

Making Connections: Conserving Landscapes for Wide-Ranging Species

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A dissertation submitted for the degree of

Doctor of Philosophy

University College London

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Declaration

I, Helen Mary Kathleen O'Neill, confirm that the work presented in this thesis is my own. The research was supported by an IMPACT award from University College London with matched funding from Zoological Society of London.

All chapters of this thesis were written by Helen O'Neill, with guidance and comments from Prof. Rosie Woodroffe and Dr Sarah Durant. Dr Richard Pearson provided comments on early drafts of chapters 2, 3, 5 and 6.

Long-term wild dog demography and movement data were collected by Prof. Rosie Woodroffe and the Kenya Rangelands Wild Dog and Cheetah Project (formerly known as the Samburu-Laikipia Wild Dog Project). Where information has been derived from other sources, I confirm this has been indicated in the thesis.

Helen O'Neill

16th January 2018

Abstract

Habitat loss and fragmentation are among the greatest threats to global biodiversity. Such threats are greatest in human-dominated landscapes, which comprise an increasing proportion of the Earth's surface. Wide-ranging species at higher trophic levels are particularly threatened by these pressures, as they need access to large areas of wildlife-friendly habitat to persist. In this thesis, the impacts of anthropogenic change to landscapes are investigated, using as case studies two extremely wide-ranging large carnivores, the cheetah and the African wild dog.

Anthropogenic habitat change affected habitat selection and movement patterns for both species. Wild dog habitat selection varied across life stages, with selection for rugged areas away from areas of high human population densities most pronounced during reproductive stages. Dispersers showed the least aversion to areas of high human population densities, suggesting that they may be more willing to use areas of suboptimal habitat.

Connectivity levels between wild dog populations across Kenya were modelled using parameters from resident packs and dispersers. Modelled connectivity was higher for dispersing animals, suggesting that wild dogs may be more able to cross the matrix between wildlife areas than appears when using parameters from resident packs. Nevertheless, the development of a major transport corridor is likely to have substantial impacts on landscape connectivity for wild dogs, and hence on population persistence.

Physical barriers impacted movement behaviour for both species. While a deliberately permeable fence had no detectable effects, fences intended to restrict wildlife movement were in fact semi-permeable. Analyses showed that crossing such fences increased cheetah travel distance, imposing an energetic cost projected to rise if fencing of properties continues to increase.

Fencing also impacted wild dog movement and demography. Wild dogs crossed more robust fences mainly through purpose-built gaps, which channelled wild dogs into particular parts of the landscape. Away from such gaps, impermeable fencing repeatedly split pack members and trapped individuals in unsuitable habitat, causing human-wildlife conflict and contributing to pack extinction.

Overall, results showed that anthropogenic landscape change had substantial impacts on wildlife populations. Future developments are likely to imperil population persistence of endangered species unless they incorporate effective, well-planned mitigation measures.

Impact Statement

Habitat loss and fragmentation are among the most urgent global concerns for wildlife conservation. Maintaining connectivity between remaining habitat patches is an important method of mitigating human impacts on wildlife. However, in order to effectively maintain connectivity it is important to understand how wild species are affected by changes to their landscapes, and what forms of management promote connectivity.

Wide-ranging species such as the African wild dog and the cheetah are among the first affected by progressive habitat loss and fragmentation as they require large areas of wildlife-friendly habitat to survive. This sensitivity to habitat loss is the major reason that both species are endangered. Conservation plans for both species have thus recommended research to identify the landscape features which facilitate, or prevent, long-distance movements and landscape connectivity.

This thesis presents novel evidence which is likely to contribute to wild dog and cheetah conservation at the local and range-wide scales. For wild dogs, it generates maps of likely landscape connections throughout Kenya which can be used immediately for species action plans, land-use plans, and environmental impact assessments. For both cheetahs and wild dogs it generates specific recommendations about the use of fencing within wildlife areas.

This thesis also presents two key findings likely to have general conservation relevance. First, the common practice of basing connectivity estimates on the habitat selection of resident animals may under-estimate connectivity (allowing unwitting destruction of movement corridors which are still open), because dispersers – the individuals most likely to move between occupied patches – have less stringent habitat preferences and can cross more human-modified lands. Second, fences constructed to block wildlife movement may in fact be semi-permeable, but crossing them impacts animals' energy budgets and may leave individuals trapped in unsuitable habitat, exacerbating human-wildlife conflict.

Finally, this research developed new methodologies for assessing connectivity and estimating the impacts of movement barriers.

These results highlight the importance of landscape connectivity for wide-ranging species, and of thoroughly evaluating the impacts on wildlife of developments such as fencing and roadbuilding.

Acknowledgements

There are many people I need to thank for their support throughout my PhD, without whom this research would not have been possible. First thanks go to my supervisors, Prof Rosie Woodroffe, Dr Sarah Durant and Dr Richard Pearson. Their guidance and support throughout the years has been completely invaluable. Thank you to Rosie for welcoming me onto the team at her long-term wild dog project and supporting me in setting up the project's cheetah monitoring work. Thank you for bringing me to the wonderful world of wild dogs, a species whose enthusiasm for life seems infinite. My time working out in the field was unforgettable; it's been a delight to work with you. Thanks go to Sarah for helping set out on my current path many years ago when she saw enough potential in me to employ me as Project Manager at the Serengeti Cheetah Project. I loved my time out there, some of the best years of my life, and it cemented in me, what I'm sure will turn out to be, a life-long love of cheetahs. Your support and guidance throughout everything has been incredible, as has the whisky! Thank you to Richard for lending your support and encouragement to the project, it couldn't have happened without you.

Also integral to the success of this work, I would also like to thank Kenya Wildlife Service (KWS) and Kenya's National Commission for Science, Technology and Innovation (NACOSTI) for their permission to spend time in Kenya and conduct my research. Kenya is a beautiful country with astonishing natural resources and it has been a privilege to work there. This work would not have been possible without the collaboration of KWS and their veterinary team who worked with me to collar my study animals. I hope that my findings prove to be useful in the work towards conserving some of the country's incredible and precious landscapes.

I would also like to thank Mpala Research Centre where I was based for my fieldwork. The support of the centre and its staff transformed my time in the field; it always helped to have access to good coffee every morning! The community of researchers at Mpala is a special one and the enthusiasm of the people I met there, and their willingness to share their cheetah and wild dog photos, was a real boon to my research.

Huge thanks must go to my fieldworker friends and colleagues from my time in Kenya, people who I hope will be friends for life. Stefanie Strebel, who was KRWDPC Project Manager while I was conducting my fieldwork as well as my

office- and house-mate, you were completely invaluable to getting me through the tough times that inevitably happen during long periods of fieldwork. Dedan Ngatia, current Project Manager for KRWDPC, thank you for continuing the project's cheetah work after I had to come back to the UK and get on with the process of writing up – I can't think of anyone better to be working on this hugely important project. Dr Adam Ferguson, thank you for the many hours of laughter and nachos eating.

Of course, the fieldwork is only half the story and writing up is so hard to do. Massive thanks must go to my ZSL officemates from the past few years: Claudia Amphlett, Harry Owen, Henrike Schulte to Bühne, Isla Watton, Tom Smallwood, Agnese Marino, Aimee McIntosh, Cally Ham, Andrew Jacobson and Susie Gold and particular thanks go to Dani Rabaiotti. You guys have made all the difference to my writing up – you've been there in good times and bad with plentiful supplies of tea/coffee/biscuits/beer as the situation requires. You've all been amazing and I can't wait to celebrate with you.

Outside of work there are also lots of people I need to thank for their unending support. To Amy Mason, thank you for your support (and the stats advice!) You're a star and never fail to cheer me up when things are getting difficult. To Ruth, Nathan and Imogen Fisher, thank you for letting me come up and visit when I needed to get away from London and for keeping me laughing throughout everything.

Most importantly, I want to thank my family. Mum, Dad and Richard – without you supporting me and helping me laugh at myself I don't know what I'd do. I appreciate your help, love and support more than I can say.

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List of Acronyms

DEE	Daily Energetic Expenditure
DEM	Digital Elevation Model
DoP	Dilution of Precision
EIA	Environmental Impact Assessment
EMCA	Environmental and Management Coordination Act
GDP	Gross Domestic Product
GLMM	Generalised Linear Mixed Model
GME	Geospatial Modelling Environment
GPS	Global Positioning System
IUCN	International Union for the Conservation of Nature
KRWDCP	Kenya Rangelands Wild Dog and Cheetah Project
KWS	Kenya Wildlife Service
LAPSSET	Lamu Port – Southern Sudan – Ethiopia Transport Corridor
LCP	Least Cost Pathway
RSF	Resource Selection Function
RSFI	Route Selection Frequency Index
RWCP	Range Wide Conservation Programme for Cheetah and African Wild Dogs
SEM	Standard Error of the Mean
SSF	Step Selection Function
VHF	Very High Frequency



Plate 2. A young African wild dog

Chapter 1.

General Introduction

Habitat loss and fragmentation represent one of the greatest threats to wildlife species across the world (Millennium Ecosystem Assessment, 2005). The global human population is growing at an unprecedented rate (United Nations, 2013), putting ever greater strain on the world's remaining natural environments. The need to support and feed rising numbers of people only increases the pressure to convert remaining patches of natural habitats to allow more intensive human use. The resulting loss of natural habitat is an important threat across many taxa; however it is of particular concern for wide-ranging species (Crooks & Sanjayan, 2006). Wide-ranging species are dependent on access to large areas of contiguous suitable habitat in order to be able to persist, thus for these species landscape level conservation over large areas is likely to be vital for their long-term survival (Ripple *et al.*, 2014). Understanding how wide-ranging species coexist with human communities and anthropogenic landscape features is likely to be key for the successful conservation of such species. It will also provide insights into the most important features in the landscape which, if sufficiently protected, will likely benefit other species also found within an area (Caro, 2003).

Identifying the remaining levels of connectivity between habitats is an important part of conservation planning (Crooks & Sanjayan, 2006). It is important because maintaining landscape connectivity is likely to confer populations with greater resilience to stochastic events and aid their persistence (Pitman *et al.*, 2017). If the locations of key movement corridors across a landscape are known, then it may be possible to mitigate the impacts of development on connectivity levels (Morrison & Reynolds, 2006). Until relatively recently, connectivity modelling for particular species was based mainly on expert opinion but, as high resolution GPS movement data are becoming available, models are increasingly empirically based (Zeller *et al.*, 2012). However, these data are collected mainly from resident animals, which are often unlikely to move long distances and therefore migrate between populations (Abrahms *et al.*, 2017). There have been few studies that have explicitly compared the differences in predicted connectivity or habitat selection preferences among individuals in different life stages (Abrahms *et al.*, 2017). Those that have done so suggest that life stage has an important effect on modelled levels

of connectivity (Elliot *et al.*, 2014b; Trainor *et al.*, 2013). Establishing whether, and how, habitat selection varies between life stages is likely to be of importance for connectivity mapping and hence future conservation planning, particularly under conditions of human population growth, land-use change, and infrastructure developments.

Over recent years, wildlife fencing has been increasingly used as a conservation intervention (Durant *et al.* 2015; Woodroffe *et al.* 2014). This is despite the reduction in landscape connectivity that inevitably results from fencing, and the important knowledge gaps regarding the long-term impacts (Durant *et al.*, 2015b). The effects of fences on the wildlife in their vicinity are poorly understood, particularly with regard to how fences change animals' movement behaviour, and how this may affect the animals' survivorship (Durant *et al.*, 2015b). Research into these areas is important, as wildlife managers heed calls for fencing to be deployed as a primary conservation tool for certain species (Packer *et al.*, 2013a) and to reduce human-wildlife conflict more generally (Hayward & Kerley, 2009).

This thesis investigates the effects of habitat fragmentation within a human-dominated landscape in northern Kenya, using two extremely wide-ranging large carnivore species, the cheetah, *Acinonyx jubatus*, and the African wild dog, *Lycaon pictus*, as case studies. Through analyses of data from collared animals, this thesis seeks to investigate how these two species move across the landscape, and how the anthropogenic features they encounter impact their populations. As wide-ranging species, cheetahs and wild dogs are good model species to evaluate the effects of anthropogenic habitat change. Adults of both species may have home ranges in excess of 2,000 sq km, and dispersing individuals often travel hundreds of kilometres (Houser *et al.*, 2009; Boast, 2014; Davies-Mostert *et al.*, 2012; Fuller & Kat, 1990). As a result there are few areas of less than 10,000 sq km that are able to support viable populations (IUCN/SSC, 2007, 2012, 2015). Both species also live at low population densities, in the region of 1-2 individuals per 100 sq km (Durant *et al.*, 2010; Woodroffe & Ginsberg, 1999). Connectivity analysis is particularly urgent for low density and wide-ranging species, as such species are particularly vulnerable to extinction as a result of habitat fragmentation (Tigas *et al.*, 2002; Ripple *et al.*, 2014; Wilcox & Murphy, 1985; Crooks, 2002).

Field data were collected within Laikipia County in northern Kenya (Figure 1.1). This area supports a variety of land-uses including traditional pastoralism, commercial livestock ranching, subsistence agriculture and tourism (Ulrich *et al.*,

2012). It includes a wide range of environmental features likely to promote or impede wildlife movement, including escarpments, river valleys of varying size, roads, settlements and game fences, and a variety of habitats ranging from grasslands to forest. Although only a very small proportion of this ecosystem comprises officially gazetted protected areas, it supports a wild dog population estimated to be the sixth largest in the world, and part of a cheetah population estimated to be the second largest in the world (IUCN/SSC, 2007, 2012, 2015; Durant *et al.*, 2017). This area therefore provides a valuable model for understanding predator use of human-dominated landscape which may be extrapolated to a wider area.



Figure 1.1. Location of the study area in Kenya.

Using data from the Laikipia populations of cheetahs and wild dogs, this thesis seeks to answer the following research questions:

1. How does habitat selection change across life stages and does it vary between different scales?
2. How connected are the remaining wild dog populations in Kenya and are they likely to be affected by planned development projects?
3. What are the likely effects of fencing on wildlife movement patterns and do fences affect animals' energy balance?
4. What are the effects of fencing on wildlife movement patterns and do fences have observable demographic effects?

The thesis begins with a review of relevant literature, as well as a more detailed introduction to the study species and study site (Chapter 2). The following four chapters address the research questions given above. In chapter 3, how wild dogs select habitat across different life stages is explored with reference to both natural and anthropogenic landscape features. In chapter 4, the levels of connectivity between resident wild dog populations in Kenya are evaluated, comparing estimates derived from the habitat selection of resident packs and dispersal groups. The resulting connectivity maps are then used to assess the potential impact of a major new infrastructure development on landscape connectivity for wild dogs in Kenya. In chapter 5, the potential energetic impact of an increase in fencing on cheetahs, and how this is affected by fence structure, is modelled. In chapter 6, the effects of fencing and fence structure on wild dog movement patterns and population demography are evaluated. Finally, Chapter 7 discusses the main results and conclusions of the preceding chapters, giving an overview of their contribution to cheetah and wild dog conservation and to the wider literature.



Plate 3. A cheetah

Chapter 2.

Literature Review

2.1. Habitat Loss and Fragmentation

Habitat loss currently constitutes the leading cause of global biodiversity loss (Schipper *et al.*, 2008; Ray *et al.*, 2005; Ripple *et al.*, 2014; Millennium Ecosystem Assessment, 2005). This is because, as land is converted from its natural state for intensive human use, it is often no longer suitable habitat for the species that were once found there (Sisk *et al.*, 1994). Major drivers of land cover change are human population growth and increasing per capita consumption rates (DeFries *et al.*, 2007; Tilman *et al.*, 2001). Between 1950 and 2013 the global human population grew from 2.5 billion to 7.1 billion people and this increase is expected to continue, with the global population projected to reach 9.5 billion people in 2050 (United Nations, 2013). Agriculture is a source of livelihoods for 86% of rural people (World Bank, 2007) and, in future, the pressure to convert natural habitats to agriculture and other more intensive human uses will only increase with the need to support and feed the growing human population.

Habitat loss affects species in a number of ways, including lowering an area's carrying capacity for a species and by increasing edge effects (Boone *et al.*, 2005). The carrying capacity of an area varies by species and habitat type but is inextricably linked with the area's size (Gilpin, 1987): small areas or fragments tend to support small populations and smaller populations are more likely to go extinct (Berger, 1990; Lande, 1988). As habitat is converted from its natural state, the overall size of the remaining area shrinks, thereby lowering the population carrying capacity of the wildlife found there (Sutherland & Anderson, 1993). This is of particular concern for species that live at low population densities; such species require large contiguous areas of habitat in order that their populations remain large enough to be sustainable in the long-term (Henle *et al.*, 2004; Woodroffe & Ginsberg, 1998). In addition, as habitat patches become smaller their perimeter to area ratio changes as the relative proportion of edge habitat will increase (Broadbent *et al.*, 2008). Edge habitat usually has differing characteristics to core habitat, with a gradation of biotic, abiotic, and often also anthropogenic, factors

which will affect the species diversity found there (Haddad *et al.*, 2015; Keeley *et al.*, 2017; Woodroffe & Ginsberg, 1998).

Habitat fragmentation is an issue frequently experienced concurrently with habitat loss (Fahrig, 2003; Haddad *et al.*, 2015). Areas of exploitation of a landscape often do not develop in an ordered fashion, instead the degraded areas expand and gradually cut off access between remnant habitat patches, leaving a patchwork of fragments behind (Kindlmann & Burel, 2008). In a fragmented landscape, pieces of habitat are no longer connected to other areas of similar habitat; instead they are surrounded by a 'matrix' of different or altered habitat, or there are movement barriers such as fences which limit animals' ability to access parts of the landscape. Fragmented habitat is often likened to islands – with each remaining patch of habitat acting as an island amidst the sea of the less suitable habitat of the matrix (Andrén, 1994; Haddad *et al.*, 2015; MacArthur & Wilson, 1967). Where connectivity is lost between habitat fragments, populations become split into several smaller populations, thereby increasing their extinction risk (Henle *et al.*, 2004). Fragmentation is frequently thought of as an issue particularly affecting those species that are poor dispersers; these species are less likely to be able to traverse areas of poor habitat to reach other habitat fragments and are therefore more likely to be split into separate populations (Henle *et al.*, 2004). However, habitat fragmentation is also a serious threat to species that have good dispersal abilities (Casagrandi & Gatto, 1999; Fischer & Lindenmayer, 2007). These species may be able to traverse the potentially hostile matrix areas and disperse between remnant habitat patches, however they may be placed at higher risk of mortality while doing so (Casagrandi & Gatto, 1999; Fischer & Lindenmayer, 2007).

2.2. Connectivity

The extent to which habitat fragments are connected is referred to as 'connectivity', and can be divided into two types: structural connectivity and functional connectivity (Kindlmann & Burel, 2008; Taylor *et al.*, 2006). When patches of habitat are left, but surrounded by unsuitable matrix habitat, it is referred to as a loss of structural connectivity (Taylor *et al.*, 2006). Whereas a loss of functional connectivity occurs when a species is no longer able to successfully move from one area of habitat to another (Taylor *et al.*, 2006). The distinction is important as, although the two types often occur together this is not always the case; a loss of structural connectivity does not necessarily mean there has been a loss of functional connectivity, likewise

a loss of functional connectivity does not mean there is no longer structural connectivity (Taylor *et al.*, 2006). Establishing the level of functional connectivity remaining in a landscape is an important factor for conservation as, even if there has been quite extensive habitat fragmentation, there may still be a high level of connectivity between remnant habitat patches. Thus, a landscape which appears to be extensively altered may still be of great conservation importance. This unexpected level of connectivity is particularly true for species with good dispersal abilities; it is only if the species' biology prevents such movement or if fragmentation has occurred to such a degree that individuals can no longer successfully traverse the matrix that there is a loss of functional connectivity (Taylor *et al.*, 2006). Equally, two areas may still be structurally connected through habitat corridors, but if the target species do not or cannot use these corridors to successfully move between habitat fragments then the areas are nonetheless functionally disconnected.

Maintaining functional connectivity between areas of suitable habitat is a key tool for mitigating the effect of land cover change and maintaining biodiversity and ecosystem function (Crooks & Sanjayan, 2006). Short-term, but often catastrophic, effects of connectivity loss centre around animals no longer being able to access basic resources such as water (Berry, 1997; Gadd, 2012; Whyte, 1988). This may be a particular problem for migratory species that are reliant on moving between different parts of a landscape to maintain adequate access to food and water throughout the year; connectivity loss has contributed to the loss of several mass ungulate migrations (Harris *et al.*, 2009). Non-migratory species and populations are also affected however, due to their often poorer ability to move across large distances compared to migratory species (Hansson, 1991). Even where there has not been a total loss of connectivity across a landscape, there may be serious implications for animals found there. If the ability of an animal to access necessary resources, such as food and water, is reduced, and the effort it must take to obtain them increases, then it may be that the animal is left in an energetically precarious position, and at risk of not being able to adequately provision itself or its offspring (Chapron *et al.*, 2008; Shine & Madsen, 1997). In addition to reducing access to resources, where a population is split into multiple separate populations, there will be an effect on the population dynamics and demography, and genetics (Dixo *et al.*, 2009; Jackson & Fahrig, 2011). For example, animals may be prevented from forming new breeding groups with unrelated individuals, leading to longer-term effects such as a loss of genetic diversity.

Where populations are split into smaller subpopulations, each with only a few individuals reproducing, populations are at risk of serious declines in their genetic diversity (Dixo *et al.*, 2009; Epps *et al.*, 2005). Without sufficient migration between populations, animals may increasingly have only closely related individuals available to mate with. This may result in animals not breeding (Becker *et al.*, 2012) or, where animals do mate with related individuals, a loss of genetic diversity (Keller, 2002). Populations where individuals have low genetic diversity tend to have lower fitness and reduced fecundity compared with genetically diverse populations (Keller, 2002). They are also at greater risk of extinction from stochastic events as they may have reduced resilience to environmental incidents such as droughts (Keller, 2002; Booy *et al.*, 2000).

Determining the level of functional connectivity remaining in a landscape is important to help determine the most appropriate interventions for preservation of threatened species (Crooks & Sanjayan, 2006). For example, in a situation where individuals have been unable to move between its remnant populations for a number of generations, and are therefore at risk of inbreeding, it may be appropriate to translocate some individuals between populations (Trinkel *et al.*, 2008). However, if it was determined that there was still some level of connectivity with occasional migration of individuals between populations then the risk of inbreeding is likely to be reduced and less active management may be more appropriate (Ingvarsson, 2001). This is to be preferred as there are multiple risks associated with translocations (Pérez *et al.*, 2012). These include threats to the individuals being transported, from immobilisations, stress and potentially being released into another individual's territory, but also to the recipient populations (Pérez *et al.*, 2012). Any pathogen that translocated individuals may be carrying will be transported with them (Cunningham, 1996). Even with careful medical and quarantine procedures risks cannot be completely eliminated. Translocations are costly to implement and, unless connectivity between populations can be re-established, are likely to be required in perpetuity to keep populations healthy. Maintaining connectivity between populations removes the necessity of such management, avoiding expensive and risky management interventions.

Whilst the importance of understanding landscape connectivity is widely recognised, to date many attempts to map landscape level connectivity have been based on expert opinion and have been conducted in the absence of empirical data on how animals actually move across landscapes (Vasudev *et al.*, 2015; Zeller *et al.*, 2012).

Without data on how animals move across landscapes it is not possible to accurately characterise which features constitute a barrier or act as a channel to movement, nor is it possible to determine where movement corridors may still exist (Chetkiewicz *et al.*, 2006). This is important as expert opinion can be less effective at predicting landscape connectivity than models based on empirical data (Zeller *et al.*, 2012). Therefore increasing the empirical basis for modelling is likely to improve the accuracy and efficacy of conservation interventions for maintaining connectivity.

2.3. Human-Dominated Landscapes

With an increasing global human population, it is inevitable that the world and its landscapes are becoming ever more human-dominated (Vitousek, 1997; Foley, 2005). A landscape can be considered as human-dominated when people are the major shapers of the environment. This could be as a result of high human population densities, widespread agriculture and land conversion, the presence of large-scale extraction industries such as mining or through a combination of such factors.

A wide variety of taxa have been found to be affected by the impacts of living in a human-dominated landscape (Bunnefeld *et al.*, 2006; Ficetola & De Bernardi, 2004; Kjoss & Litvaitis, 2001; Graham *et al.*, 2009) however large carnivores have been found to be particularly at risk (Woodroffe, 2000; Linnell *et al.*, 2001; Ripple *et al.*, 2014). A key factor is that human-dominated landscapes tend to be associated with habitat loss, degradation and/or a loss of connectivity between areas of habitat (Kindlmann & Burel, 2008). As areas of previously remote habitat become more accessible, then they may begin to be used by the local human population more intensively. For example, where roads are built by logging companies to enable timber extraction, previously inaccessible areas of forest are opened up for exploitation (Laurance *et al.*, 2009). Exploitation may take many forms, from extraction of natural resources such as timber or minerals to clearing of natural habitat for cultivation (Laurance *et al.*, 2009). Once remote areas become more accessible there may be cascading impacts, for example livestock may be grazed in these areas more often than was formerly possible. This may lead to increased competition with wild ungulate species and the possibility of overgrazing, which in turn leads to the habitat becoming further degraded (Reid *et al.*, 2013). As intact habitat patches become smaller, the likelihood of wildlife moving into community or farming areas increases; particularly if the wildlife's natural food source has been

negatively affected, for example through competition for resources such as water or through hunting (Hartter *et al.*, 2011). This may lead to human-wildlife conflict resulting in retaliatory killings (Dickman *et al.*, 2014; Gusset *et al.*, 2009; Hoare, 2000; Inskip & Zimmermann, 2009; Marker *et al.*, 2003) which may miss, or extend beyond, the individual problem animal, either accidentally or as a pre-emptive attempt to prevent further conflict (Ray *et al.*, 2005).

Whilst there are a number of threats to wildlife associated with human-dominated landscapes, such areas are nonetheless likely to be of vital importance for future conservation (Durant *et al.*, 2017). Protected areas are undoubtedly extremely important refuges for wildlife but the global protected area network only covers approximately 12% of the world's land surface; and is therefore unlikely to be able to sustain the world's biodiversity on its own (Chape *et al.*, 2005; Rodrigues *et al.*, 2004). In addition to covering only a relatively small proportion of the terrestrial surface, areas that have been gazetted are also not fully representative of the world's terrestrial habitats (Rodrigues *et al.*, 2004). Areas that are unsuitable for alternative uses such as agriculture, for example mountainous regions, are over-represented (Chape *et al.*, 2005). Human-dominated landscapes are likely to be particularly important for those species which are wide-ranging and live at low population densities. Such species need large contiguous areas of wildlife-friendly habitat in order to persist, and they are unlikely to be able to be sustained solely in protected areas (Durant *et al.*, 2017).

2.4. Movement Ecology

Movement ecology refers to the study of how species move in relation to their environments (Nathan *et al.*, 2008). By studying how an animal moves through its landscape it is possible to determine the key aspects of its habitat that relate to its resource use and distribution (Nathan *et al.*, 2008). The increase in recent years of the availability of high quality, high resolution GPS tag data means that the literature on movement ecology has dramatically increased.

Movement ecology is important to the study of animals living in human-dominated landscapes because although populations may persist in such areas, individuals may change their behaviour or movement patterns whilst there. Studies show that wide-ranging wildlife species employ diverse responses to human impacts, for example Graham *et al.* (2009) found that African elephants, *Loxodonta africana*, were more likely to make use of human-dominated areas at night and that they

would move through these areas, which were associated with an increased mortality risk, more quickly than they moved through the surrounding areas. Šálek *et al.* (2014) conducted a review which showed that eight carnivore species (red fox, *Vulpes vulpes*; grey fox, *Urocyon cinereoargenteus*; coyote, *Canis latrans*; bobcat, *Lynx rufus*; raccoon, *Procyon lotor*; striped skunk, *Mephitis mephitis*; Eurasian badger, *Meles meles* and stone marten, *Martes foina*) change their home range sizes and population densities in relation to human settlements, with home range size decreasing and population density increasing with higher levels of urbanisation. This suggests that some species may be able to successfully adapt their behaviour in order to persist in urban landscapes; Šálek *et al.* did note that there was no strong evidence that the species studied had greater fitness or survival rates in urban environments compared to natural ones. Tigas *et al.* (2002) found that coyotes and bobcats tended to avoid developed areas, particularly during the day when the level of human activity was at its highest. However, Randa & Yunger (2006) investigated the distribution of raccoons, red foxes and coyotes along an urban to rural gradient and found that the species had differing responses. Red foxes and coyotes were found at the rural end of the spectrum, however raccoons were found in relatively developed areas. Basille *et al.* (2009) also found that Eurasian lynx, *Lynx lynx*, in Norway did not avoid areas of high human densities, as was expected, instead selecting areas of intermediate human density. A previous study in Laikipia found that African wild dogs preferred areas with no human settlements (Woodroffe, 2010). These differing responses highlight the behavioural adaptability of many species, and that animals employ a diversity of strategies to minimise the negative impacts they experience from living within a human-dominated landscape. However, the ability of wildlife to adapt to, and their overall tolerance of, human impacts is likely to vary substantially between species.

As well as determining the areas used by an animal, movement ecology allows the examination of how movement patterns are affected by the presence of linear geographical features, such as roads, rivers and fences (Cozzi *et al.*, 2013; Dickie *et al.*, 2017). Natural barriers have always been important in the structuring of wild populations but increasingly anthropogenic barriers are appearing in natural landscapes and altering the way that animals are able to move across those landscapes (Durant *et al.*, 2015b; Linnell *et al.*, 2016; Wingard *et al.*, 2014). Anthropogenic barriers may include roads, fences, agricultural land or human settlements and have the potential to have long-term impacts similar to those caused by natural barriers, and prevent free gene flow across previously contiguous

areas and populations (Epps *et al.*, 2005). The effect of man-made barriers on wildlife has received increasing attention in the scientific literature over recent years, particularly relating to roads and other transport routes. This is partly due to various high profile infrastructure building plans, such as those for roads in Serengeti National Park in Tanzania and Cross River National Park in Nigeria, and the trans Mongolia railway (Cannon, 2017; Dobson *et al.*, 2010; Sanjmyatav, 2011). Fahrig & Rytwinski (2009) conducted a review into the effects of roads on a wide range of different wildlife species. Although they found there were some positive effects of roads on some species, they also found that overall the negative effects massively outweighed any positives. The impacts of roads varied across taxa and body sizes, with small mammals experiencing either no effect or a mildly positive one, whereas amphibian and reptile species tended to experience negative effects. Of the large mammals included in their study, most exhibited negative effects; with all of the canid species (red fox; grey wolf and black-backed jackal, *Canis mesomelas*) and all of the felid species (bobcat; Eurasian lynx; Iberian lynx, *Lynx pardinus*; Amur tiger, *Panthera tigris altaica* and cougar, *Puma concolor*) that were evaluated were reported as showing only negative effects.

In relation to conservation within human-dominated landscapes, it is possible to look at the areas and habitats within the landscape where animals are found and whether and how they can move between isolated patches in a fragmented habitat. This is important because having such information makes it possible to conserve these areas thereby promoting population persistence. It is also possible to look at the levels of remaining connectivity across a landscape, and to identify key movement corridors that remain and which might be in need of protection. For example, the annual migration of the Gourma elephant population in Mali is reliant on being able to move through a 1 mile wide valley, in order to move between their wet and dry season ranges (Wall *et al.*, 2013). This valley, which has been dubbed *La Porte des Éléphants* (the elephant doorway) is the last remaining valley which does not have a human settlement nearby (Wall *et al.*, 2013). A similar phenomenon is seen in the migration of pronghorn, *Antilocapra americana*, in the Greater Yellowstone Ecosystem, where animals move along a movement corridor with an average width of just 2km (Berger, 2004; Berger *et al.*, 2006). Whilst these are quite extreme examples, they do show that the way animals move across a landscape is likely to be affected not only by the different habitat types found there but also by different geographical features which may alter their movement patterns. Landscape features, such as rivers, valleys, roads and human settlements, can

impact on the movement patterns of wildlife in a number of ways. Firstly they may act to channel the animals' movements; making it more likely that individuals would move along a certain course rather than maintain their natural movement patterns (Brody & Pelton, 1989; Cozzi *et al.*, 2013; Dyer *et al.*, 2002; Loarie *et al.*, 2009; McDonald & St. Clair, 2004; Shepard *et al.*, 2008; Vanak *et al.*, 2010). Another impact may be to prevent species from moving between certain areas, creating a barrier to movement (Bartzke *et al.*, 2015; Blanco *et al.*, 2005; Cozzi *et al.*, 2013; Dyer *et al.*, 2002; Frantz *et al.*, 2010; Rondinini & Doncaster, 2002). These impacts are not exclusive and the effects may work in combination, for example channelling animals' movements along a feature until they reach an area where the barrier is more permeable and they are therefore able to cross it. The impact of such barriers can be severe; preventing movement between patches even for relatively mobile species such as various species of tropical birds who have been found not to cross even relatively narrow water-bodies (Diamond, 1975). This barrier effect can lead to the geographical features having a major influence on the structure of wild populations, and may restrict gene flow which can eventually lead to allopatric speciation, making it a potentially important evolutionary factor (Orr & Smith, 1998).

In many cases the locations of key movement corridors are less clear-cut than those of the Mali elephants or pronghorns and an alternative approach may be required to identify them. For species where there is little empirical data, expert opinion may be used to characterise the ability of that species either to make use of different habitat types or the extent to which the species will be able to traverse certain areas (Zeller *et al.*, 2012). However, as greater levels of empirical movement data have become available, analyses such as resource selection functions (RSF) and step selection functions (SSF) are increasingly being used to map connectivity. RSFs are a form of habitat selection analysis which compare the characteristics of habitat available to an animal with the habitat it actually used (Manly *et al.*, 2002). RSFs divide the landscape into resource units, which are effectively sampling units such as pixels within a raster layer, which have attributes, such as slope or habitat type, associated with them (Manly *et al.*, 2002). Location data are then overlaid on the resource layers and the probability of different landscape resource units being used by the animal is modelled and used to identify habitat associations (Manly *et al.*, 2002; Chetkiewicz *et al.*, 2006). SSFs work in a similar way, but on a smaller scale, by evaluating the locations to which an animal could potentially have moved at a specific time point, with where it actually went (Fortin *et al.*, 2005). RSFs and SSFs have been used across a wide range of taxa to investigate habitat selection

preferences, these models have then been used to investigate landscape connectivity (Chetkiewicz & Boyce, 2009).

RSFs and SSFs can be used in combination with connectivity analysis techniques, the most common form of which is Least Cost Pathways (LCP) (Sawyer *et al.*, 2011). The characteristics of a landscape are assigned cost values based on their modelled habitat suitability values (Chetkiewicz & Boyce, 2009). The costs of the possible routes across the landscape are then calculated and the route with the lowest cost is the route the animal is considered most likely to take (Chetkiewicz & Boyce, 2009). This type of connectivity analysis has been employed to model connectivity across a wide range of taxa including amphibians (Joly *et al.*, 2003; Stevens *et al.*, 2006), birds (Beazley *et al.*, 2005), large mammals (Beazley *et al.*, 2005; Osborn & Parker, 2003) and large carnivores (Chetkiewicz & Boyce, 2009; Cushman *et al.*, 2009; Larkin *et al.*, 2004). A problem with this type of analysis is that it assumes that animals have a perfect knowledge of their landscape and so are able to select the best route (McRae *et al.*, 2008), therefore it only produces a single pathway between patches. A new connectivity methodology has recently been developed, *LSCorridors* (Ribeiro *et al.*, 2017). This method works on the same principles as least cost pathways, but introduces a level of stochasticity to the landscape cost values as well as a moving window of landscape influence, rather than working on a pixel to pixel basis (Ribeiro *et al.*, 2017). This produces multiple-path corridor maps which can be used for conservation planning.

2.5. Behavioural Effects on Movement Patterns

An aspect of both habitat selection and connectivity analyses that is receiving increasing amounts of attention in the literature is the effect of different behaviours and life history stages (Abrahms *et al.*, 2017; Roever *et al.*, 2014). This increasing interest is because changes that species exhibit in response to human-dominated environments may change during different behaviours and life stages. Dispersing individuals, which are more exploratory in their behaviour, are likely to tolerate different habitats than resident individuals, thus altering what we may perceive as a connected landscape (Elliot *et al.*, 2014b; Keeley *et al.*, 2017). Taking such responses into consideration when investigating habitat selection leads to a more detailed and accurate picture of the impacts of these environments and therefore the conservation measures required (Roever *et al.*, 2014). For example, Roever *et al.*, (2014) used movement data from elephants to evaluate the effect of behaviour

on the elephants' probability of using different areas of their landscape. They found that there were significant differences in the elephants' movement patterns when they compared the habitat selection models for encamped and exploratory behaviours, and that the models which incorporated behaviour consistently outperformed the models which did not (Roever *et al.*, 2014).

Behaviour has also been found to impact carnivore habitat selection, for example a difference in responses to different habitats by cougars in relation to different behavioural states was found by Zeller *et al.* (2014). Cougars moving across the landscape selected habitat differently from individuals exhibiting resource use behaviour (e.g. finding food and using day-beds); urban and agricultural areas were generally avoided but to a greater extent when the cougars were in a resource-use behavioural state (Zeller *et al.*, 2014). Bunnefeld *et al.* (2006) found that Eurasian lynxes responded differently to the presence of human settlements and infrastructure depending on their sex and reproductive status. Male lynxes and females without kittens tended to be found nearer to man-made features than were females with young kittens. However, as their kittens aged, females with kittens would go closer to human environments. In this case a large proportion of mortality for the lynx population was caused by humans and therefore having young kittens appears to have caused the female lynxes to become significantly more risk averse.

Animals may make use of particular areas within their home ranges for certain behaviours; some areas may be of greater importance for foraging, or the animal may have particular requirements for denning locations (Balme *et al.*, 2007; Jackson *et al.*, 2014). Many species exhibit different behaviour or ranging patterns according to aspects of their life histories such as their age, sex or reproductive status. For example, ranging patterns of cheetahs living in Serengeti National Park were found to vary between males and females (Caro, 1994). Females were recorded as having home ranges of 833 sq km on average; the home range size of males varied depending on whether they were territorial: non-territorial males also had large home ranges of 777 sq km on average, however territorial males averaged only 37 sq km – less than 5% of an average female home range (Caro, 1994).

Studies which have looked at the difference between resident and dispersal groups have shown differences in their habitat requirements and movement ecology (Elliot *et al.*, 2014b; Tobin *et al.*, 2010; Trainor *et al.*, 2013). For example, male African lion, *Panthera leo*, dispersal groups were shown to have habitat selection patterns significantly different from those of groups of resident adults (Elliot *et al.*, 2014b).

These differences meant that modelled connectivity levels were much higher for the dispersal groups because they had less stringent habitat preferences and so were projected to be more able to move through lower quality habitat (Elliot *et al.*, 2014b). However, there have been relatively few studies that have focussed on the different habitat preferences and tolerances of dispersing and resident animals (Abrahms *et al.*, 2017). This is likely due to the logistical difficulties associated with tracking dispersal behaviour as this is usually a relatively short period in most animals' lives, the timing of which is unpredictable and can vary substantially between individuals (McNutt, 1996). Unless a population is the subject of in-depth study it can also be difficult to determine whether an individual or group is in the middle of a dispersal; this has led to some studies making assumptions, based on factors such as group size, in categorising animals dispersing or non-dispersing (Jackson *et al.*, 2016).

2.6. Fences

Fencing has long been a controversial topic in conservation (Woodroffe *et al.*, 2014). There have been global and regional differences in approaches to the use of wildlife fences. Fencing has been used extensively in Australia to control invasive species, and in southern Africa to prevent disease transmission and to fence property or reserve boundaries; whereas in areas such as Asia, Europe and East Africa, fencing has historically been little used (Beale *et al.*, 2013; Hayward & Somers, 2012; Hayward & Kerley, 2009).

Game fences were widely used in the middle of the 20th century in southern Africa as a way of separating humans and livestock from populations of wildlife (Gadd, 2012). Many of these fences were erected primarily to prevent the transmission of diseases, particularly foot and mouth disease, from wild ungulates to domestic cattle, as affected livestock would not be accepted into international meat markets (Gadd, 2012). These fences were therefore often erected in areas that caused significant problems for wild species, by blocking key access routes to water and grazing during dry seasons, and were widely implicated in the collapse of the southern African wildebeest, *Connochaetes taurinus*, population (Ben-Shahar, 1993; Berry, 1997; Whyte, 1988). Towards the end of the 20th century, the tide within conservation began to turn against the use of fences with greater emphasis placed on maintaining connectivity between habitats (Durant *et al.*, 2015b). This is because there has been increasing recognition of the, often serious, negative effects which fences can have on wildlife populations. In southern Africa – an area

which, as mentioned above, historically made extensive use of fencing to control the spread of disease, there has been a move towards dismantling of fences (WCS, 2008; Lindsey *et al.*, 2009).

In recent years the debate over the utility of fences within conservation has once again come to the fore (Creel *et al.*, 2013; Durant *et al.*, 2015b; Packer *et al.*, 2013a, 2013b; Woodroffe *et al.*, 2014). There has been a move to return to using fences to reduce human-wildlife conflict and to enclose populations of threatened species in order to better protect them (Lindsey *et al.*, 2012). In many areas across Africa fences are being used in an attempt to reduce incidents of human-elephant conflict; by erecting fences around protected areas these projects aim to reduce the level of crop-raiding by elephants and so reduce the negative impacts felt by local communities who live in close proximity to them (Lindsey *et al.*, 2012). Fences have also been advanced as a method of protecting endangered species such as the African lion. Packer *et al.* (2013a) argued that, with respect to lion conservation, fenced reserves had higher levels of success in maintaining their lion populations for a comparatively small sum of money compared with unfenced reserves. The validity of this conclusion was questioned by Creel *et al.* (2013), who argued that using the estimated lion carrying capacity of a reserve rather than population size skewed the results, as some small fenced reserves had artificially high lion densities. In addition it suggested that large unfenced reserves which may have lion populations numbering several hundred individuals but which were not at their estimated carrying capacity were less valuable than small fenced reserves containing a handful of individuals but which were at, or above, carrying capacity. This analysis also only looked at the effect on lion populations, and did not take into account the effects that fencing may have on other species. This would likely be particularly important for species such as African wild dogs and cheetahs as they are negatively affected by high lion densities (Durant, 2004; Mills & Gorman, 1997; Chauvenet *et al.*, 2012; Creel & Creel, 1996; Woodroffe *et al.*, 2014).

Hayward & Kerley (2009) discussed the pros and cons of wildlife and conservation fencing. They concluded that the problems associated with fencing, which included immediate issues, such as its high financial cost, as well as longer term consequences including inbreeding and loss of genetic diversity, outweighed the benefits that could be gained from fencing (Hayward & Kerley, 2009). One key potential negative impact of wildlife fences is that they may have unintended effects on other species in the ecosystem. An example of this effect on a small scale can

be seen in South Africa, where in fenced reserves African wild dogs have been shown to use fences to prevent prey escaping thereby increasing their hunting success (Davies-Mostert *et al.*, 2013). This only resulted in a change in the wild dogs' hunting behaviour, as they were able to hunt larger prey species and therefore needed to hunt less often, but it could then lead to an alteration of the overall species composition of an area (Davies-Mostert *et al.*, 2013). This behaviour has also led to conflict with land managers as chasing large ungulates into the fences damages the fences, which are then expensive to repair – this has led to wild dogs being removed from some ranches (Lindsey *et al.*, 2005b; Woodroffe *et al.*, 2014).

Nonetheless, despite calls for fencing to be employed sparingly and as a last resort, large-scale fencing has become government policy in some countries. These include plans to fence all of the National Parks in Uganda (Durant *et al.*, 2015b), and in Kenya the government requires that all areas with rhino populations must be fenced (Kenya Wildlife Service, 2012).

Whilst the use of fencing is an important issue within conservation, it is important to remember that most fences are not erected for conservation purposes. Landscape connectivity will likely be affected whether a fence is erected in an attempt to mitigate human-wildlife conflict or to delineate property boundaries. The increasing levels of fencing around private properties that were previously common ground has been identified as a significant threat to the Greater Mara ecosystem in southern Kenya (Løvschal *et al.*, 2017).

Much of the literature surrounding fencing concentrates on the effects it has on connectivity and how a reduction in connectivity is likely to affect species populations, for example by preventing animals from accessing important resources at certain times of year. The ultimate driver of much of animal behaviour and ecology is the requirement for individuals to be able to access and consume enough energy to equal, or exceed, their daily energetic expenditure in order to survive (Tomlinson *et al.*, 2014). This need influences every aspect of an animal's life, from its ranging and feeding behaviour to its reproductive success (Tomlinson *et al.*, 2014). Movement behaviour e.g. patrolling the animal's territory, is often an important cause of energy expenditure (Halsey, 2016) thus it is likely that changes to its landscape will affect the animal's energy intake and expenditure. As energetic expenditure scales with body size, i.e. larger bodied animals have higher energetic requirements (Tomlinson *et al.*, 2014), and is higher in endothermic species (Nagy,

2005), changes in a landscape are likely to particularly affect large-bodied mammals and most of all, large carnivores. This is because large carnivores live at high trophic levels and in order to access their energy source – their prey, they can be required to move considerable distances, thereby expending additional energy in excess of their, often energetically demanding, hunting strategies (Carbone *et al.*, 2007; McNab, 1963). As such, if fences are erected and they prevent species from accessing important resource areas this may seriously affect animals' abilities to balance their energy budgets. Even if the fence is semi-permeable, for example when there are crossing points, if the distance an animal has to travel in order to traverse it is large, accessing the area may prove to be energetically untenable. This will affect all animals in the landscape which have their movement patterns altered by the fence; however due to their marginal energetic balance large carnivores are likely to be among the most effected.

2.7. Large Carnivore Conservation

Large carnivores are often wide-ranging and tend to live at low populations densities (Ripple *et al.*, 2014). Carnivores exist at high trophic levels and are therefore reliant on having access to a suitable prey base in order to survive, however large carnivores have particularly high energetic requirements due to their large body size, meaning they need access to large areas with adequate prey densities (Carbone *et al.*, 2007; Ripple *et al.*, 2014). These characteristics make them particularly vulnerable to many of the pressures associated with modern biodiversity loss such as habitat loss and fragmentation (Ripple *et al.*, 2014). They are also vulnerable to human persecution, this is because large carnivores can be a threat to human life and livelihoods and so may be killed as a result (Kissui, 2008; Treves & Karanth, 2003). As species often experience these pressures simultaneously, large carnivores are among the groups that are most threatened with extinction (Ripple *et al.*, 2014).

The key threats to the survival of large carnivore species can generally be classified within the broader terms of habitat loss and human-wildlife conflict as well as loss of prey and the illegal wildlife trade (Ripple *et al.*, 2014). The wide-ranging natures of most large carnivore species mean that they require large expanses of carnivore-friendly habitat in order to persist in an area. Compounding the problems associated with habitat loss, carnivore species that inhabited these areas are likely to be forced into closer contact with the local human population. Increased contact

between large carnivores and local communities is often associated with a rise in levels of conflict (Inskip & Zimmermann, 2009). Human-carnivore conflict takes many forms, and the drivers behind conflicts are often complex (Dickman *et al.*, 2014). Arguably the most commonly reported conflict is that which results from livestock depredation (Inskip & Zimmermann, 2009). The livelihoods of many rural communities rely on livestock farming (Boone *et al.*, 2005) however, these livestock may also represent an easy source of food for local wild predator species. Livestock depredation by wild carnivores has been recognised as a problem across the globe (Europe: Meriggi & Lovari, 1996; Kaczensky, 1999; Rigg *et al.*, 2011; North America: Musiani *et al.*, 2003; Morehouse & Boyce, 2017, 2011; Naughton-Treves *et al.*, 2003; Africa: Thorn *et al.*, 2012; Dickman *et al.*, 2014; Ogada *et al.*, 2003; Asia: Johnson *et al.*, 2006; Dar *et al.*, 2009; globally: Ripple *et al.*, 2014; Inskip & Zimmermann, 2009; Treves & Karanth, 2003) and the carnivores in question are at high risk of being killed in retaliation for, or to prevent, such attacks (Treves & Karanth, 2003; Kissui, 2008). In some cultures this is actively encouraged; for example some tribes in East Africa, such as the Barabaig, men who kill livestock raiding lions are rewarded by the whole community (Dickman & Hazzah, 2016; Dickman *et al.*, 2013).

Whilst large carnivores are amongst the most threatened groups of species (Ripple *et al.*, 2014), they are also among the most charismatic; as a result they are often used as flagship species. Flagship species are used to gain public, and/or political, interest in a conservation issue thereby helping to secure the resources required for their protection (Verissimo *et al.*, 2011). An argument for using large carnivores as flagship species is that not only are they charismatic, they also have ecological characteristics which mean they also may work as umbrella species (Belbachir *et al.*, 2015; Caro, 2003; Noss *et al.*, 1996). Umbrella species require large areas of habitat, therefore by conserving enough habitat so that a population of the umbrella species can persist in an area, other species will also be conserved (Simberloff, 1998). Large carnivores can act as umbrella species; they tend to be wide-ranging and therefore require large areas of useable habitat to persist – if action is taken to conserve them then other species will also be conserved as a result (Belbachir *et al.*, 2015; Caro, 2003; Noss *et al.*, 1996).

2.8. Study Species

2.8.1. African Wild Dog

The African wild dog is a highly social species and animals live almost exclusively in groups throughout their lives. Packs consist of an alpha male and female who are usually the only members of the pack that produce pups (Creel & Creel, 1991). The rest of the pack is made up by other founding individuals – usually the alpha pair’s siblings – and the offspring of the alpha pair (Fuller *et al.*, 1992; Woodroffe *et al.*, 2009). They are cooperative breeders; all members of the pack are involved in pup-rearing even though it is normally only the alpha pair that actually reproduce (Fuller *et al.*, 1992; Woodroffe *et al.*, 2009). Packs are initially formed by two dispersal groups joining together; dispersal groups are usually a single sex group of related individuals, often littermates (McNutt, 1996). Wild dogs are somewhat territorial and packs will defend their territories against intruders.

Although previously found throughout sub Saharan Africa, wild dogs have suffered from extensive habitat loss and are now only known to occur in 7% of their former range (Figure 2.1; IUCN/SSC, 2007). Wild dogs are categorised as Endangered by the IUCN Red list with their global population estimated to be approximately 6600 individuals (Woodroffe & Sillero-Zubiri, 2012). Their endangered status is partly as a result of habitat loss but also as a result of human persecution. Wild dogs have historically had a bad reputation, with government policy in some countries actively encouraging their eradication (Fanshawe *et al.*, 1997, 1991). In recent decades attitudes have changed and wild dogs are increasingly valued, particularly as a draw for tourists (Lindsey *et al.*, 2005b). Wild dogs are extremely wide-ranging, with resident packs recorded as having home ranges of more than 2000 sq km in some areas (Fuller *et al.*, 1992). Dispersing and translocated groups are also known to sometimes travel thousands of kilometres in search of new territories and mates (Masenga *et al.*, 2016).

The effect of potential movement barriers on wild dog behaviour is somewhat complicated. There have been several documented cases of packs using fences to their advantage during hunting to restrict their prey’s ability to escape by flushing them towards the fences (van Dyk & Slotow, 2003; Davies-Mostert *et al.*, 2013). This has been shown to increase their hunting success for larger ungulate species, meaning they need to hunt less often (Davies-Mostert *et al.*, 2013). However such

behaviour has only been reported on a relatively small number of reserves and so only a small proportion of animals are likely to benefit from the associated increase in hunting efficiency. Even if packs elsewhere learnt to employ this behaviour it may only be for a short-term gain as the damage to fences that results has led to increased antipathy towards wild dogs from land managers and has resulted in the removal of wild dog packs from reserves (Lindsey *et al.*, 2005b; Woodroffe *et al.*, 2014). Overall, as a wide-ranging species, wild dogs are likely to be primarily negatively affected by the loss of connectivity that is associated with increased levels of fencing. Other anthropogenic landscape features also affect wild dog movement patterns, for example there have been suggestions that wild dogs preferentially use roads to move around their territories (Woodroffe, 2010); this is potentially problematic, as roadkill is an important cause of mortality for the species (Woodroffe *et al.*, 2007a).

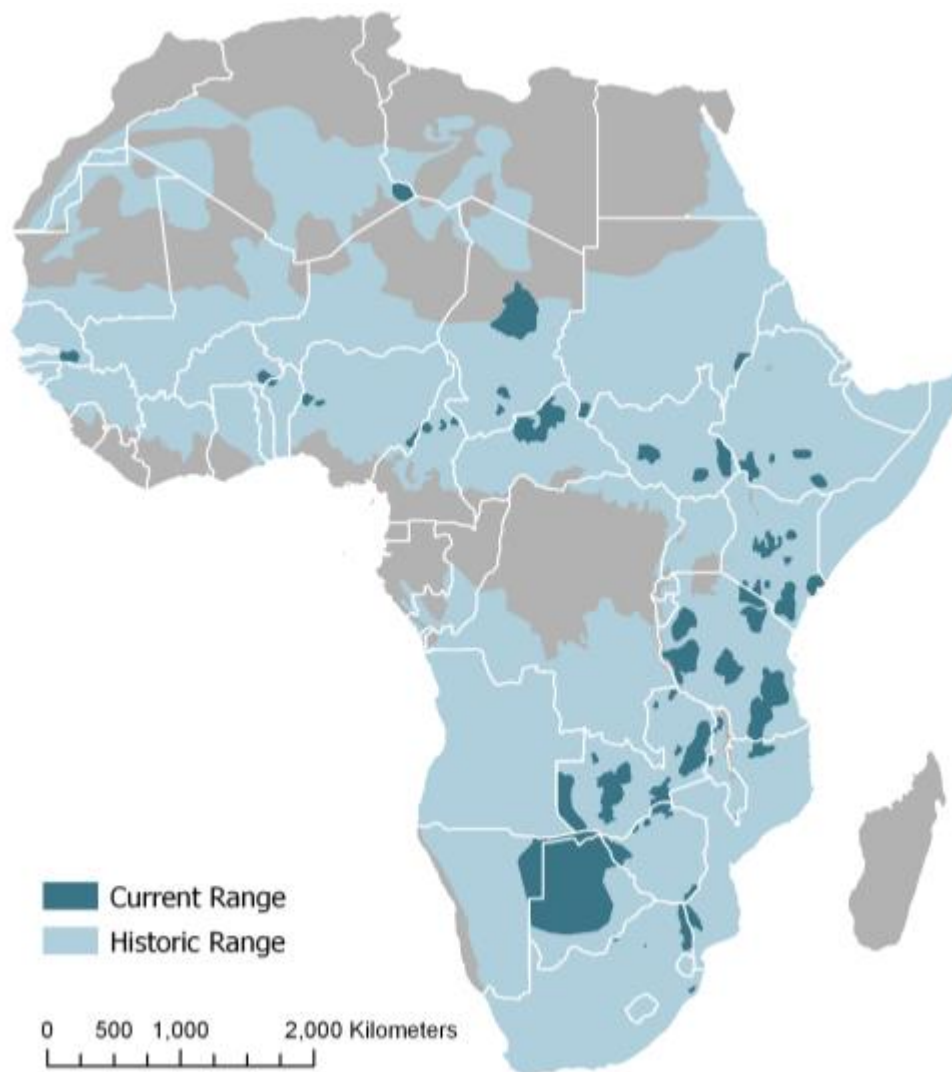


Figure 2.1. Historic and current range of the African wild dog, *Lycaon pictus*. Data from IUCN/SSC (2007) and Woodroffe & Sillero-Zubiri (2012)

2.8.2. Cheetah

The cheetah is a member of the *Felidae* family and is most famous as the world's fastest land animal (Myers, 1975). A significant proportion of research into the biology and ecology of cheetahs originates from the Serengeti Cheetah Project which focusses on the cheetah population of the Serengeti National Park's open grass plains (Durant *et al.*, 2007); as a result cheetahs have often been referred to as a species that specialises in living on open plains (Mills *et al.*, 2004). As the volume of literature from other systems has increased, there has been a greater amount of evidence to show that the cheetah is a generalist species, and is able to live in a variety of different habitats ranging from savannah woodland to desert (Bissett & Bernard, 2006; Belbachir *et al.*, 2015; Houser *et al.*, 2009; Broomhall *et al.*, 2003; Mills *et al.*, 2004; Durant *et al.*, 2015a). The species used to be found throughout the African continent, across the Middle East and into Asia, however their range has now significantly decreased and they are estimated to still be resident in just 9% of their historic range (Figure 2.2; Durant *et al.*, 2017). Habitat loss and fragmentation have been identified as the primary cause of the cheetah's continuing decline; this has led to the species being categorised as Vulnerable to extinction by the IUCN Red List (Durant *et al.*, 2015a) although there have been recent calls to uplist the species to Endangered (Durant *et al.*, 2017).

Cheetahs have a unique social structure among felids; females are solitary, except for when rearing cubs, and are not territorial – instead roaming across large home ranges (Durant, 2004), in some areas they have been recorded as having home ranges over 2000 sq km in size (Marker *et al.*, 2008). Males are sometimes solitary, although often live in coalitions and are sometimes territorial. When they are territorial, males may hold small territories; however when they are non-territorial, which is often the case, they have large home ranges, similar in size to those of females (Durant, 2004). Purchase & Du Toit (2000) observed that, within their home ranges, cheetahs used habitat differently depending on their behavioural state. There was a preference for treeline habitat at the interface between woodland and grassland areas, and this preference was also significantly higher during resting periods. Mills *et al.* (2004) found that cheetahs preferentially used open areas for hunting which seemed to be linked to an increase in hunting success.

Although both wild dogs and cheetahs are large carnivores, they nonetheless suffer the effects of coexisting with other larger and more powerful carnivore species, particularly the lion and the spotted hyaena, *Crocuta crocuta*; this takes the form of competition for resources, kleptoparasitism and direct predation (Durant, 2004; Mills & Gorman, 1997; Creel & Creel, 1996). It is this suppression that is likely to be the cause of the two species' wide-ranging behaviour and the reason that they live at very low population densities (Groom *et al.*, 2016; IUCN/SSC, 2007). This coexistence also affects their movement patterns; wild dogs have been found to proactively avoid these larger predators (Broekhuis *et al.*, 2013; Mills & Gorman, 1997; Creel & Creel, 1996; Swanson *et al.*, 2014) and cheetahs will actively move away from lions and hyaenas and are less likely to hunt when these other large predators are nearby (Durant, 2000).

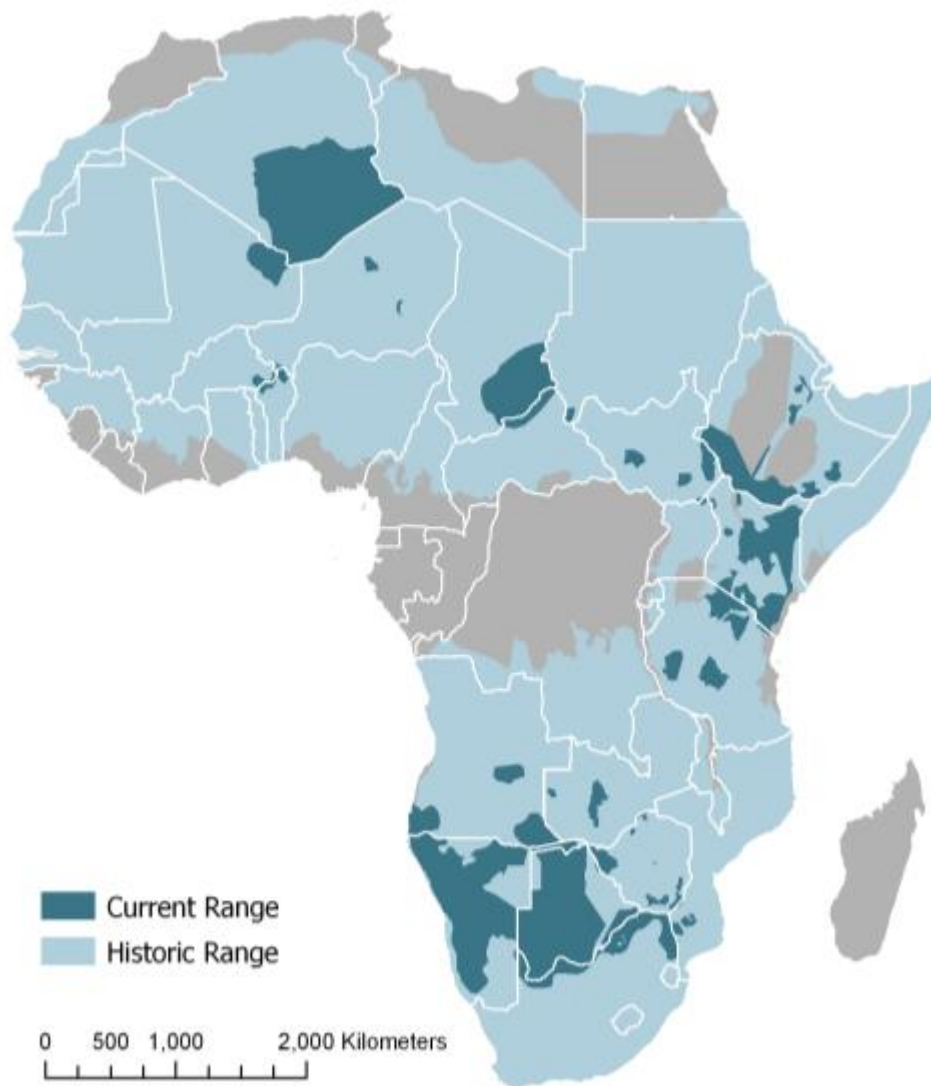


Figure 2.2. Current and historic range of the cheetah, *Acinonyx jubatus*, in Africa. Data from IUCN (2007) and Durant *et al.* (2017)

2.9. Study Site

Laikipia County covers approximately 9800 sq km of north-central Kenya. The county is to the north of the Aberdare highlands (3999 metres above sea level) and north west of Mount Kenya (5199m; Figure 2.3; Georgiadis *et al.*, 2007). The elevation in the county varies from 2000m in the south of the county to 1700m in the north (Graham *et al.*, 2009). The mean daily maximum temperature in the area is 28°C and the minimum is 14°C (Shorrocks *et al.*, 2008). Rainfall is strongly affected by the County's vicinity to Mt Kenya and the Aberdares; areas in the south of county close to the equator have annual rainfall of 900mm but in the north this falls to 400mm (Kinnaird & O'Brien, 2012). Rainfall is bimodal with long rains expected from April to June and short rains from October to December (Graham *et al.*, 2009); however, rain may fall at any time of year, it is highly variable both across and within years (Ulrich *et al.*, 2012). The area has many ephemeral and permanent water points, including man-made dams and water holes used by both livestock and wildlife. Droughts, of varying severity, are relatively common and can have substantial negative impacts on people, livestock and wildlife living in the area (Huho *et al.*, 2010).



Figure 2.3. Location of Laikipia County in relation to Mount Kenya and the Aberdares as well as nearby major towns

The main vegetation type in the county is *Acacia* woodland (Kinnaird & O'Brien, 2012). There are two other common vegetation types in Laikipia: savannah grassland, areas covered by perennial grasses and widely spaced trees, and bushland, areas of intermittent perennial grasses and acacia tree species with >30% canopy cover (Kinnaird & O'Brien, 2012).

A wide variety of land use types are found within the county (Figure 2.4). Cropland and other more intensive farming types tend to be found in the south of the county due to the higher levels of rainfall in these areas. Large-scale, privately-owned cattle ranches are a major land use type across the centre of the county. Many of these ranches rely primarily on their cattle ranching business for income, however a significant proportion also have ecotourism businesses and thus manage their land with the intention of encouraging wildlife. There are also group ranches, where many people rely on traditional pastoralism for their livelihoods. Group ranches tend to have high livestock densities, as do the commercial large-scale cattle ranches (Kinnaird & O'Brien, 2012). Ranches where land is managed for wildlife

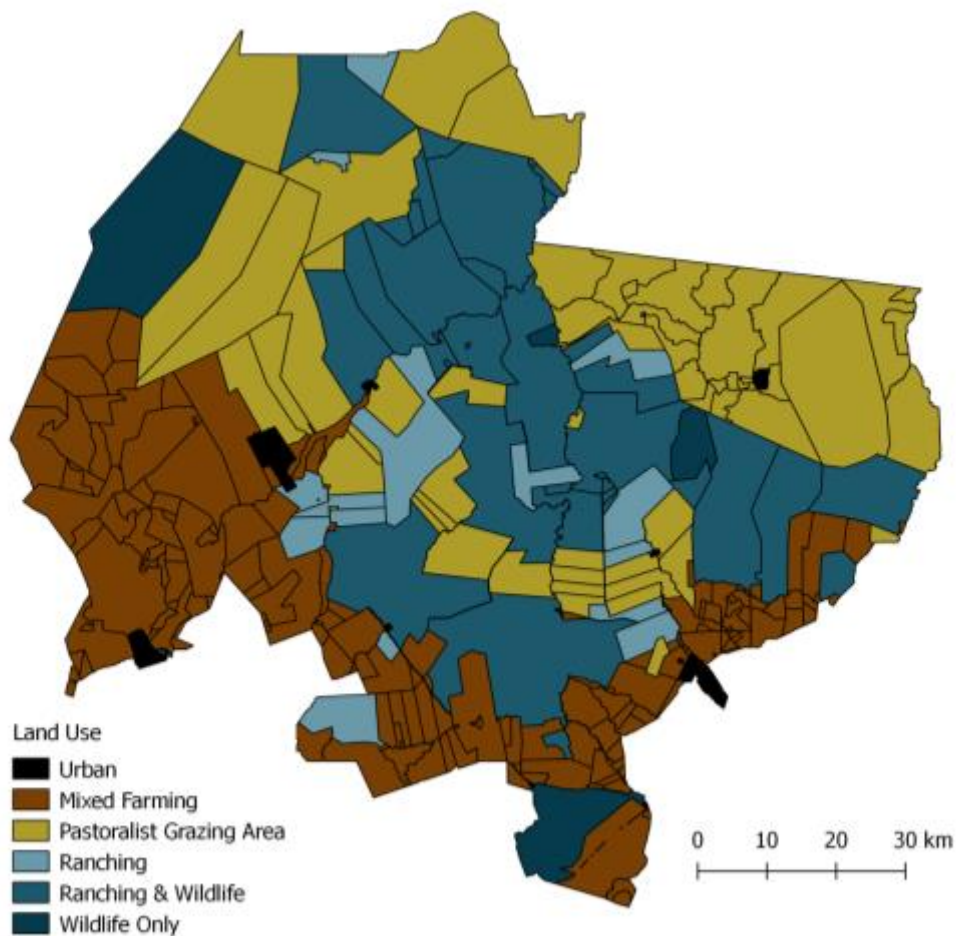


Figure 2.4. Land use types in Laikipia County, Kenya

have lower stocking densities. Laikipia does not have government gazetted wildlife areas (Graham *et al.*, 2009) however there are some areas of privately owned land which are managed as wildlife sanctuaries and which do not have livestock.

Despite not having government-enforced wildlife areas, Laikipia is one of Kenya's most important wildlife areas (Kinnaird & O'Brien, 2012). The county has the second highest wildlife densities in the country, second only to the Maasai Mara (Kinnaird & O'Brien, 2012). Much of the wildlife is found on lower density livestock ranches and in the area's few wildlife sanctuaries; however groups ranches and communities lands are also home to many wildlife species albeit generally at lower densities than elsewhere in the county (Georgiadis *et al.*, 2007). The most common ungulate species in the area, in terms of biomass and abundance, are elephants, impala and dik dik (Augustine, 2010), however it is home to many other ungulate species including Grevy's and common zebra, *Equus grevyi* and *E. burchelli*, giraffe, *Giraffa camelopardalis*, buffalo, *Syncerus cafer*, and Grant's gazelle *Gazella granti* (Keesing, 1998). The area is still home to populations of all of its native large carnivores; these include lions, leopards, cheetahs, wild dogs, spotted hyaenas and striped hyaenas (Frank *et al.*, 2005).

Over the past 50 years, Laikipia's landscape has undergone large-scale changes. The local human population has increased from approximately 66,000 in 1969 to almost 400,000 in 2009 (Kenya National Bureau of Statistics, 1969, 2009) with inevitable impacts on local natural resources and changes in local land-uses. In particular there has been a shift towards small-scale mixed farming for subsistence alongside large-scale horticultural farms (Ulrich *et al.*, 2012).

Currently, there are several planned development projects which threaten the integrity of wildlife habitat in the area, these include: major water extraction (Abdi, 2013), large-scale fencing projects (Pearce, 2015), an oil pipeline (LAPSSET Corridor Development Authority, 2015), and a power line which threatens ecotourism – a major source of revenue for the region (Waweru, 2013). In addition to these major infrastructure projects and changes in land-use there are new potential movement barriers, such as property boundary and wildlife fences, which are increasingly being erected and reinforced. This is partly as a result of the recent increase in levels of poaching and the illegal trade in wildlife across East Africa; numerous rhinos are known to have been poached from local rhino sanctuaries (Jorgic, 2014). All properties which have rhino on their land are required, by Kenya Wildlife Service (KWS), to be fenced (Kenya Wildlife Service, 2012). This is in an

attempt to better protect the rhino population from illegal killing and in light of the recent upswing in poaching levels; it is unlikely that this requirement will be dropped from future management plans.

Laikipia is an important area for cheetah and wild dog conservation, being home to parts of globally important populations for both species (IUCN/SSC, 2007, 2012, 2015). Evidence of recent functional connectivity of Laikipia to adjoining areas is illustrated by the wild dog population itself. The species was locally extirpated in the 1980s but in the early 2000s Laikipia was naturally recolonised by individuals migrating into the area (Woodroffe, 2011). Over subsequent years the population has established itself and grown to become one of the largest in the world (Woodroffe, 2011). Establishing how the two species survive in Laikipia's human-dominated landscape will enable recommendations to be made for future land-use planning which will likely also benefit other species in the ecosystem. Such recommendations are also likely to be highly applicable to species living in other human-dominated areas.

2.10. Field Methods

2.10.1. GPS Collars

Three types of GPS collar (Table 2.1) have been used in the course of the long-term research project, the Kenya Rangelands Wild Dog and Cheetah Project (KRWDPC; formerly known as the Samburu-Laikipia Wild Dog Project). The weight of GPS collars available has largely determined the type of collar used throughout the study. In the interests of animal welfare, collar weights were restricted to less than 1.5% of the animal's body weight. Wild dogs in the study population have a mean weight of 23kg (Woodroffe et al., 2007c). Cheetahs in the study population have a mean weight of 43kg (O'Neill, unpublished data). Additional information about animals collared and included in this study is in Appendix 1.

2.10.2. Immobilisations

All immobilisations conducted during the course of this study and KRWDPC have been in collaboration with Kenya Wildlife Service. Permission for immobilisations was given by Kenya's National Commission for Science, Technology and

Table 2.1. Details of GPS collar manufacturers and collar models used to collect data analysed in this thesis

Collar Manufacturer and Location	Collar Model	Communication type	Approx. Weight of Collar	Species Used On
Televilt Lindesberg, Sweden	Posrec-300	None (data stored on board)		Wild dog
Vectronics Berlin, Germany	GPS Plus 1c	Bidirectional VHF	250g	Wild dog
Sirtrack Hawkes Bay, New Zealand	Pinnacle LITE G5C-275D	Iridium	400g	Cheetah

Innovation. Immobilisations followed protocols approved by the Ethics Committee of Zoological Society of London. Details of the protocols followed are given below.

2.10.2.1. Wild dogs

The wild dogs whose GPS collar data were used in these analyses were immobilised by free darting from a vehicle. Immobilisations were conducted during daylight hours, between dawn and early afternoon. This is to ensure that immobilised animals were fully recovered before nightfall. Once an individual had been selected for collaring, the vehicle would slowly approach to a distance of <15m. Individuals were darted when lying away from any other wild dogs to ensure that if the dart missed, that non-target animals would not be struck by the dart. Individuals were darted into the muscle mass of their hindquarters, using a dart fired from a CO₂ powered rifle. After darting wild dogs usually move 10-30m before lying down again, during which time the pack stays with the individual. No aggressive or other potential harmful behaviour has been observed directed at a darted wild dog by other members of its pack. No injuries were sustained by wild dogs during immobilisations, other than a small wound from the dart penetrating the skin which was treated with antiseptic spray.

Wild dogs were immobilized with a combination of approximately 26 mg/kg of medetomidine (Domitor; Pfizer Animal Health, Walton Oaks, Surrey, United Kingdom) and approximately 2.6 mg/kg of ketamine. After between 45 and 60 minutes, animals were reversed with approximately 130 mg/kg of atipamezole (Antisedan; Pfizer Animal Health).

During immobilisations animals were moved into shaded areas, their body temperature was monitored and they were cooled with water as necessary. During immobilisations other pack members would move away but remain within a few hundred metres. Packs were rapidly reunited after the immobilisations.

2.10.2.2. Cheetahs

Cheetahs were also immobilised by free darting from a vehicle in a similar fashion to the darting of wild dogs, however due to their larger body size cheetahs were darted from up to 20m distance. Immobilisations were conducted between dawn and early afternoon to ensure the animal could recover before nightfall. Cheetahs moved <50m after darting. No aggressive behaviour was exhibited towards darted cheetahs by other members of their social groups. No injuries were sustained by immobilised cheetahs other than the dart wound which was treated with antiseptic spray.

Cheetahs were also immobilised with a combination of medetomidine and ketamine although in slightly different dosages to those given to the wild dogs; approximately 25mg/kg medetomidine and 3mg/kg ketamine. After approx. 45 to 60 minutes animals were reversed with 120 mg/kg of atipamezole.

During immobilisations cheetahs were moved into shaded areas, their body temperature monitored and they were cooled with water as required. Other members of the cheetahs' social groups moved away during immobilisations however all groups reunited within a few hours of the immobilisation and before nightfall.



Plate 4. A pack of African wild dogs resting

Chapter 3.

What Wild Dogs Want: Habitat Selection Differs Across Life Stages in African Wild Dogs

3.1. Abstract

Habitat loss is a key threat to the survival of many species. Habitat selection studies can help inform conservation initiatives by identifying the most important habitat characteristics for the persistence of threatened species living in changing landscapes. However, there may be differences between animals' regional and local habitat selection preferences, and these preferences may alter as an individual's life stage changes. Using GPS collar data collected from a free-ranging population of African wild dogs living in a human-dominated landscape in Kenya to develop resource selection function and step selection function models, this study investigates the differences between second order (selection of home range across a landscape) and third order (selection of habitat within the home range) habitat selection across four life history stages relevant to this species: resident-non-denning, resident-heavily-pregnant, resident-denning and dispersing. Analyses showed strong second order selection for areas with low human population densities and areas close to rivers and roads. More rugged areas were also generally selected for, as were areas with lower percentage tree cover. Habitat selection was similar between the two orders of selection, although not all factors significantly affected selection across both orders. Habitat selection was also broadly similar across the four life stages; however the magnitude of selection varied significantly, with dispersers more tolerant to higher human population densities. This analysis demonstrates that connectivity across a landscape will vary for individuals at different life stages. This variation needs to be taken into account during conservation planning of connectivity across a landscape.

3.2. Introduction

Habitat loss and fragmentation are recognised as one of the leading causes of global biodiversity loss (Brooks *et al.*, 2002; Millennium Ecosystem Assessment, 2005). In order to prevent and reduce further biodiversity loss, it is vital to know which elements of a habitat are the most crucial to preserve for threatened species to be able to persist (Giam *et al.*, 2010; Lee & Jetz, 2008). This information will be of particular importance in areas where there are growing human populations; in these areas the resource needs of vulnerable local communities must be balanced against the conservation of any wildlife with whom they share a landscape (Kaimowitz & Sheil, 2007; Sanderson *et al.*, 2002). Whilst the global protected area network is undoubtedly vital for conservation (Chape *et al.*, 2005), unprotected areas, where local communities and wild species coexist, are likely to be of great importance for the conservation of many species (Durant *et al.*, 2017; Lee & Jetz, 2008; Margules & Pressey, 2000; Naughton-Treves *et al.*, 2005). For unprotected areas to reach their full conservation potential, it is important to know what habitat characteristics are favoured by wildlife species. Where this information is available, it can be incorporated into development and land-use planning to try to foster successful coexistence between people and wildlife (Burdett *et al.*, 2010; Lee & Jetz, 2008; Polasky *et al.*, 2005).

Among the groups of species most threatened by the deleterious effects of habitat loss and fragmentation are large-bodied mammals (Cardillo *et al.*, 2005; Fisher & Owens, 2004), and in particular large carnivores (Crooks *et al.*, 2011; Ripple *et al.*, 2014). There are several reasons for this, primarily stemming from larger-bodied species tending to have larger home ranges (Lindstedt *et al.*, 1986; Woodroffe & Ginsberg, 1998). If a terrestrial species has a large home range, it will need a large area of contiguous, suitable habitat in order to find the resources it requires to survive. Large carnivores are particularly at risk, not only because they usually have comparatively large home ranges, but also because they tend to be under higher levels of threat where they come into contact with humans (Ripple *et al.*, 2014; Woodroffe & Ginsberg, 1998). In areas where humans and carnivores live in close proximity, carnivores are often at risk of being killed by members of local communities because they are perceived, or prove, to be a threat to livestock and/or people (Andrén *et al.*, 2006; Ogada *et al.*, 2003). This means that while carnivores may be able to cross through areas of suboptimal habitat, they are likely to be at high risk when doing so (Bouyer *et al.*, 2015; Bunnfeld *et al.*, 2006).

This study investigates habitat selection by wide-ranging species in a human-dominated landscape, using the African wild dog population of Laikipia County in Kenya as a case study. The African wild dog is one of the widest-ranging large carnivores (Woodroffe, 2010). Laikipia County is home to a globally important wild dog population, which naturally recolonised the area after being locally extirpated in the 1980s (Woodroffe, 2011). The species was able to successfully re-establish itself despite the landscape having been extensively modified by the county's rapidly expanding human population (Ulrich *et al.*, 2012). This study will use wild dogs as a model species to improve our knowledge as to how wide-ranging species move across human modified landscapes, in order to inform conservation planning.

3.2.1. Orders of Habitat Selection

Where species are found, and the habitats they use, are central aspects of their biology and therefore are important factors in planning which areas need to be conserved for the species to be able to persist (Cody, 1985). Habitat selection can be classified into three scales (Johnson, 1980). The coarsest scale, or first order selection, refers to the geographic or physical range of a species (Johnson, 1980) – for example a species may be a rainforest specialist which is only found within the Congo basin. Second order selection is at a finer scale and refers to the choice of home range of an individual or social group within the species' geographic range (Johnson, 1980), for example a particular area of that rainforest. Third order selection is the use of habitat within an animal's home range (Johnson, 1980), for example if certain areas of the home range are preferentially used for foraging or denning. Many studies focus on the habitat selection exhibited at one order rather than several (McGarigal *et al.*, 2016). However, species (or individual) preferences may vary across orders of selection and so restricting analyses to only one hierarchical level could result in important information not being apparent (Bradshaw *et al.*, 1995; Zeller *et al.*, 2017).

3.2.2. The Effect of Life Stage

As animals move through different life stages, they are likely to have varying requirements and therefore select habitat differently. The majority of habitat selection studies focus on the preferences of adult and/or resident individuals or groups, as this age group is usually the easiest to study (Abrahms *et al.*, 2016). Whilst it is undoubtedly important to know which habitats individuals in this life stage require for their survival, as they often form the largest proportion of a population

and it is the stage in which animals reproduce, there is increasing recognition that understanding the habitat selection of individuals in other life history stages is also important (Abrahms *et al.*, 2016). A clear example of this is shown by studies of habitat connectivity – resident adults usually remain in their established home ranges and seldom go on long excursions whereas dispersing individuals may travel large distances in search of mates and new territories (Elliot *et al.*, 2014a). Dispersal, where individuals leave their natal range and set up new territories or home ranges elsewhere, is likely to be the life stage where connectivity between remnant populations is most vital and hence needs to be considered in understanding how different habitats contribute to connectivity. There have been relatively few studies which have focussed on the habitat preferences of dispersers (Abrahms *et al.*, 2017), this study aims to address a knowledge gap about how dispersing and resident animals differ in how they select habitat as they move across a landscape.

3.2.3. African Wild Dogs

The African wild dog is an extremely wide-ranging large carnivore. Resident packs have been recorded as having territories of over 2000 sq km and groups of young individuals may travel hundreds of kilometres when dispersing from their natal pack (Davies-Mostert *et al.*, 2012; Fuller & Kat, 1990; Masenga *et al.*, 2016). Currently categorised as Endangered by the IUCN Red List, wild dogs have been extirpated from as much as 93% of their former resident range (IUCN/SSC, 2007, 2012, 2015). Although once found across Sub-Saharan Africa, a combination of habitat loss, deliberate and accidental killing by people, and disease, means that the species is now restricted to 39 subpopulations scattered across the continent; all but three of these subpopulations are thought to number fewer than 50 packs and none is estimated to comprise more than 150 packs (Woodroffe & Sillero-Zubiri, 2012). Much of the species' remaining range is outside of protected areas, and so it remains under threat from further habitat loss and the negative effects of land-use change (IUCN/SSC, 2007, 2012, 2015). Establishing the habitat selection patterns of the species is a key first step in developing land-use planning and management recommendations for its conservation.

Wild dogs are obligate cooperative breeders, and pups normally stay with their natal pack until they reach approximately two years of age (Fuller *et al.*, 1992; McNutt, 1996). During this time, they will help raise the subsequent years' pups. Once they

reach sexual maturity most wild dogs leave their natal packs in single sex dispersal groups (McNutt, 1996); these groups often travel very long distances (Davies-Mostert *et al.*, 2012) before encountering opposite sex wild dogs and establishing new packs. As dispersal groups are often more wide-ranging than resident packs, dispersal groups are likely to have differing habitat preferences to those of resident packs. This has been suggested in previous work on habitat selection by dispersing and resident African wild dogs; however previous studies have relied on opportunistic sightings, which can suffer from detection bias, and crude methods of assigning dispersal status (Jackson *et al.*, 2016) or small sample sizes which have prevented direct analysis of dispersal group preferences (Abrahms *et al.*, 2017).

3.2.4. Hypotheses and Predictions

Hypothesis A: Wild dogs do not move across a landscape randomly in relationship to human impacts and geographical features

Prediction A.1: Second order habitat selection of wild dogs will be influenced by human population density

Prediction A.2: Second order habitat selection of wild dogs will avoid areas that impede movement across the landscape, such as rugged areas and those with dense tree cover

Prediction A.3: Second order habitat selection of wild dogs will favour areas close to linear features, such as rivers and roads, that facilitate rapid movement across the landscape

Hypothesis B: Wild dogs select habitats differently across life stages

Prediction B.1: Denning wild dogs will select for inaccessible areas with the lowest human densities, highest ruggedness, most trees and furthest from roads and rivers

Prediction B.2: Dispersing wild dogs will show least avoidance of high human population densities and will be most selective of areas that facilitate movement across the landscape e.g. roads.

Hypothesis C: Wild dog habitat selection will differ according to scale

Prediction C.1: The strength of habitat selection for different geographical and anthropogenic features will differ between second and third order habitat selection.

3.3. Methods

3.3.1. Study Area

Laikipia County is a mixed-use, human-dominated landscape in Northern Kenya. Land-use types in the county include ranch land, traditional pastoralist areas and wildlife conservancies (Ulrich *et al.*, 2012). The county is one of the most important wildlife areas in Kenya, with globally important populations of several endangered species (Kinnaird & O'Brien, 2012). The area was naturally recolonised by wild dogs in the early 2000s, after the species went locally extinct in the 1980s (Woodroffe, 2011). Laikipia is now home to a key part of one of the largest free-ranging wild dog populations in Africa (IUCN/SSC, 2015, 2012, 2007).

Although an important area for wildlife, Laikipia has a large and growing human population (Kenya National Bureau of Statistics, 1969, 2009) which is putting increasing pressure on the county's remaining natural resources, this has recently resulted in violent clashes over resources such as access to water and areas to graze livestock (Cruise & van der Zee, 2017).

3.3.2. Wild Dog Movement Data

Data collected from GPS (Global Positioning System) collars were used to explore wild dog habitat selection patterns. Between January 2011 and February 2017 18 wild dogs were immobilised and fitted with GPS collars (Vectronic GPS-plus mini; Figure 3.1) as described in Woodroffe (2011). Some individuals were from the same natal pack; however no two individuals were fitted with GPS collars in the same pack at the same time. Packs are highly cohesive and members normally only separate for short periods during denning periods, when some individuals remain at the den to guard the pups; as a result collaring one individual in each pack (or dispersal group) effectively monitors the movements of all pack members. Individuals were collared for an average of 236 days (range: 114 – 388 days) before the collar's battery expired, the individual dispersed and was lost to monitoring, or the collar was removed.

Wild dogs are extremely crepuscular (Woodroffe *et al.*, 2017) and so only data collected during the animals' active periods at dawn and dusk were used in these analyses. Morning locations were recorded at 06:30 and 08:00, and evening locations at 18:00 and 19:30 local time (UTC + 3). These timings correspond to the



Figure 3.1. An African wild dog wearing a GPS collar

beginning (06:30 and 18:00) and end (08:00 and 19:30) of wild dog morning and evening periods of activity (Woodroffe *et al.*, 2017). Dilution of Precision (DoP), a measure of the effect of satellite spatial configuration on the accuracy of the GPS location data (Langley, 1999), was used to determine the accuracy of locations. All GPS collar locations where the DoP was more than 5 (indicating a potentially inaccurate location) were excluded from the analysis.

3.3.3. Wild Dog Life Stage Data

Collared wild dogs were visually monitored throughout the study. Frequency of visual observation varied due to logistical constraints but packs were usually located at least once every 1-4 weeks throughout the study. Observational data, including individual identification of pack members and pack reproductive state, were recorded. These data, in combination with data collected from the GPS collars, were used to determine each collared individual's life stage. Collar data were divided into four categories: resident-non-breeding (hereafter referred to as resident), resident-heavily-pregnant (hereafter referred to as pregnant), resident-denning (hereafter referred to as denning) and dispersing.

Individuals were categorised as denning during the period of approximately three months when packs had pups in the den; the exact dates of this period were determined by mapping the GPS collar data and using the distinctive “starburst” movement pattern created by dogs leaving to hunt and then returning to the den to tend the pups twice a day (Figure 3.2).

Data for all individuals were categorised as pregnant for the 28 days before the start of denning. This was not in reference to whether the collared individual was pregnant, as none of the collared animals produced pups themselves; instead this categorisation refers to the weeks when the alpha female of the collared individual’s pack was heavily pregnant. This is because if the alpha female shows differing habitat selection during this time then this would be reflected for all individuals within the pack. Wild dog gestation is approximately 70 days (Creel *et al.*, 1997); endocrine levels of alpha female wild dogs differ during this time from the levels observed during oestrus and lactation (Creel *et al.*, 1997) with levels of oestrogen and progesterone metabolites excreted, increasing throughout pregnancy and peaking at birth (Monfort *et al.*, 1997). Wild dogs have large litters (Creel & Creel, 1991) and females are visibly pregnant less than half way through their gestation (Creel *et al.*, 1997), which may impact on their mobility later in their pregnancy. If the combination of changes in hormonal levels and locomotive ability during pregnancy, as well as the need to locate potential den sites, affects wild dog habitat selection then this is likely to be most distinctive towards the end of gestation, therefore only data from the last 28 days of gestation were used for these analyses.

Individuals were categorised as resident when they were part of a pack which had an established territory and were not denning and the alpha female was not heavily pregnant.

Individuals were defined as dispersing for a period beginning when a single sex group left its natal pack permanently. This could be determined because, although only one individual in each pack was fitted with a GPS collar, other individuals in the pack were fitted with VHF (Very High Frequency) radio collars to facilitate ground tracking. Dispersals were defined as ending either when the dispersal group was seen with opposite sex dogs or when its ranging patterns became a consistent home range, whichever happened sooner. A home range was defined as being consistent when weekly home ranges (defined as minimum convex polygons drawn around all the locations recorded in a week) consistently overlapped and the overall area size plateaued (Figure 3.3).

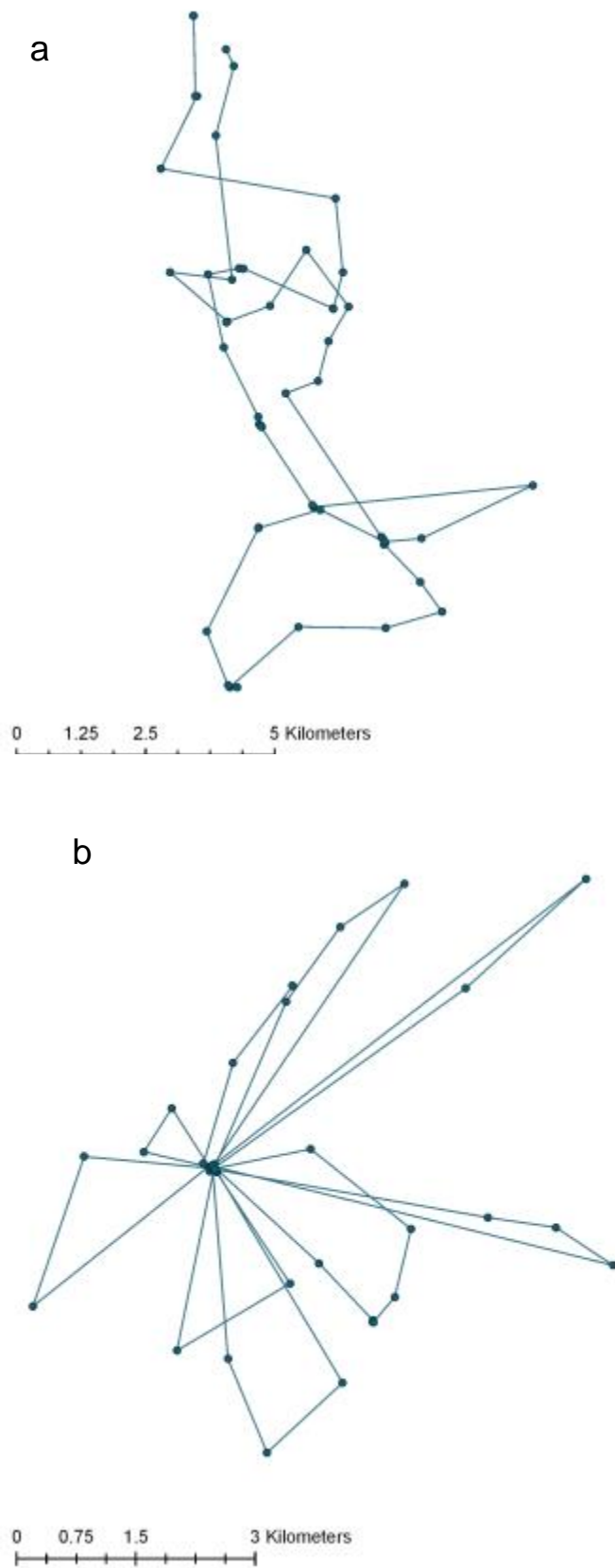


Figure 3.2. Maps showing 7 days of movement data from a GPS collared wild dog during a resident-non-breeding life stage (map a) and a resident-denning life stage (map b)

Any data where the individual's life stage did not fit into the above categories, e.g. periods around a pack break up following the death of an alpha female, were excluded from analyses; a total of 383 datapoints from 3 individuals, leaving a total of 7009 datapoints (Table 3.1).

3.3.4. *Habitat Characteristics*

Wild dog habitat selection was investigated in relation to five key habitat variables that are likely to affect foraging choices, den selection and movement patterns: human population density, distance to roads, distance to rivers, percentage tree cover and Terrain Ruggedness Index. All variables were analysed at 100m resolution.

Gridded Population of the World, Version 4 (GPWv4) was used for human population density data (CIESIN, 2016). Data were downloaded at 30 arc-second resolution (approximately 900 metres) and resampled using bilinear interpolation to 100m grid cells.

Location data for Kenyan main roads and rivers were downloaded (Japan International Cooperation Agency, 2013; Survey of Kenya, 1997) and converted into raster files in *R* (R Core Team, 2016) using the *rasterise* function of the *raster* package (Hijmans, 2015). For each layer a distance grid was calculated using the *raster* package's *distance* function. The distance grids give the distance in kilometres for each grid square to the nearest road or river; hence larger values indicate greater distance from roads and rivers, signifying avoidance. It was these distance grids which were used in the subsequent analysis.

Percentage tree cover was downloaded from USGS MODIS MOD44B (DiMiceli & Carroll, 2017) at 250m resolution then resampled to 100m grid cells using bilinear interpolation.

Terrain Ruggedness Index is a measure of the roughness of an area calculated, from a digital elevation model (DEM) raster layer (90m resolution), as the mean of the absolute differences between the value of a cell and the values of its 8 surrounding cells. Terrain Ruggedness Index was calculated in *R* using the *terrain* function in the *raster* package using DEM data downloaded from World Resources Institute (World Resources Institute, 2007). The terrain ruggedness raster was resampled to 100m grid cells using bilinear interpolation.

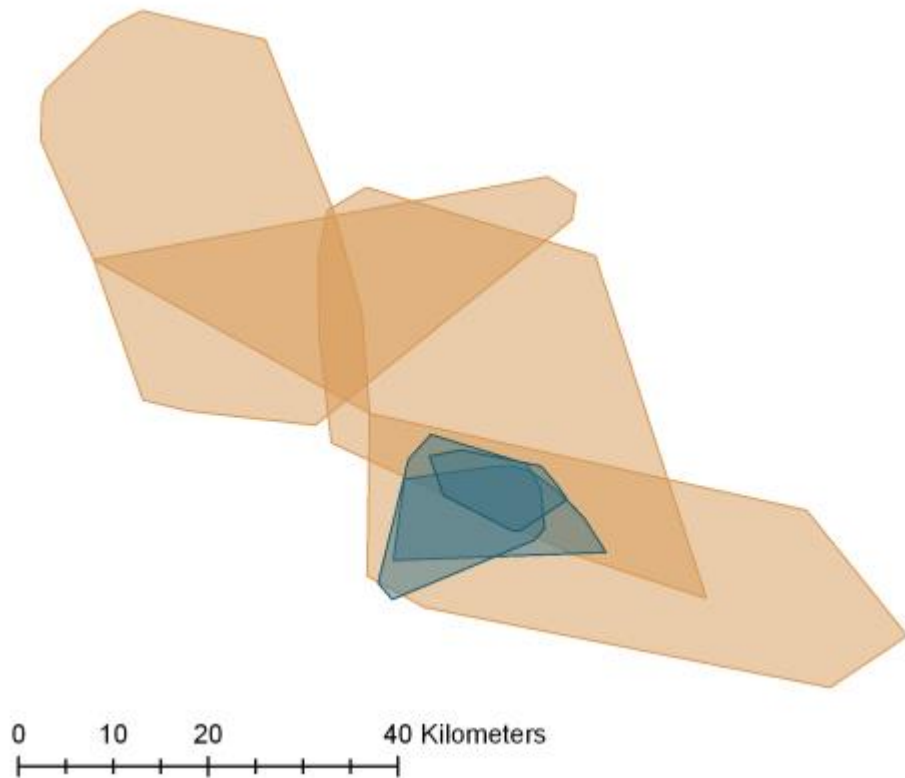


Figure 3.3. Minimum convex polygons drawn around weekly GPS collar data from a wild dog defined as dispersing (orange polygons) and resident (blue polygons)

Table 3.1. Number of data points included in analyses for each life stage

Life Stage	Number of Individuals	Mean Number of Data Points per Individual	Range of Number of Data Points	Total Number of Data Points Included in Analysis
Denning	15	106.0	25 – 185	1590
Pregnant	14	57.4	27 – 155	803
Resident	16	233.8	23 – 473	3741
Dispersing	7	125.0	5 – 424	875

3.3.5. Second Order Habitat Selection

Second order habitat selection was analysed using resource selection function (RSF) models. RSFs are widely used for evaluating habitat selection (Manly *et al.*, 2002). RSFs model habitat selection by comparing the habitat characteristics of an animal's observed locations with the characteristics of its available habitat. By investigating these differences, it is possible to infer which aspects of the habitat significantly affect whether an animal species is found in an area.

Determining the habitat areas that are available to an animal is an important step in developing an RSF model. If too wide an area is chosen then it may be that the study animals were not found in an area because the distance from their core range was too great, or there was an impermeable barrier, rather than as a result of its habitat characteristics and may therefore lead to erroneous results. Equally if too narrow an area is chosen then the magnitude of selection may be hidden as the comparison area is not sufficiently broad.

In this study, the area available to the wild dogs was calculated by drawing a minimum convex polygon around the entire wild dog GPS collar dataset; the central point of this polygon was determined, using the *polygon centroids* tool in *QGIS* (QGIS Development Team, 2012) and a circle was drawn around it; the radius of which was 90km, i.e. the distance between the centre point and the most distant wild dog location (Figure 3.4). There were no significant movement barriers that would prohibit movement by GPS collared wild dogs across the expanse of this area and the whole area could be considered available to them due to wild dogs' wide-ranging nature (Davies-Mostert *et al.*, 2012). In order to determine the habitat characteristics of the area available to the wild dogs, 10000 random points were generated within the "available" area and overlaid onto the landscape rasters described above. The habitat characteristics of each random point were extracted using the *extract* function of the *raster* package in *R*.

To determine the habitats used by the GPS-collared wild dogs, the GPS locations recorded by the GPS collars at 08:00 and 19:30 were used. Only two points were used each day in order to minimise spatial autocorrelation, and these time points correspond with the end of the period each day when wild dogs move the greatest distance (Woodroffe, 2010). These data were overlaid onto the landscape rasters and their habitat characteristics extracted.

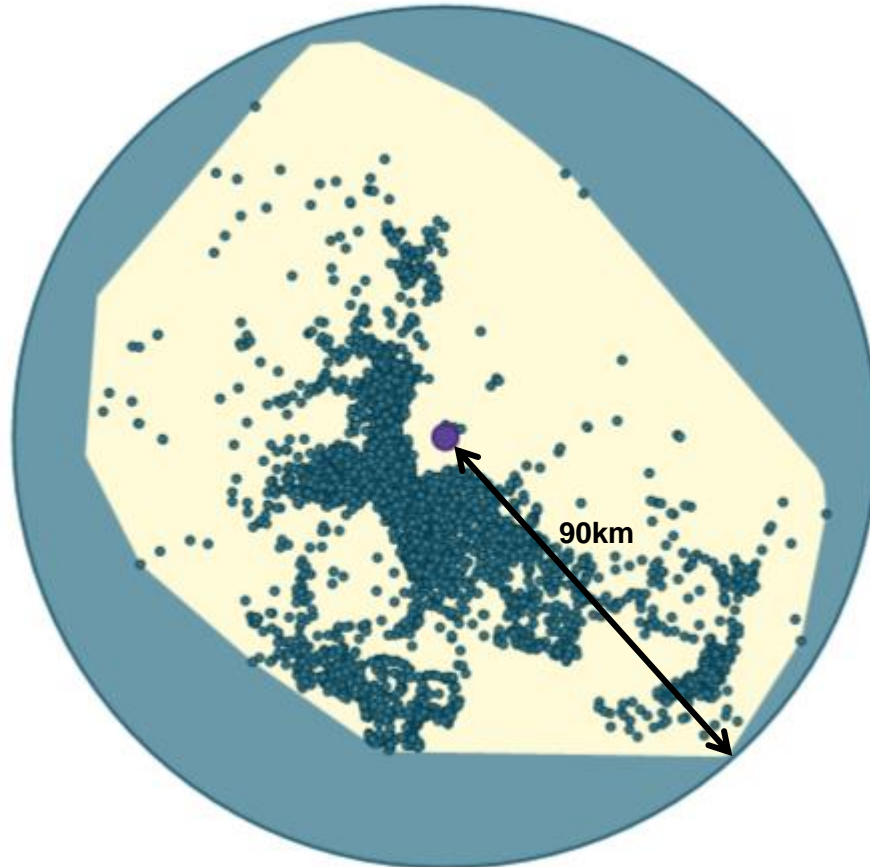


Figure 3.4. Diagram showing how available habitat was determined for the second order habitat selection analysis. Dark blue dots show wild dog GPS collar locations. Yellow polygon shows the minimum convex polygon drawn around the GPS locations with a purple dot marking the central point. Blue circle shows the area used to represent the background habitat available to the wild dog packs.

The differences between used and available habitat were analysed using generalised linear mixed models (GLMM) using the *lme4* package (Bates *et al.*, 2015, p.4) in *R*. Human population density, distance to roads, distance to rivers, percentage tree cover and terrain ruggedness index were modelled as fixed variables and wild dog identity as a random variable. Each life history category was analysed separately and the resulting coefficients compared using Chi-squared tests.

3.3.6. Third Order Habitat Selection

Third order habitat selection was analysed using Step Selection Function (SSF) models. SSF models are modified version of RSF which incorporate movement behaviour into evaluating habitat selection (Fortin *et al.*, 2005). SSFs model habitat selection by comparing the habitat characteristics of an animal's observed locations with the characteristics of simulated locations, the positions of which are generated

based on the animal's movement patterns; effectively comparing where the animal could have gone at each step with where it actually went. SSFs require relatively high-resolution movement data, which have become increasingly available with the growth in the use of GPS tracking collars and tags. Using the location data collected by an animal's GPS tag, it is possible to approximate the path taken by the animal as it moves through its habitat; by extracting parameters of step length (Figure 3.5; the straight-line distance between two GPS locations) and turn angle (the degree of direction change between two steps) and then simulating potential steps which the animal could have taken if the differing habitat characteristics had no effect on its movement choices. These simulated steps are analogous to the available habitat in RSF analyses. Step lengths and turn angles for the 06:30 to 08:00 and 18:00 to 19:30 steps were extracted from the wild dog GPS collar data (Table 3.2) using the *movement.pathmetrics* function in the *Geospatial Modelling Environment* (hereafter referred to as GME; Beyer, 2010). Using the *movement.ssfsamples* function in GME, 30 simulated steps were generated for each observed step. Simulated steps were generated using the step length and turn angle distributions extracted from the GPS collar data. To minimise circularity, for each individual the combined distributions of all of the other collared individuals were used to parameterise the step lengths and turn angle distributions for their

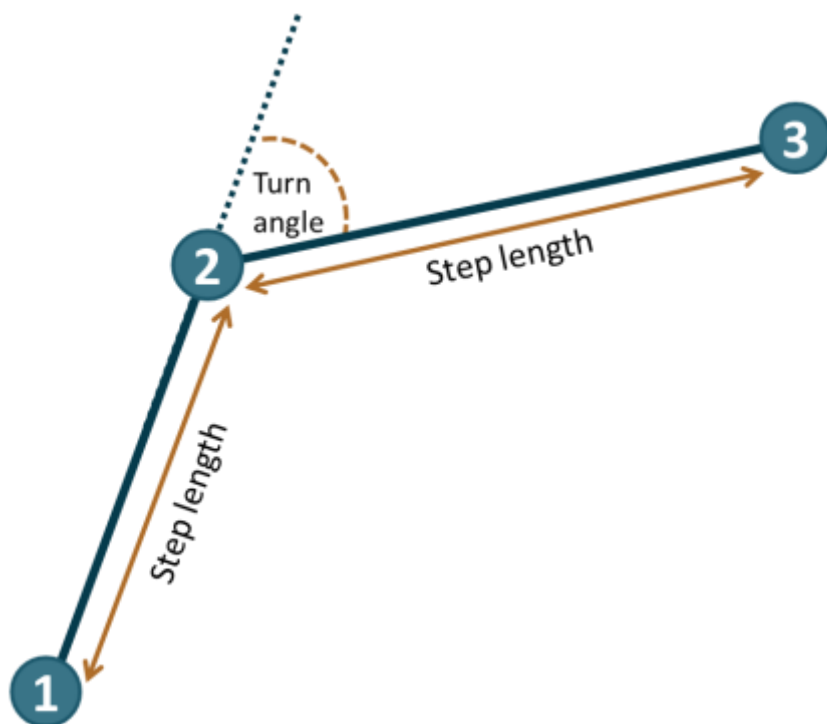


Figure 3.5. Diagram illustrating step length and turn angle. Points 1,2 & 3 represent location data from GPS collars, step lengths are the straight line distance between subsequent locations, turn angle is the degree of direction change between steps.

simulated steps following Fortin *et al.* (2005). The locations of the end points of each of each simulated step and its corresponding observed step (the 08:00 location for the 0630-0800h step, and the 19:30 location for the 1800-1930 step) were then overlaid onto the landscape rasters described above. The habitat characteristics of each point were extracted using the *extract* function in the *raster* package in *R*.

Table 3.2. Mean step lengths of different life stages

Life Stage	Mean Step Length (m)	Standard Deviation (m)
Denning	1808.1	1756.9
Pregnant	2036.3	2065.9
Resident	2015.2	2499.3
Dispersing	3315.4	4183.3

Differences between the observed locations and their associated simulated locations were analysed using a conditional logistic regression. Conditional logistic regression stratifies data into groups for comparison, allowing each observed location to be directly compared with its corresponding simulated locations. Data for each life history stage (resident, pregnant, denning and dispersing) were analysed separately. Regressions were run using the *mcllogit* function of the *mcllogit* package (Elff, 2014) in *R*, with human population density, distance to roads, distance to rivers, percentage tree cover and terrain ruggedness as fixed variables and wild dog identity as a random variable.

3.4. Results

3.4.1. Second Order Habitat Selection

Resource selection functions revealed that the habitat characteristics of wild dog GPS locations were significantly different from those of randomly generated points across the landscape showing strong evidence of habitat selection (Table 3.3, Figure 3.6, Figure 3.7, Figure 3.8, Figure 3.9 & Figure 3.10). At all life stages there was a significant preference for areas with low human population densities, low percentage tree cover and which are close to roads and rivers (Table 3.3). However

Table 3.3. Second order (home range) habitat selection models results

*** denotes $p < 0.001$, ** denotes $p < 0.01$, * denotes $p < 0.05$, ns denotes non significant result

	Habitat Variable	Coefficient	Standard Error	z-value	P-value	Sig
Denning	Intercept	0.169	0.150	1.123	0.262	ns
	Human Population Density	-0.110	0.005	-20.742	<0.001	***
	Distance to Roads (km)	-0.045	0.005	-8.287	<0.001	***
	Distance to Rivers (km)	-0.172	0.025	-6.897	<0.001	***
	Percentage Tree Cover	-0.118	0.008	-14.412	<0.001	***
	Terrain Ruggedness Index	0.059	0.003	17.203	<0.001	***
Dispersing	Intercept	-1.330	0.496	-2.681	0.007	**
	Human Population Density	-0.027	0.002	-11.548	<0.001	***
	Distance to Roads (km)	-0.121	0.009	-14.020	<0.001	***
	Distance to Rivers (km)	-0.292	0.033	-8.726	<0.001	***
	Percentage Tree Cover	-0.016	0.005	-3.505	<0.001	***
	Terrain Ruggedness Index	0.018	0.005	3.523	<0.001	***
Pregnant	Intercept	0.183	0.153	1.196	0.232	ns
	Human Population Density	-0.119	0.007	-16.363	<0.001	***
	Distance to Roads (km)	-0.051	0.007	-7.355	<0.001	***
	Distance to Rivers (km)	-0.392	0.037	-10.470	<0.001	***
	Percentage Tree Cover	-0.091	0.010	-8.650	<0.001	***
	Terrain Ruggedness Index	0.008	0.006	1.450	0.147	ns
Resident	Intercept	1.000	0.105	9.516	<0.001	***
	Human Population Density	-0.028	0.001	-23.194	<0.001	***
	Distance to Roads (km)	-0.094	0.004	-21.928	<0.001	***
	Distance to Rivers (km)	-0.417	0.020	-21.347	<0.001	***
	Percentage Tree Cover	-0.028	0.003	-10.163	<0.001	***
	Terrain Ruggedness Index	-0.002	0.003	-0.718	0.473	ns

whilst denning packs and dispersal groups selected for more rugged areas, pregnant and resident packs did not (Table 3.3).

Packs across all life stages showed significant selection for areas with low human population densities (Table 3.3). Dispersal groups showed a degree of selection for areas with low human population density similar to that of resident packs (Table 3.4). The magnitude of selection with respect to human population densities was significantly greater for denning and pregnant packs, with these life stages found in the areas with the lowest human densities (Table 3.4).

All life stages showed a preference for being close to roads, with the strongest preference shown by dispersal groups and the weakest by denning packs (Table 3.3 & Table 3.4). All life stages also preferred areas close to rivers, the strongest selection was shown by pregnant packs (packs with heavily pregnant alpha females) and resident packs, the weakest selection was by denning packs (Table 3.3 & Table 3.4).

All life history categories avoided areas with high percentage tree cover (Table 3.3), with denning packs showing the strongest avoidance (Table 3.4). Pregnant packs showed stronger avoidance than did resident packs and dispersal groups showed the weakest avoidance (Table 3.4).

Packs with heavily pregnant alpha females, like resident packs, showed no significant selection preferences with respect to terrain ruggedness (Table 3.3). Dispersal groups preferred more rugged areas, however the strongest effect was seen with denning packs which strongly selected more rugged areas (Table 3.4).

3.4.2. Third Order Habitat Selection

Step selection functions showed that, overall, wild dogs had third order habitat selection patterns (within their home ranges) similar to those they showed at second order (a landscape scale). The direction of selection (whether the wild dogs selected for or against a habitat characteristic) was generally the same, however wild dogs showed significant selection for some habitat variables at second order selection were not significantly selected for at third order, and vice versa.

Wild dog third order habitat selection was significantly affected by human population density for all life stages (Table 3.5). Denning, pregnant and resident packs as well

Table 3.4. Chi squared values comparing second order habitat selection coefficients across life stages.

*** denotes $p < 0.001$, ** denotes $p < 0.01$, * denotes $p < 0.05$, ns denotes non significant result

		Denning	Dispersing	Pregnant
Human Population Density	Resident	229.90 ***	0.05 ns	154.08 ***
	Pregnant	1.06 ns	145.37 ***	
	Dispersing	205.24 ***		
Distance to Roads	Resident	49.11 ***	7.84 **	26.89 ***
	Pregnant	0.48 ns	39.17 ***	
	Dispersing	54.87 ***		
Distance to Rivers	Resident	60.05 ***	10.32 **	0.35 ns
	Pregnant	23.99 ***	3.93 *	
	Dispersing	8.35 **		
Percentage Tree Cover	Resident	107.21 ***	4.75 *	33.01 ***
	Pregnant	4.15 *	41.76 ***	
	Dispersing	115.56 ***		
Terrain Ruggedness Index	Resident	171.64 ***	11.31 ***	2.61 ns
	Pregnant	61.46 ***	1.71 ns	
	Dispersing	45.58 ***		

as dispersal groups all showed a significant preference for areas with low human population densities, as in the second order selection analyses.

Proximity to rivers was also a significant factor across life stages, with all wild dog life stages showing a significant preference for areas closer to rivers (Table 3.5). Proximity to roads was only a significant factor in habitat selection for dispersal groups and resident packs. The third order habitat selection models for packs with heavily pregnant alpha females and denning packs revealed no evidence of selection for areas close to roads (Table 3.5).

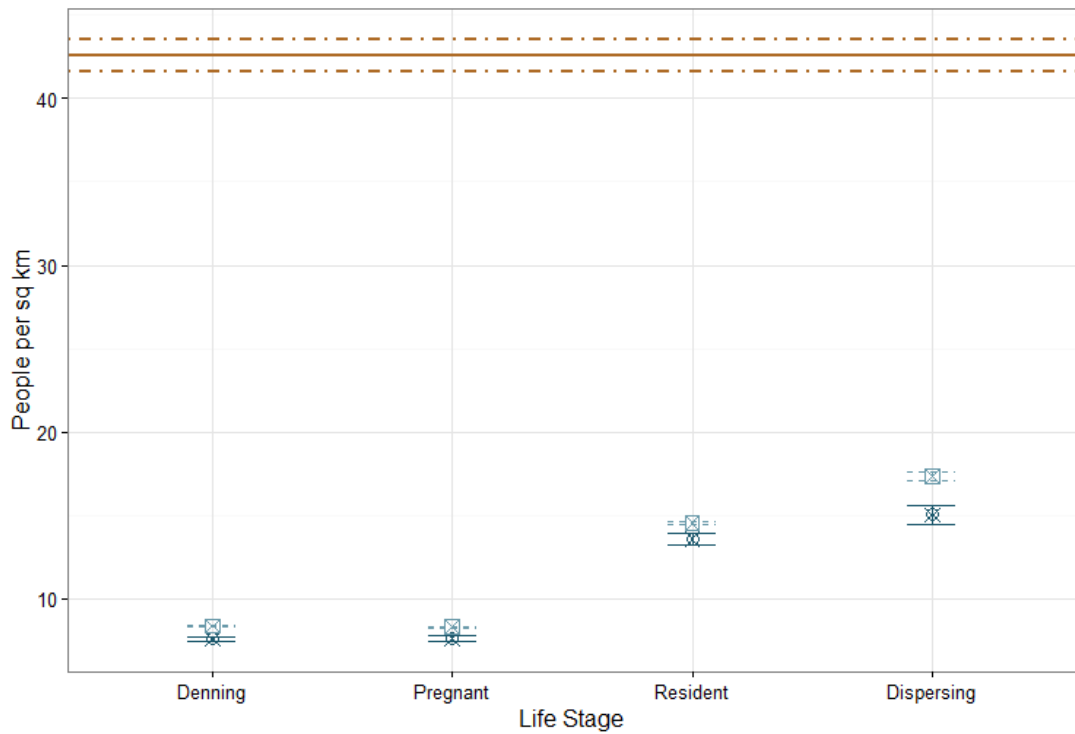


Figure 3.6. Comparison of mean values for human population density. Wild dog location data are shown by dark blue circles with solid line \pm SEM, SSF simulated values are shown by light blue squares with dashed lines \pm SEM and landscape level average is shown by brown solid line \pm SEM shown as dash-dot brown line

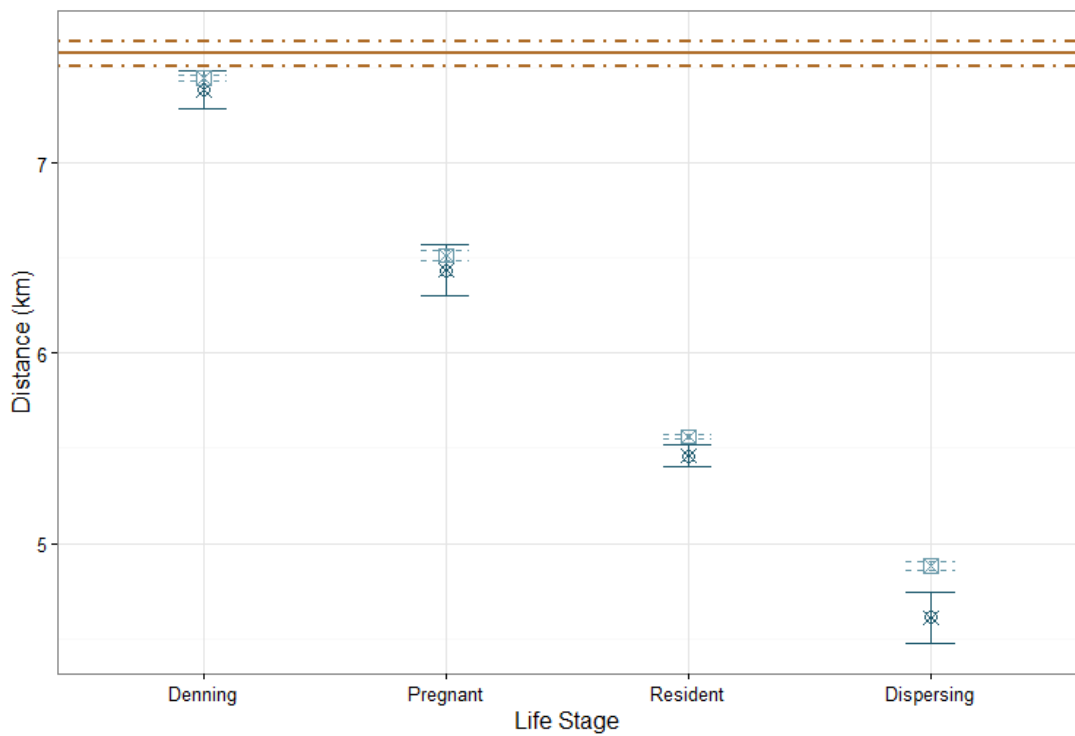


Figure 3.7. Comparison of mean distance to the nearest road. Wild dog location data are shown by dark blue circles with solid line \pm SEM, SSF simulated values are shown by light blue squares with dashed lines \pm SEM and landscape level average is shown by brown solid line \pm SEM shown as dash-dot brown line

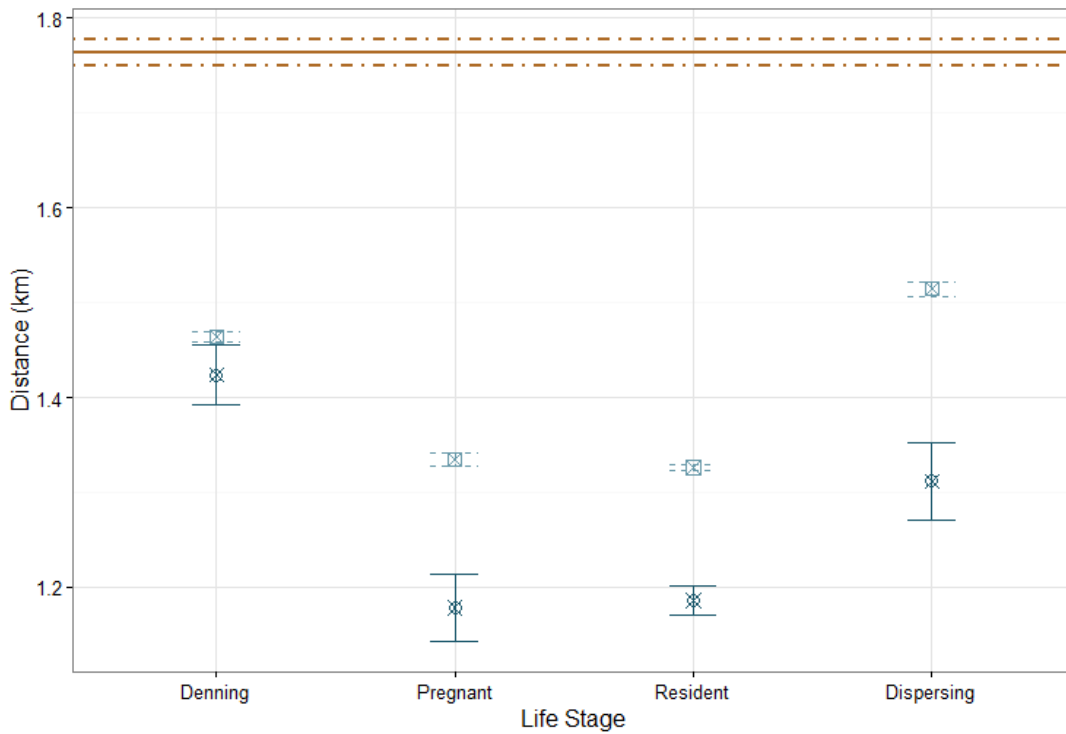


Figure 3.8. Comparison of mean distance to the nearest river. Wild dog location data are shown by dark blue circles with solid line \pm SEM, SSF simulated values are shown by light blue squares with dashed lines \pm SEM and landscape level average is shown by brown solid line \pm SEM shown as dash-dot brown line

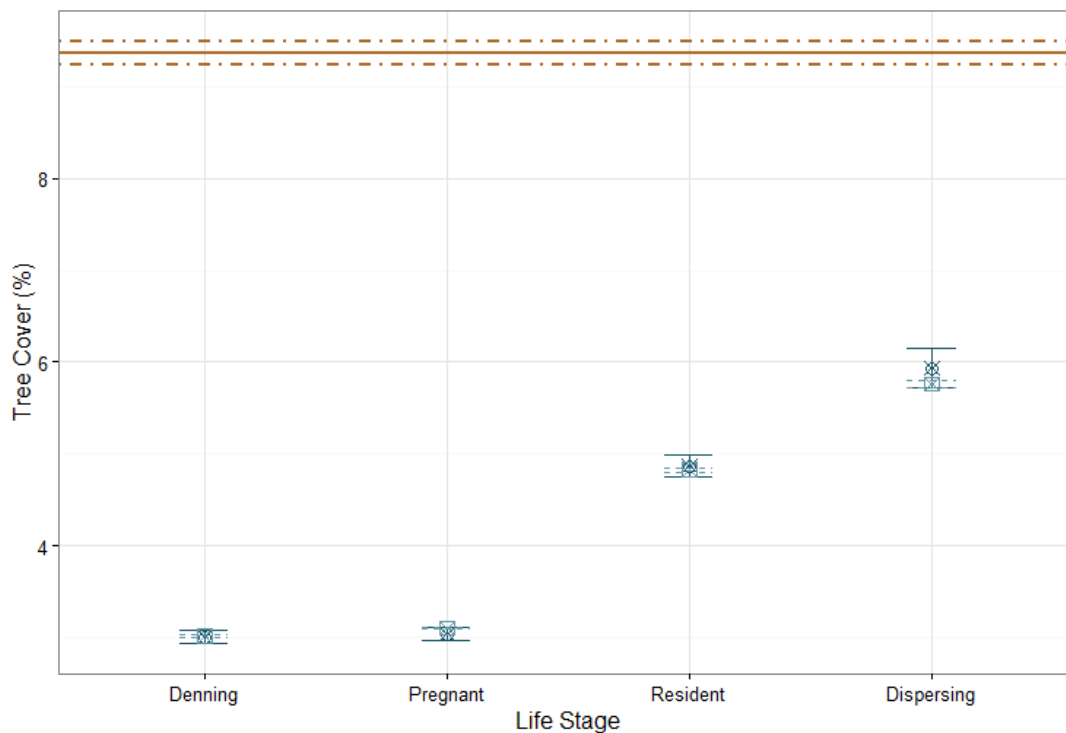


Figure 3.9. Comparison of mean percentage tree cover. Wild dog location data are shown by dark blue circles with solid line \pm SEM, SSF simulated values are shown by light blue squares with dashed lines \pm SEM and landscape level average is shown by brown solid line \pm SEM shown as dash-dot brown line

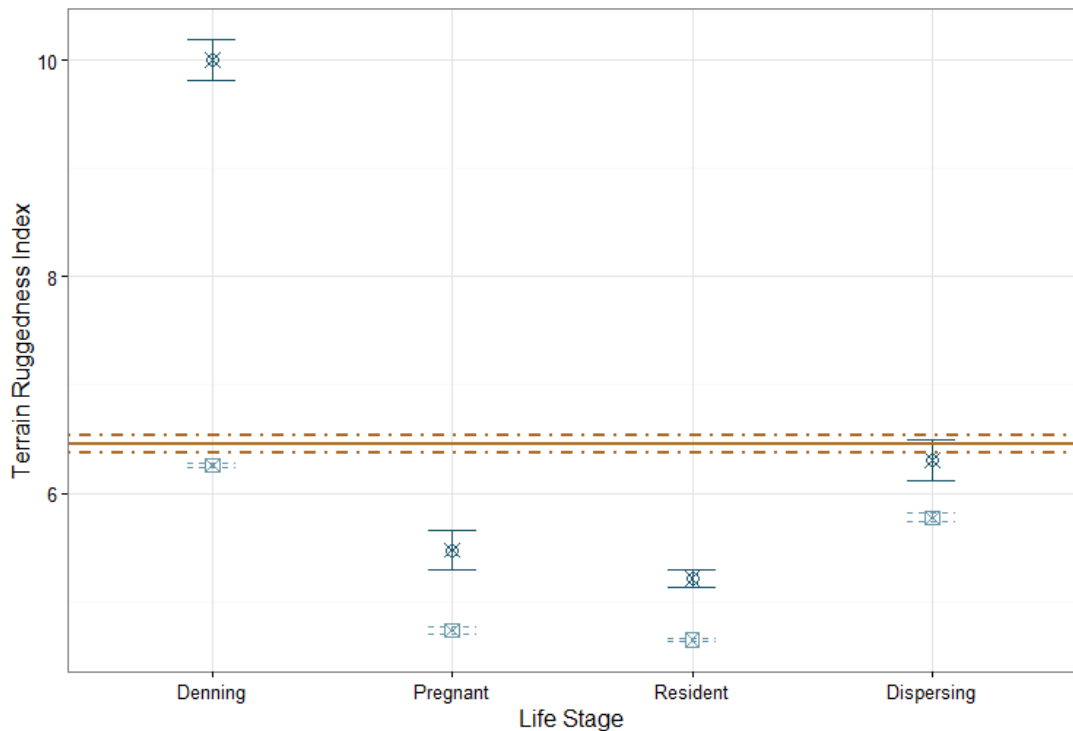


Figure 3.10. Comparison of mean terrain ruggedness. Wild dog location data are shown by dark blue circles with solid line \pm SEM, SSF simulated values are shown by light blue squares with dashed lines \pm SEM and landscape level average is shown by brown solid line \pm SEM shown as dash-dot brown line

All life stages showed no significant selection with respect to percentage tree cover at the third order of selection. Whereas all of the life stages showed significant preference for more rugged areas within their home ranges (third order selection).

3.5. Discussion

This study found evidence suggesting that home range (second order) habitat selection by African wild dogs was affected by geographical features in the landscape (Hypothesis A). Wild dogs showed preference for areas close to rivers and roads, but with low human population densities, low percentage tree cover and low levels of terrain ruggedness. Although the direction of selection (i.e. preference or avoidance) was similar across life stages, the magnitude of selection varied significantly (Hypothesis B). Habitat selection was broadly consistent across second order (home range) selection, and third order (within home range) selection (Hypothesis C). However the models revealed that some habitat features, for example low percentage tree cover, which wild dogs had significantly preferred at second order selection did not significantly affect third order (within home range) selection or vice versa.

Table 3.5. Third order (within home range) habitat selection models results*** denotes $p < 0.001$, ** denotes $p < 0.01$, * denotes $p < 0.05$, ns denotes non significant result

	Habitat Variable	SSF Coefficient	Standard Error	z-value	P-value	Sig
Denning	Human Population Density	-0.029	0.009	-3.319	<0.001	***
	Distance to Roads (km)	-0.011	0.024	-0.477	0.633	ns
	Distance to Rivers (km)	-0.086	0.037	-2.326	0.020	*
	Percentage Tree Cover	0.005	0.018	0.269	0.788	ns
	Terrain Ruggedness Index	0.113	0.004	26.617	<0.001	***
	Dog ID			1.666	0.096	ns
Dispersing	Human Population Density	-0.021	0.005	-4.035	<0.001	***
	Distance to Roads (km)	-0.093	0.021	-4.478	<0.001	***
	Distance to Rivers (km)	-0.218	0.039	-5.552	<0.001	***
	Percentage Tree Cover	0.012	0.009	1.330	0.183	ns
	Terrain Ruggedness Index	0.014	0.006	2.212	0.027	*
	Dog ID			1.095	0.273	ns
Pregnant	Human Population Density	-0.044	0.012	-3.624	<0.001	***
	Distance to Roads (km)	0.002	0.029	0.066	0.948	ns
	Distance to Rivers (km)	-0.224	0.048	-4.691	<0.001	***
	Percentage Tree Cover	-0.023	0.027	4.860	0.395	ns
	Terrain Ruggedness Index	0.039	0.008	-0.850	<0.001	***
	Dog ID			0.613	0.540	ns
Resident	Human Population Density	-0.006	0.002	-3.631	<0.001	***
	Distance to Roads (km)	-0.029	0.012	-2.424	0.015	*
	Distance to Rivers (km)	-0.216	0.022	-10.005	<0.001	***
	Percentage Tree Cover	-0.003	0.004	-0.766	0.444	ns
	Terrain Ruggedness Index	0.036	0.004	9.199	<0.001	***
	Dog ID			0.882	0.378	ns

Wild dogs showed a high level of avoidance of areas with high human population densities across all life history stages and at both orders of selection. Whilst this is not necessarily surprising, this is a wild dog population that began to recolonise Laikipia County in 2001 when the landscape was already human-dominated. Therefore all wild dog packs in the current population have become established alongside local human communities. These results suggest that wild dogs may be able to coexist with local communities primarily through avoidance of areas with high human densities (Woodroffe & Donnelly, 2011). Wild dogs in Laikipia live at high population densities relative to other wild dog populations in other areas (Woodroffe, 2011), and yet there are only low levels of conflict with the local human population and low levels of livestock depredation reported (Woodroffe *et al.*,

2005a). These low levels of conflict may be in part due to the apparent avoidance of the more human-dominated parts of the landscape.

Wild dogs in Laikipia selected areas closer to roads across all life history stages at the second order level of selection, however denning packs and those with heavily pregnant alpha females did not show a significant preference at third order selection. Wild dog selection for areas close to roads has been observed by another study (Abrahms *et al.*, 2016) and is consistent with the findings of Woodroffe (2010). The roads included in the analysis in Woodroffe (2010) were smaller, private bush roads used to travel within properties whereas in this study the roads were main roads and part of Kenya's wider road network. Although the majority of these main roads are not paved, and instead have murrum surfaces, they are important transport routes between the towns across Laikipia. Nonetheless, despite having a greater volume of traffic than the bush roads, wild dogs were found to select for areas closer to these roads. Much of Laikipia is covered by relatively thick *Acacia* bushland, and it is likely that the wild dog population uses roads as an easy route for travelling through the vegetation (Woodroffe, 2010). This inclination for using areas close to roads is unusual; many wildlife species avoid roads (Forman, 2003). Across a wide variety of taxa roads have been shown to act as important movement barriers (Dyer *et al.*, 2002; Mader, 1984; Marsh *et al.*, 2005; McGregor *et al.*, 2008; Waller & Servheen, 2005), with many species showing population level negative effects such as a reduction in abundance (Fahrig & Rytwinski, 2009). However, whilst for many species the presence of roads may make them avoid areas, or for which roads may act as movement barriers, some canid species have been shown to use roads or tracks made by humans to facilitate movement across landscapes. For example both wolves and coyotes are known to use the compacted snow left by snowmobile trails to move through areas with deep snow cover more easily (Gese *et al.*, 2013; Paquet *et al.*, 2010). Wild dogs' propensity for using roads to travel around their landscapes has conservation implications as it leaves wild dogs at risk from being hit and killed by road traffic (van der Meer *et al.*, 2014). The relatively high risk of roadkill has led to its inclusion as a significant threat in regional strategies and national plans for wild dog conservation (IUCN/SSC, 2015, 2012, 2007).

Wild dogs were also found to select areas closer to rivers across all life history categories at both orders of selection. Mean distance from rivers for wild dog locations varied from 1.2km for resident packs and packs with heavily pregnant

alpha females, to 1.4 km for denning packs, all substantially less than the mean distance for random points of 1.8km (Figure 3.8). Wild dogs have been reported to use rivers during hunts (Rhodes & Rhodes, 2004) as they act as barriers increasing the wild dogs' hunting success, similar to their use of fences (Davies-Mostert *et al.*, 2013). The use of rivers to increase hunting success has been observed in other carnivore species including lions, resulting in increased reproductive success for individuals in riverine areas (Hopcraft *et al.*, 2005; Mosser *et al.*, 2009).

Terrain ruggedness and percentage tree cover both had significant effects on wild dog habitat selection, but not across all life stages and orders. Areas with higher terrain ruggedness values were preferred by all life stages at third order selection, but had no significant impact on second order selection for pregnant and resident packs. Percentage tree cover had a significant effect at second order, with all life stages selecting for areas with less tree cover, however it was not significant at third order. This may be because by selecting for preferred habitat at one order of selection, there is no need for animals to select at the other. For example, if packs have chosen areas in the landscape with lower levels of percentage tree cover to establish their territories, i.e. avoiding forested areas, then at third order selection there may be no need for further selection as they are already in their preferred habitat.

Although all life stages showed similar patterns of habitat selection, the strength of selection varied between life stages. Denning packs showed significantly stronger preference for areas with lower human population densities, and less attraction to roads, than did dispersal groups or resident packs. Denning packs were also found in areas that were significantly more rugged than any other life history category. In Laikipia wild dog packs tend to den in rocky areas on the side of steep hills (Woodroffe, 2011), unlike in other areas where it is common for packs to take over holes previously dug by other species such as aardvarks, *Orycteropus afer* (Robbins & McCreery, 2003). When packs have pups in the den they are at their most vulnerable – this is because for approximately three months, until the pups are old enough to join and follow the rest of the pack, the whole pack is extremely restricted in their movement patterns (Woodroffe *et al.*, 2017). In order to provision the pups and their guardians, the pack usually go out and return from hunting twice a day, behaviour that if noticed by a predator, or human, may lead to discovery of the den and the pups. Other studies focussing on wild dog den site selection have shown similar patterns of preference, particularly with respect to rugged areas

(Jackson *et al.*, 2014; van der Meer *et al.*, 2013). This analysis did not distinguish between days when the collared individuals remained at the den to guard the pups and days when they took part in the morning and evening hunts, therefore these results will reflect a mixture of habitat selection when hunting, areas close to the den and the den location itself.

These results also show evidence of packs changing their habitat selection preferences in the weeks before the alpha female whelps. Packs with heavily pregnant alpha females exhibited habitat selection behaviour which had some similarities with resident packs, for example with respect to distance to rivers and terrain ruggedness, but others that were similar to denning packs, for example being found in areas with lower human population densities. Studies have investigated the effect of gestation on home ranges and movement patterns in species including white-nosed coati, *Nasua narica* (Valenzuela & Ceballos, 2000) and mule deer *Odocoileus hemionus* (Long *et al.*, 2009), showing that females exhibit significant behavioural changes in the weeks before birth. In the case of coatis, pregnant females were found to use smaller ranges than non-breeding, though not as small as home ranges during nesting periods (Valenzuela & Ceballos, 2000). Pregnant mule deer were found to move more slowly in the final week of gestation (Long *et al.*, 2009). It may be that these changes in behaviour partly result from females experiencing increased locomotive difficulties as they become increasingly heavily pregnant. In addition to changes in range size and movement speed, mule deer were also shown to change their habitat selection preferences whilst heavily pregnant, for example selecting for areas with better grazing thereby increasing their nutritional intake (Long *et al.*, 2009). Previous studies focussing on habitat selection in African wild dogs have tended to focus on the denning period (van der Meer *et al.*, 2013; Jackson *et al.*, 2014), however these results suggest that some behavioural changes begin in the weeks before denning takes begins.

Dispersal groups showed selection behaviour significantly different from that of other life history categories. For example, the average human population densities of dispersal groups' GPS locations were the highest among the categories investigated (Figure 3.6). However, when looking at their second and third order habitat selection, dispersal groups were nonetheless found to select for areas with lower human population densities than expected by chance (Table 3.3 & Table 3.5). This suggest that, while dispersal groups are less risk averse than other life stages, they will select the least risky habitat from the options available to them at their

location. This apparent willingness to use suboptimal habitat could be as a result of avoiding entering the territories of existing wild dog packs, or because they are searching for uninhabited areas to establish new territories. Resident wild dog packs are territorial, and so straying into the territory held by an established pack has an associated risk of injury or even death (Creel & Creel, 2002). This avoidance of entering into another pack's territory has been used to change wild dog pack ranging patterns by using translocated scent-marks to prevent packs from moving out of their usual range (Jackson *et al.*, 2012). However, in this wild dog population, packs have large overlaps in their territories (Woodroffe, 2010), suggesting that a desire to avoid existing pack territories may not be the main driver of why dispersal groups may be found in suboptimal habitat in this case. That they spend more time in suboptimal habitat could at least partly explain why dispersal groups are recorded travelling extremely long distances. Groups not only need to continue travelling until they meet an opposite sex group with which they can form a new pack, but they then need to find a suitable, preferably uninhabited, area to establish their new territory.

Whilst this study strongly suggests that there are significant differences in the habitat selection of different life stages, it is nonetheless based on a relatively small number of individuals. This is particularly true regarding dispersal behaviour, which is based only on 7 individuals for which movement data were collected over a relatively short period of time as dispersals only lasted for a few weeks. The small sample size is due to the logistical challenges of collecting dispersal data; predicting when an individual is likely to leave their natal group in order to fit them with a GPS collar before they disperse is difficult as the timings of dispersals can be highly variable, especially in areas like Laikipia which are non-seasonal meaning dispersals can happen at any point throughout the year. Following individuals during dispersals is also difficult as their movement patterns are often very unpredictable; this adds an extra layer of logistical difficulty especially when the animals are moving across private or inaccessible land.

This study highlights the importance of considering life history stage when investigating habitat selection behaviour, as wild dog habitat preferences differed across life stages. Other studies have shown behavioural state (e.g., foraging, travelling etc.) to have an important impact on habitat selection, however to date there are still relatively few studies exploring the differences between resident and dispersing groups (Abrahms *et al.*, 2016). The few studies that there have been,

have shown important contrasts in habitat selection between resident animals and dispersal groups. For example, Elliot *et al.* (2014b) found that dispersing groups of lions travelled across areas that were avoided by adult males and groups of adult females. Jackson *et al.* (2016) also looked at dispersal behaviour in African wild dogs, using opportunistic reports of groups where groups numbering fewer than 9 individuals were assumed to be dispersal groups. That study found significant differences in the habitat characteristics of areas where smaller groups, assumed to be dispersers, and larger groups, assumed to be resident, were found. Both these studies found that there were highly significant differences in projected levels of connectivity depending on whether the connectivity model was based upon data from residents or dispersers.

This study highlights the importance of considering changes in habitat requirements across individuals' life histories when planning for conservation. The habitat selection preferences of wild dogs differed significantly across life stages, which is likely to impact on levels of habitat connectivity. For example, habitat selection was shown to be different for resident-denning packs compared with resident-non-denning packs. These differing preferences are likely to be important for future land-use planning as a loss of suitable denning sites may impact future reproductive success. The results also show the importance of accounting for scales of selection as habitat selection choices at one scale may not be the same as choices at a different scale. For example while dispersal groups preferred lower risk areas at third order selection, at second order selection they used areas of higher human population density, suggesting they could be at higher risk of coming into conflict with local communities. Awareness of the impact of scale on wildlife movement patterns across a landscape is likely to be critical for conservation planning.

For conservation planning to be most effective it needs to be based on the requirements of the animals which are likely to be most affected by it. If connectivity planning is based around a life stage which does not normally travel outside of an established territory, it may erroneously appear that remnant habitat patches are no longer functionally connected and so connectivity conservation may not be prioritised in these areas. Planning based upon data from individuals which are unlikely to make long distance movements is unlikely to accurately plan for the needs of individuals that do. Such behavioural differences are important to account for when making recommendations for future conservation and land-use planning as they are likely to affect which strategies are most appropriate and effective.



Plate 5. A lactating alpha female African wild dog with houses from a local community visible in the background

Chapter 4.

Landscape Connectivity for African Wild Dogs across Kenya: Effects of Life Stage and Infrastructure Development

4.1. Abstract

Habitat loss and fragmentation are two of the greatest threats to global biodiversity; maintaining connectivity between remnant populations is a key conservation tool for threatened species. However, in many areas, the aim of maintaining movement corridors for wildlife conservation must be balanced against the need for poverty alleviation and large-scale development projects. This study investigates the levels of connectivity still present across Kenya for a wide-ranging species which is under serious threat from habitat and connectivity loss, the African wild dog, and evaluates the potential impact of a major new infrastructure development, the Lamu Port - South Sudan - Ethiopia Transport (LAPSSET) corridor. Resource selection functions, fitted to GPS collar data, were used to develop landscape resistance-to-movement layers. Resistance layers were then used to model connectivity between known patches of wild dog resident range. Connectivity levels based on data from dispersal groups and resident packs were compared to evaluate the impact of an animal's life stage on the results of connectivity mapping.

Wild dogs are likely to be extensively affected by the construction of LAPSSET. Two of the seven known remaining populations in Kenya are in the route of the LAPSSET corridor, and as the project trisects the country connectivity between the northern and southern populations is likely to be substantially reduced.

4.2. Introduction

4.2.1. Connectivity

For many species fragmentation of their remaining areas of habitat is one of the greatest threats to their long-term survival (Millennium Ecosystem Assessment, 2005). Maintaining functional connectivity between remnant habitat patches is a key conservation tool to safeguard the viability of populations of threatened species (Crooks & Sanjayan, 2006). By securing functional connectivity between habitat patches, it is possible for individuals to migrate between the subpopulations in these patches. This prevents each subpopulation from becoming isolated, vulnerable to stochasticity and at risk of threats such as a loss of genetic diversity (Ingvarsson, 2001). Key to the maintenance of functional connectivity are movement corridors: areas which a species can move through in order to reach another suitable habitat patch (Hilty *et al.*, 2012). The corridors themselves do not necessarily need to be suitable habitat for permanent residency of the species in question, but they must be of sufficient quality to enable the passage of individuals (Chetkiewicz *et al.*, 2006).

Identifying the locations of movement or dispersal corridors can present difficulties as they may differ from animals' resident habitat (Chetkiewicz *et al.*, 2006). In addition animals may only use them irregularly and for relatively short periods of time, making it difficult to detect and observe animals moving through corridors. As a result a modelling approach is often used in order to identify the locations of potential movement corridors (Abrahms *et al.*, 2017). Many habitat connectivity studies rely upon expert opinion and records of the locations of opportunistic sightings; however as GPS collaring has become more common, and fine-scaled movement data more readily available, modelling has become more empirically based (Zeller *et al.*, 2012). Even where empirical data are used, the behavioural state of the animal has seldom been taken into account, with many studies basing their models on data collected from resident or territorial animals (Abrahms *et al.*, 2017). In many species, resident and territorial animals are less likely to make long-distance journeys and may have habitat requirements and tolerances differing from those of dispersers (see Chapter 3; Elliot *et al.* 2014). Basing connectivity models on habitat requirements of resident animals could therefore lead to erroneous conclusions as to the location or existence of movement corridors. In addition, remnant habitat patches, which may appear to no longer be connected when

modelled using data from resident animals, may actually still be available to dispersers. This is an important consideration as where land is no longer thought to be of value for conservation it may have an increased chance of being developed thereby having a negative impact on connectivity.

Whilst habitat loss and fragmentation are recognised as important drivers of global biodiversity loss (Millennium Ecosystem Assessment, 2005), there is also recognition that in many situations the costs of biodiversity conservation fall disproportionately upon vulnerable communities (Balmford & Whitten, 2003). Development projects are often focused around such communities, attempting to improve peoples' livelihoods and access to resources. The necessities and urgency of helping these vulnerable communities can mean that the environmental impact of such projects is given lower priority than the development benefits (Lee, 2013). Perhaps one of the most famous of these is the proposed highway across the Serengeti National Park in Tanzania (Dobson *et al.*, 2010). This proposed road would cut across important linkages for the mass migration of wildebeest, zebra and other ungulates, which occurs between the Serengeti National Park and the Maasai Mara National Reserve (Dobson *et al.*, 2010). The road would likely have serious negative impacts on wildlife populations in the area. However, some argue that it would provide an important linkage to markets for the towns on the western side of the park and help with poverty alleviation (Fyumagwa *et al.*, 2013), despite comparisons between the proposed routes of the highway suggesting that the alternative routes would have greater effects on poverty alleviation than the route through Serengeti National Park (Hopcraft *et al.*, 2015). A high-profile court case found that the building of the road would likely threaten the ecosystem's ecological stability (Ubwani, 2014) and therefore the plans have been shelved, meaning that to date the projected ecological and economic costs of the road have taken priority, but it is an issue that is often revisited. This is not an isolated case and there are many other instances where infrastructure development is in conflict with conservation goals. For example, there are proposals for a road to be built through the Cross River Protected Area in Nigeria (Cannon, 2017) and for the development of the Trans-Mongolia railway which would threaten the migration of the critically endangered Saiga antelope, *Saiga tatarica* (Sanjmyatav, 2011). All of these linear infrastructure developments are likely to have substantial impacts on threatened species in their vicinity as they will likely form important movement barriers.

Wide-ranging species are particularly likely to be affected by habitat loss, as they require large areas of wildlife friendly habitat to survive (Crooks & Sanjayan, 2006). However, as such species generally have good dispersal abilities, they may also be able to traverse relatively long distances in the search for areas of suitable habitat (Beck & Kitching, 2007). However, linear infrastructure can act as movement barriers, preventing animals from being able to access parts of the landscape. For example, the international railway which bisects Mongolia's Gobi-Steppe ecosystem is an important movement barrier for species such as the Asiatic wild ass, *Equus hemionus*, and the Mongolian gazelle, *Procapra gutturosa* (Ito *et al.*, 2017).

Large carnivores are especially vulnerable to connectivity loss (Crooks *et al.*, 2011). This is because, as well as being wide-ranging, these species live at particularly low population densities (Ripple *et al.*, 2014). They are also often adversely affected by increases in human densities as they are frequently perceived (sometimes correctly) as a threat to human life and livelihoods (Woodroffe, 2000). In addition to the direct effects of human-carnivore conflict, large carnivores can be negatively affected by increases in linear barriers and infrastructure. For example, roads have been linked to population declines in cougars (Fahrig & Rytwinski, 2009). Cougars are also affected by the expansion of human development, with landscape connectivity negatively affected by increases in human infrastructure (Burdett *et al.*, 2010).

4.2.2. African Wild Dogs

The African wild dog is an extremely wide-ranging large carnivore species (Davies-Mostert *et al.*, 2012) which requires large areas of contiguous carnivore-friendly habitat for populations to persist. Resident packs in some areas have home ranges of over 2000 sq km and dispersal groups have been recorded travelling hundreds of kilometres in search of mates and territory (Davies-Mostert *et al.*, 2012; Masenga *et al.*, 2016; Fuller & Kat, 1990). This wide-ranging nature makes the species particularly vulnerable to the effects of habitat loss (Woodroffe & Ginsberg, 1998). Despite the species' ability to traverse large distances, they have been shown to be vulnerable to loss of connectivity. For example, the population of the Greater Limpopo Transfrontier Conservation Area has been found to not be a genetically homogenous population (Tensen *et al.*, 2016). This suggests that connectivity has been lost between the subpopulations of Kruger National Park and Gonarezhou National Park despite them existing within a transfrontier conservation area (Tensen *et al.*, 2016). A recent study has shown that wild dogs are significantly negatively

affected by higher temperatures and therefore are likely to be vulnerable to the effects of climate change (Woodroffe *et al.*, 2017). Maintaining connectivity between remnant populations is therefore likely to be of high importance for the species to maintain the potential for animals to move into new areas to mitigate the effects of rising temperatures.

Kenya is an important stronghold for the species and is home to several resident populations. However, despite being charismatic large carnivores, much is still unknown about the distribution of African wild dogs in Kenya (Kenya Wildlife Service, 2010). The remaining known populations within Kenya are small, all are thought to number fewer than 30 packs (Woodroffe & Sillero-Zubiri, 2012), and so maintaining connectivity between populations is likely to be extremely important for their long-term persistence (IUCN/SSC, 2007). The locations of patches of wild dog resident range across Africa have been mapped, based on observations and expert opinion, through the Range Wide Conservation Programme for Cheetahs and African Wild Dogs (hereafter RWCP; IUCN/SSC, 2007, 2012, 2015). The map of patches of wild dog resident range in Kenya suggests that there may still be connectivity between all the identified patches (Figure 4.1; IUCN/SSC, 2007). However, across much of the country there is little information on the presence or absence of wild dogs and there has not previously been an attempt to model connectivity levels between populations using empirical data.

The locations of wild dog movement corridors are important to identify in light of the major development and construction projects currently underway in Kenya. Planned projects include building a fence across the Kenya-Somalia border (AFIC, 2017) and as part of Kenya's Vision 2030, a major new infrastructure project is under construction, LAPSSET: the Lamu Port – South Sudan – Ethiopia Transport Corridor (LAPSSET Corridor Development Authority, 2015). This project involves the construction of a new oil pipeline, gas pipeline, highway and railway from South Sudan across the centre of Kenya to the coast, with a branch also running up to Ethiopia (Figure 4.2; LAPSSET Corridor Development Authority, 2015). The inner corridor, comprising the pipelines, highway and railway, will be between 500m and 10km wide as required by the terrain. There are also plans for an outer corridor spanning 50km on either side of the inner corridor which will be a "Special Investment Zone", where the government is encouraging the development of businesses such as farming, factories and industrial parks (LAPSSET Corridor Development Authority, 2015). These developments are likely to form a significant

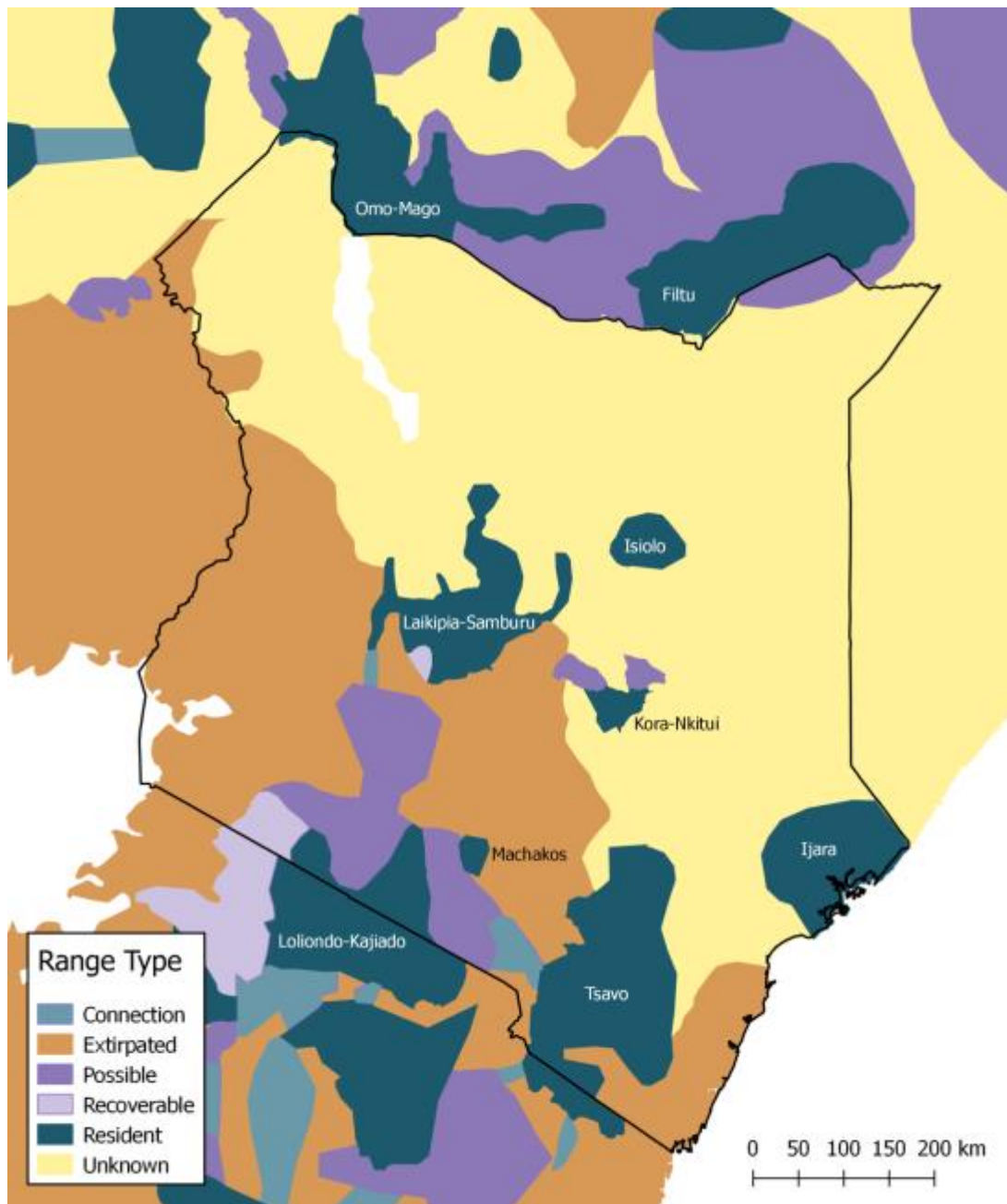


Figure 4.1. Locations of known patches of resident African wild dog range in Kenya, mapped using expert opinion and sightings data by the Range Wide Conservation Program for Cheetah and African Wild Dog

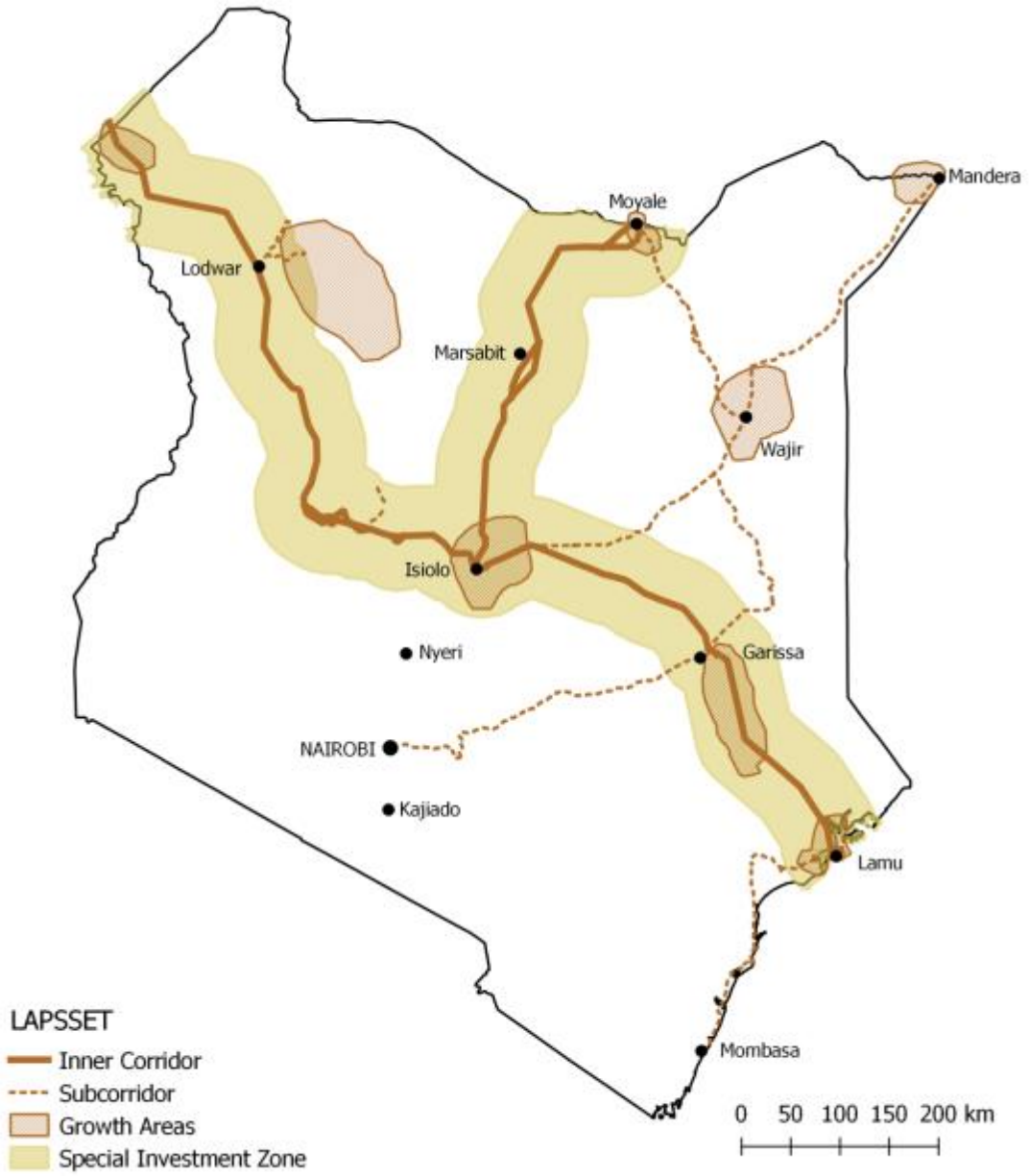


Figure 4.2. Location of the Lamu Port Southern Sudan Ethiopia Transport (LAPSSET) corridor and its associated development projects. Data from World Resources Institute (2010).

wildlife movement barrier which trisects the country. In addition to the central LAPSSET corridor, original plans included the construction of three resort cities, at Lake Turkana, Isiolo and Lamu; and four growth areas (LAPSSET Corridor Development Authority, 2015).

Tourism is an extremely important source of revenue for Kenya. It was estimated to contribute 9.8% of the country's Gross Domestic Product (GDP) in 2016 (World Travel & Tourism Council, 2017). Wildlife viewing is an important draw for tourists to visit Kenya and, as a charismatic large carnivore, African wild dogs are among the species that attract visitors (Lindsey *et al.*, 2005a). It is important to ensure that infrastructure development is done in such a way that it ensures sustainable wildlife-based revenue generation, which benefits both local communities and the national economy. This study evaluates the levels of landscape connectivity that persist for wild dogs across Kenya and evaluates how LAPSSET may affect connectivity for the species.

4.2.3. Hypotheses and Predictions

Hypothesis A: Human density is associated with lower connectivity for large carnivores

Prediction A.1: Direct movement routes persist across areas of low human population density

Prediction A.2: Connectivity will be under greatest threat where human population densities are highest, such as in the south of Kenya

Hypothesis B: Dispersing animals will be able to use more of the landscape than resident animals

Prediction B.1: Modelled levels of connectivity will be higher for wild dog dispersal groups than for resident packs

Hypothesis C: Large linear infrastructure will reduce landscape connectivity

Prediction C.1: Important movement pathways intersect with the planned routing of LAPSSET in Kenya

4.3. Methods

4.3.1. Study Area

Kenya is a crucial stronghold for the African wild dog, and is home to several globally important populations (IUCN/SSC, 2007). The location of known wild dog populations across East Africa have been mapped as part of the Regional and National Conservation Action Planning Workshops coordinated by the Range Wide Conservation Programme for Cheetahs and African Wild Dogs (RWCP; IUCN/SSC, 2007). These distributions were first mapped in 2007 and then updated as part of a review of Kenya's National Conservation Action Plan in 2015. During these workshops, using sightings data and expert opinion, the country was classified with respect to wild dogs into the categories Resident, Possible, Connection, Extirpated, Recoverable and Unknown (Figure 4.1). This resulted in the identification of seven patches of wild dog resident range, two of which are contiguous with patches across Kenya's southern border with Tanzania. There are also two patches of wild dog resident range across the northern border with Ethiopia (Figure 4.1). Although these nine areas have been identified as resident range, there remains substantial uncertainty regarding the distribution of the species across East Africa (Figure 4.1). Much of north Kenya is categorised as unknown, as is all of Somalia, and it is possible that resident populations of wild dogs may persist there. For the purposes of this research, however, the connectivity analysis was restricted to the locations of the nine known patches of wild dog resident range within, or directly bordering, Kenya. Shapefiles of the locations of resident range were obtained from RWCP and were then converted into 300m resolution raster files using the *rasterise* function of the *raster* package in *R* (Hijmans, 2015; R Core Team, 2016).

Connectivity models were parameterised using data from the Laikipia-Samburu wild dog population. Habitat selection by wild dogs from this population is likely to provide a good basis for connectivity modelling as this population persists within a human-dominated landscape that also includes a diversity of habitats. This therefore provides information on how wild dogs interact with human activity and anthropogenic landscape features. High levels of human activity and anthropogenic landscape features are likely to have the greatest impacts on connectivity levels.

4.3.2. Connectivity between Patches of Wild Dog Resident Range

4.3.2.1. Resistance Layers

Landscape resistance-to-movement raster layers (hereafter referred to as resistance layers) were calculated based on wild dog second order habitat selection preferences. Second order habitat selection relates to the choice of habitat that makes up an animal's home range within the geographic range of the species (Johnson, 1980) and thus is an appropriate scale for mapping landscape connectivity. In Chapter 3, Resource Selection Functions (RSF) were used to characterise second order habitat selection preferences of dispersing and resident-non-breeding (hereafter referred to as resident) wild dogs. Using these RSF models, landscape resistance layers were calculated for each life stage (dispersing and resident) as follows.

RSF models were fitted separately to data from wild dogs at different life stages and GPS collar data which were prepared in the same manner as described in Chapter 3 (Section 3.3.2; page 66). RSF models were fitted using all habitat variables: human population density, distance to roads, distance to rivers, percentage tree cover and Terrain Ruggedness Index; as described in Chapter 3 (Section 3.3.4; Page 70). Raster layers of habitat variables used in the analyses were sourced from the same locations and prepared as described in Chapter 3 (Section 3.3.4; Page 70), however raster layer extents were set to the entire of Kenya and resampled to 300m resolution. This resolution was used because the connectivity analysis study area was expanded to the whole of Kenya and 300m was both computationally feasible and proved sufficient detail for the purposes of this analysis.

Resistance layers were calculated from the RSF models using the formula:

$$z = \beta_1 v_1 + \beta_2 v_2 + \dots + \beta_n v_n$$

where z is the resistance value and β_n is the coefficient for variable v_n (Manly *et al.*, 2002). Extreme outliers were removed by rescaling the top 1% of raster values to the value of the 99th percentile. The raster was then divided by the maximum value of the resistance layer to rescale it in preparation for the connectivity analysis.

In order to evaluate the sensitivity of the connectivity models to the inclusion of the different habitat variables, the RSF models were rerun excluding each habitat

variable one at a time. The resultant partial models were then used to calculate resistance layers as described above. This meant that for both dispersers and resident wild dogs six resistance layers were calculated (full model (i), and models excluding: distance to roads (ii), distance to rivers (iii), human population density (iv), percentage tree cover (v) and terrain ruggedness index (vi)).

4.3.2.2. Connectivity Analyses

Connectivity between patches of wild dog resident range was modelled using *LSCorridors* (Ribeiro *et al.*, 2017), a software package which works through *GRASS GIS* (GRASS Development Team, 2016). *LSCorridors* simulates potential movement pathways between populations, based on resistance-to-movement raster layers and a multiple least cost pathways approach. For each source and target population multiple movement pathways can be simulated, in this case 250 iterations were run between each patch of wild dog resident range and every other patch. *LSCorridors* adds stochasticity into the models by incorporating variation in the resistance rasters by multiplying the raster layer value by a variability raster layer. The variability raster layer is created by multiplying a raster layer, that has a uniform distribution between 0 and 1, with the designated variability parameter (in this case 2) and adding 1 (Ribeiro *et al.*, 2017). An additional source of variability between iterations is the selection of random start and end points for the pathway. In traditional least-cost pathway analyses animals are expected to depart from the point in their habitat patch which is nearest to their target habitat patch. *LSCorridors* randomly selects a departure point from within the source patch, thereby increasing the stochasticity in the models. *LSCorridors* can also include the perceptual range of the species in question by incorporating a moving window into the analysis which, rather than assuming the animal decides on its next movement based on the resistance value of the next pixel, works across a larger area. In this analysis, 250 iterations were run between each resident population, the variability parameter was set to 2 and the perceptual range was set to 3000m using the *MLAvg* option. *MLAvg* uses the average value of the moving window to determine the next step, and is recommended for more habitat generalist species such as African wild dogs (Ribeiro *et al.*, 2017). The moving window was set to 3000m as this is slightly larger than the average step lengths during morning and evening active periods (90 minutes between GPS collar locations) for both resident and dispersing wild dogs (Table 3.2; page 75). In order to evaluate the impact of changes in the size of the window used, models were also run with the window set to 1500m and 4500m.

LSCorridors combines the modelled movement pathways into a single raster layer for each model. These Route Selection Frequency Index (RSFI) raster corridor maps show the frequency with which each raster cell is passed through by modelled movement pathways. Cells that have higher RSFI values are used more often in the simulations and are therefore likely to be particularly important for maintaining connectivity.

To evaluate the connectivity maps, they were compared with the range map developed by RWCP (Figure 4.1) and with published data from dispersing wild dogs in southern Kenya (IUCN/SSC, 2007; Masenga *et al.*, 2016).

4.3.3. Impact of Planned Linear Infrastructure Development

A shapefile of the route of the LAPSSET corridor was downloaded from World Resources Institute (2010) and was mapped over the connectivity maps developed as described above. A 50km buffer was created on either side of the LAPSSET route (100km total width) to describe the outer corridor's planned Special Investment Zone. The shapefiles of resort cities and projected growth areas were also downloaded from the World Resources Institute (World Resources Institute, 2010) and compared with the connectivity maps.

4.4. Results

4.4.1. Connectivity between Patches of Wild Dog Resident Range

4.4.1.1. Resistance Layers

Resistance to movement layers developed using data from both dispersal groups and resident packs indicated high resistance in areas of Kenya with high human population densities (Figure 4.3 & Figure 4.4). This was particularly noticeable in the southern half of the country, with very high resistance values in the areas around Nairobi and Lake Victoria.

Wild dogs tend to select for areas that are close to roads and rivers (Chapter 3), thus the connectivity model generated high resistance values for those parts of Kenya that were far from roads and rivers (Figure 4.3). For example, large swathes of northern Kenya and the coast north of Lamu, showed unexpectedly high resistance values, despite low human population density. When distance to roads

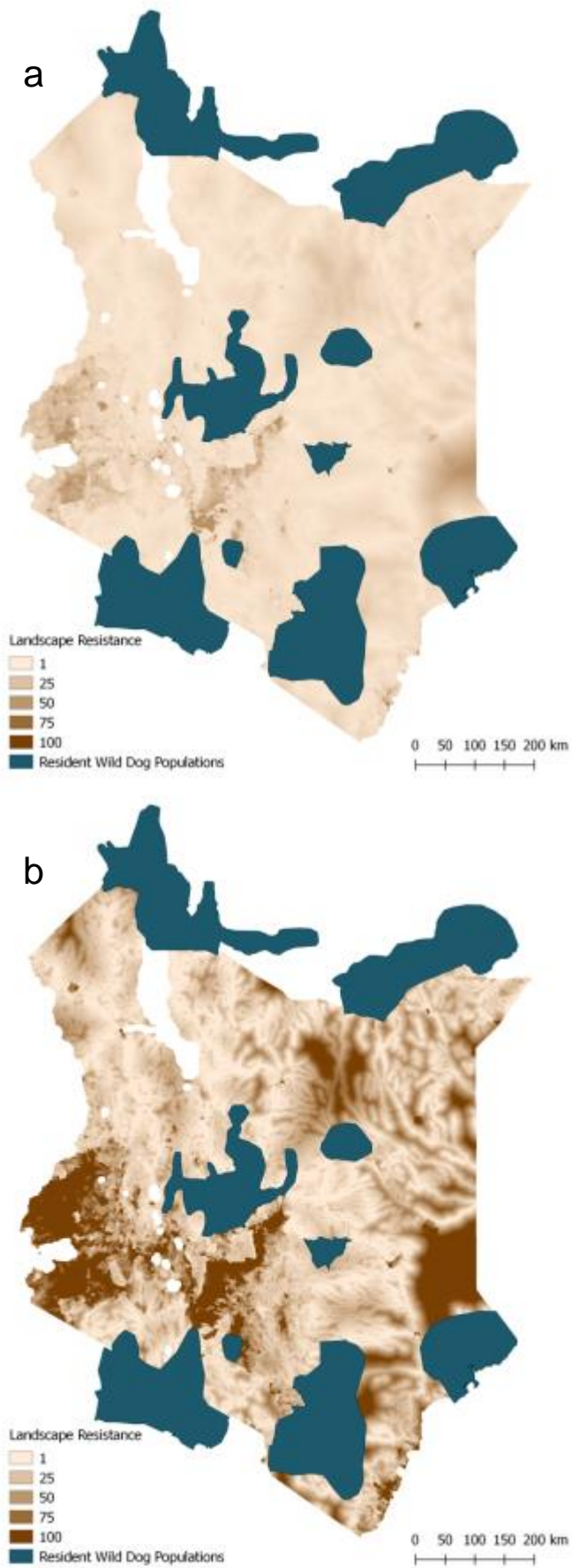


Figure 4.3. Landscape resistance rasters calculated using the full RSF model (i), using data from dispersal groups (panel a) and resident packs (panel b). Darker colours indicate higher resistance.

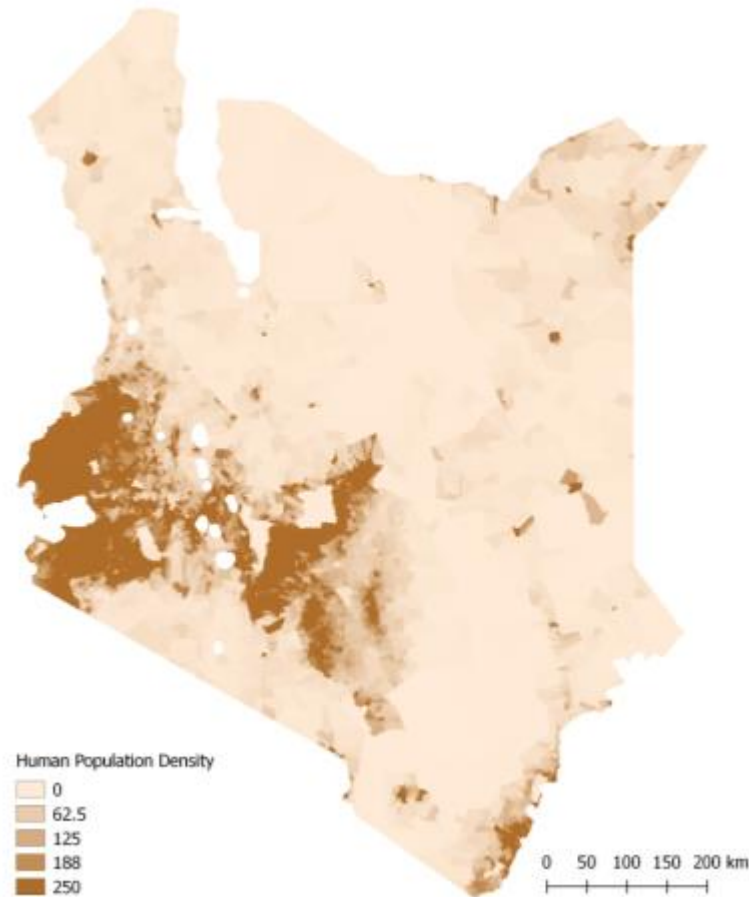


Figure 4.4. Human population densities (people per square kilometre) across Kenya. Data from CIESIN 2016.

was removed from the RSF model, the resistance to movement values in the northern parts of Kenya, where there are relatively few roads, changed substantially (Figure 4.5).

Dispersal groups had lower resistance values across the country than resident packs, when comparing the resistance layers developed using data from the two different life stages (Figure 4.3).

4.4.1.2. Connectivity Analyses

The connectivity analysis using the full RSF model predicted relatively narrow movement pathways between many of the patches of wild dog resident range, particularly for resident packs (Figure 4.6 & Figure 4.7). There were some areas where there were high concentrations of potential movement pathways, suggesting that according to the model, animals will likely be channelled along certain routes. This channelling is particularly noticeable in northern Kenya where the model

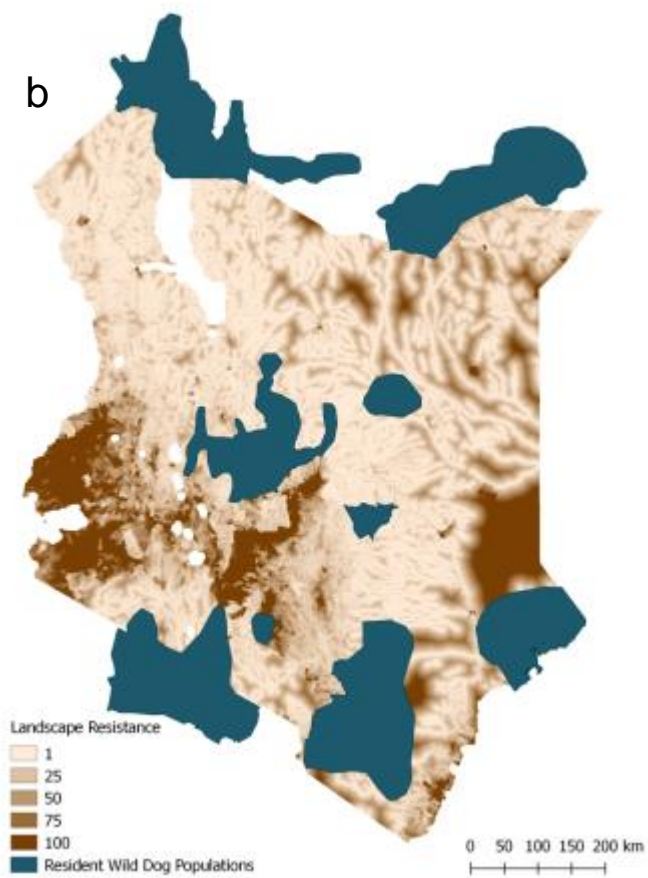
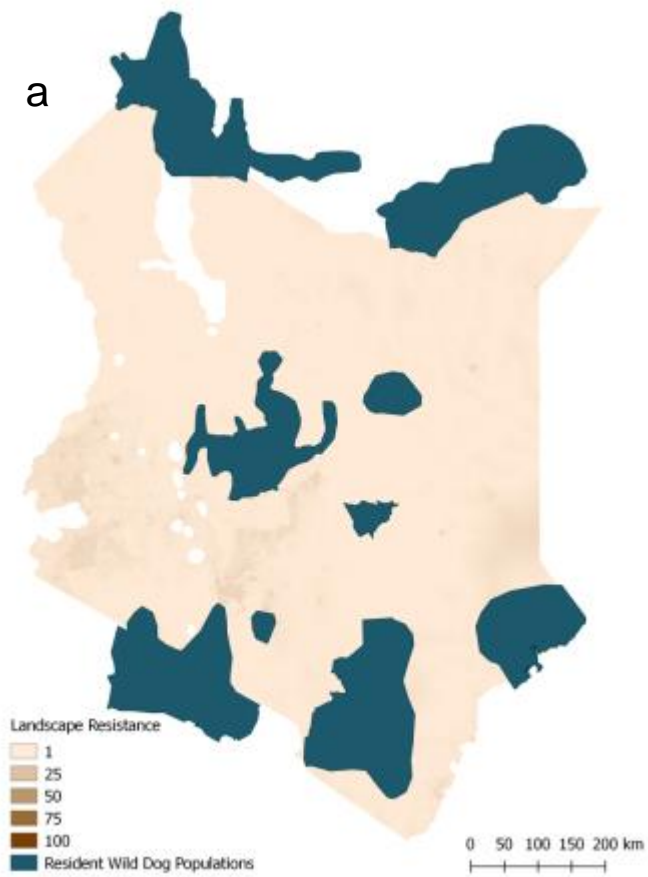


Figure 4.5. Landscape resistance rasters calculated using the RSF model not including distance to roads (ii) as a variable, using data from dispersal groups (panel a) and resident packs (panel b). Darker colours indicate higher resistance.

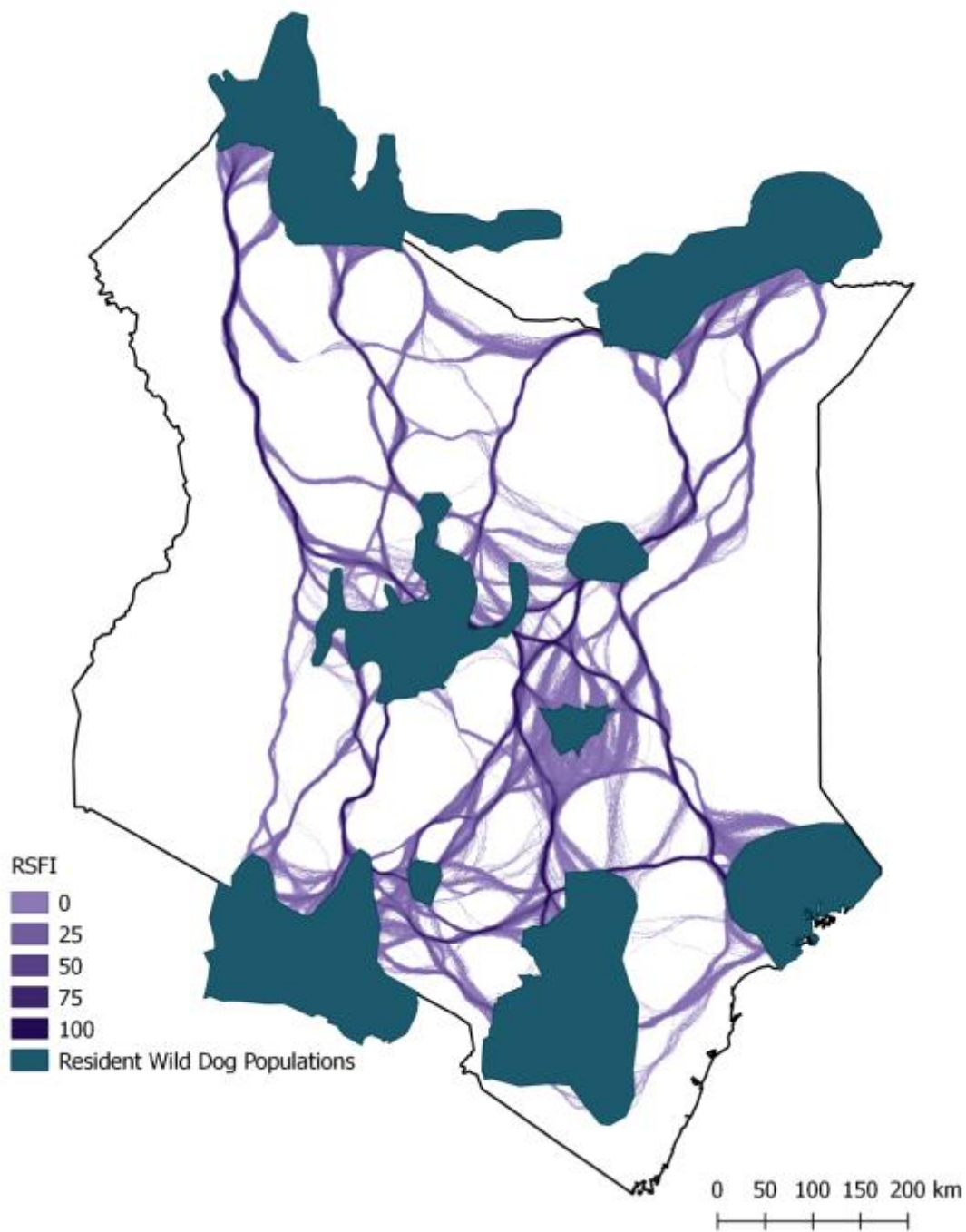


Figure 4.6. Connectivity map based on the full RSF model (i) using GPS data from dispersal groups and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.

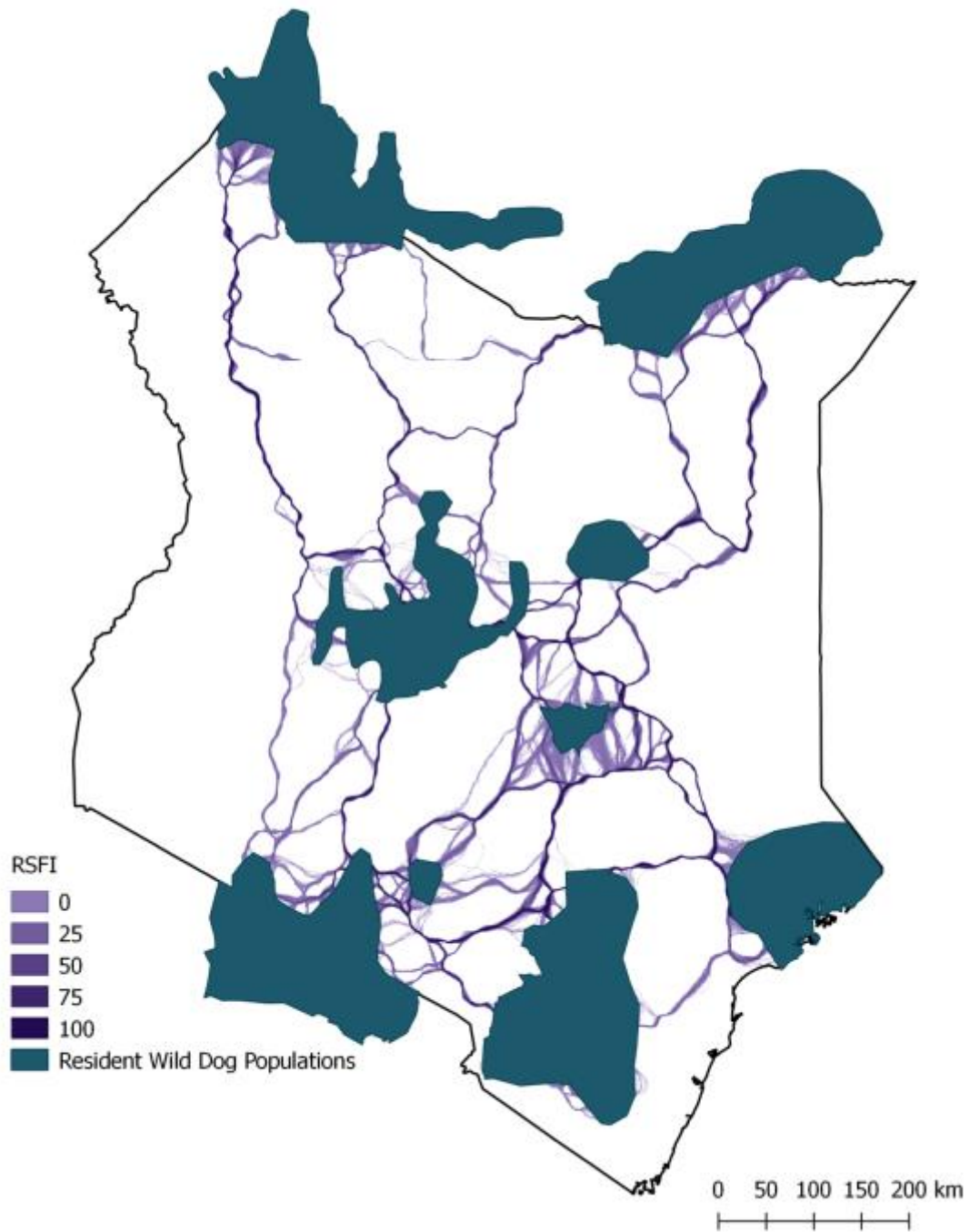


Figure 4.7. Connectivity map based on the full RSF model (i) using GPS data from resident packs and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.

generates narrow, highly concentrated movement pathways (Figure 4.6 & Figure 4.7).

The sensitivity analysis suggested that the inclusion of distance to roads as a variable has an important impact on the modelled location of movement pathways. Many of the movement pathways generated by the full RSF models, for both life stages, were closely associated with the location of roads. When the connectivity analysis was run without including distance to roads, the level of connectivity across northern Kenya in particular increased substantially (Figure 4.8 & Figure 4.9). Other sensitivity analyses showed some differences in connectivity levels but the majority of the main corridors remained similar to the full model (see Appendix 2 Figure 1. to Appendix 2 Figure 8.). Changes to the scale parameter also only resulted in minor changes to the models (see Appendix 2 Figure 9. to Appendix 2 Figure 16.).

Connectivity maps predicted that the link between the Laikipia-Samburu wild dog population and the Loliondo-Kajiado population was at high risk (Figure 4.6 & Figure 4.7). A movement pathway was predicted to pass through the Aberdare National Park; however, there are high human population densities around the Park. This means that there is a very narrow area through which wildlife would have the greatest chance of passing, and even this route would require them to pass through areas with relatively high human population densities (Figure 4.10).

The locations of the potential movement corridors differed from the areas identified during the RWCP mapping process (Figure 4.11). There are records in the literature of wild dogs which had been fitted with GPS collars, dispersing from the Tanzanian side of the Loliondo-Kajiado population and moving northwards into Kenya (Masenga *et al.*, 2016). Overlaying these data onto the connectivity maps from this analysis shows large amounts of overlap between the projected movement pathways and those taken by the collared wild dogs from the Loliondo-Kajiado population (Figure 4.12).

4.4.1.3. Comparison between Connectivity Levels for Dispersing and Resident Animals

The location of movement pathways for the full model for both life stages were similar (Figure 4.6 & Figure 4.7). Areas with the highest RSFI values, which correspond to the areas where the most movement pathways were predicted to pass through, were also in similar places. The major difference between the two life

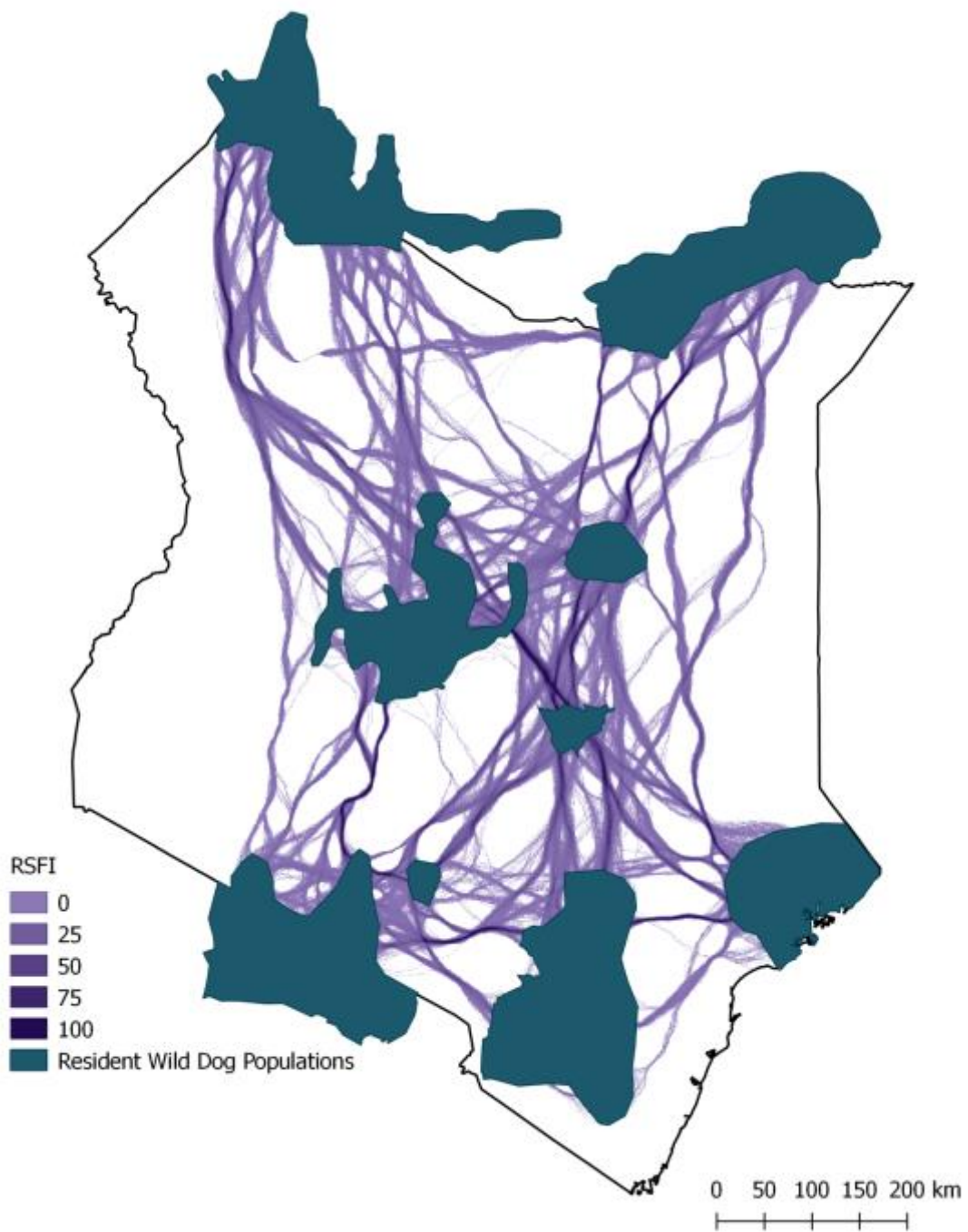


Figure 4.8. Connectivity map based on the RSF model not including roads (ii), using GPS data from dispersal groups and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.

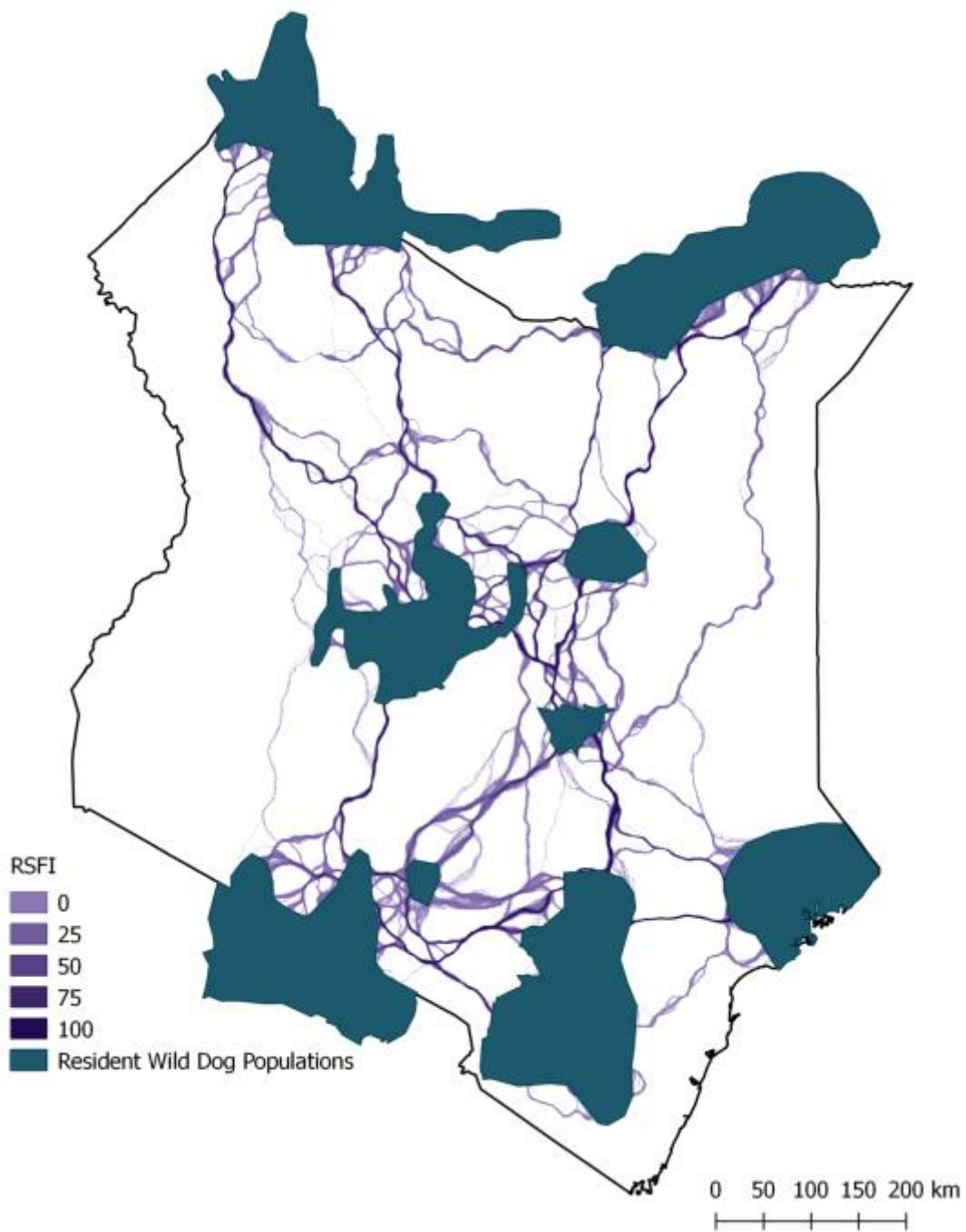


Figure 4.9. Connectivity map based on the RSF model not including roads (ii), using GPS data from resident packs and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.

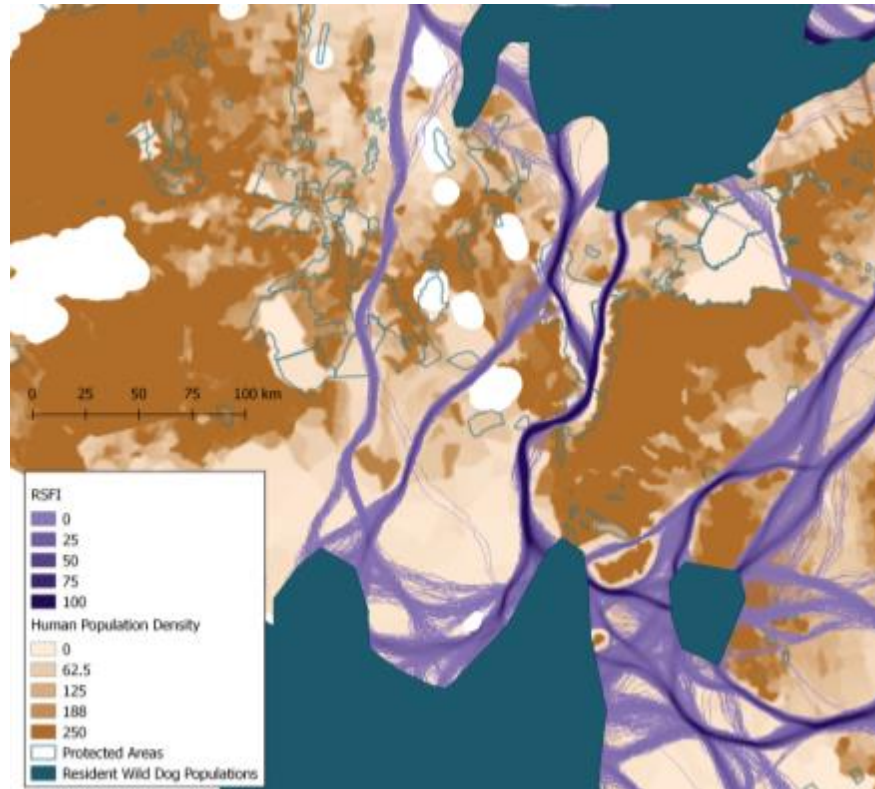


Figure 4.10. Movement pathways modelled for dispersal groups (using the full RSF model (i) and a 3000m moving window) between the Loliondo-Kajiado and Laikipia-Samburu range patches shown against the locations of protected areas and human population density

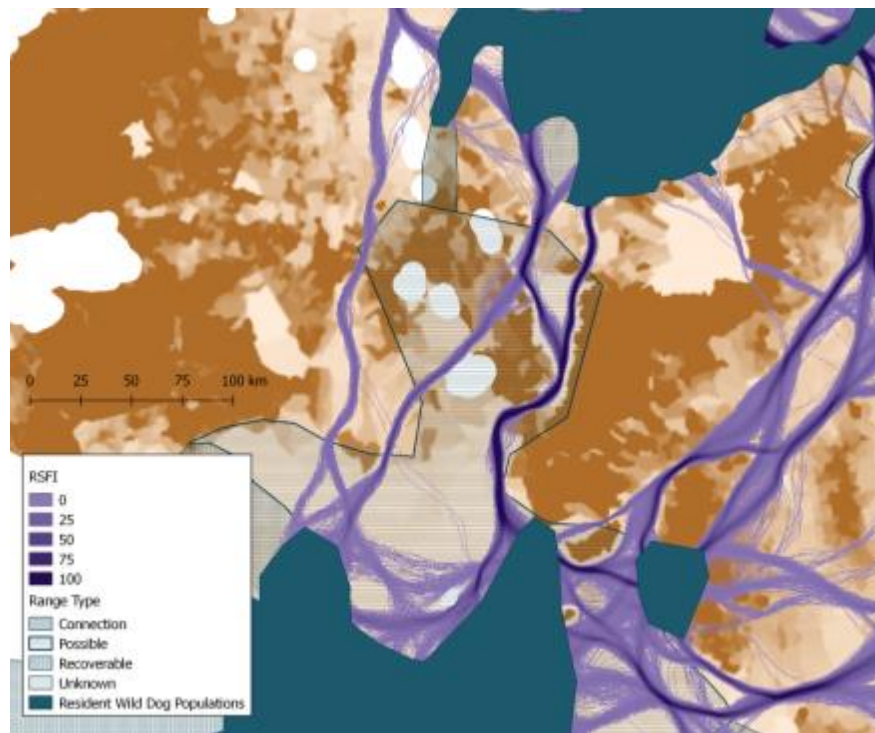


Figure 4.11. Movement pathways modelled for dispersal groups (using the full RSF model (i) and a 3000m moving window) between the Loliondo-Kajiado and Laikipia-Samburu range patches shown against RWCP range map and human population density

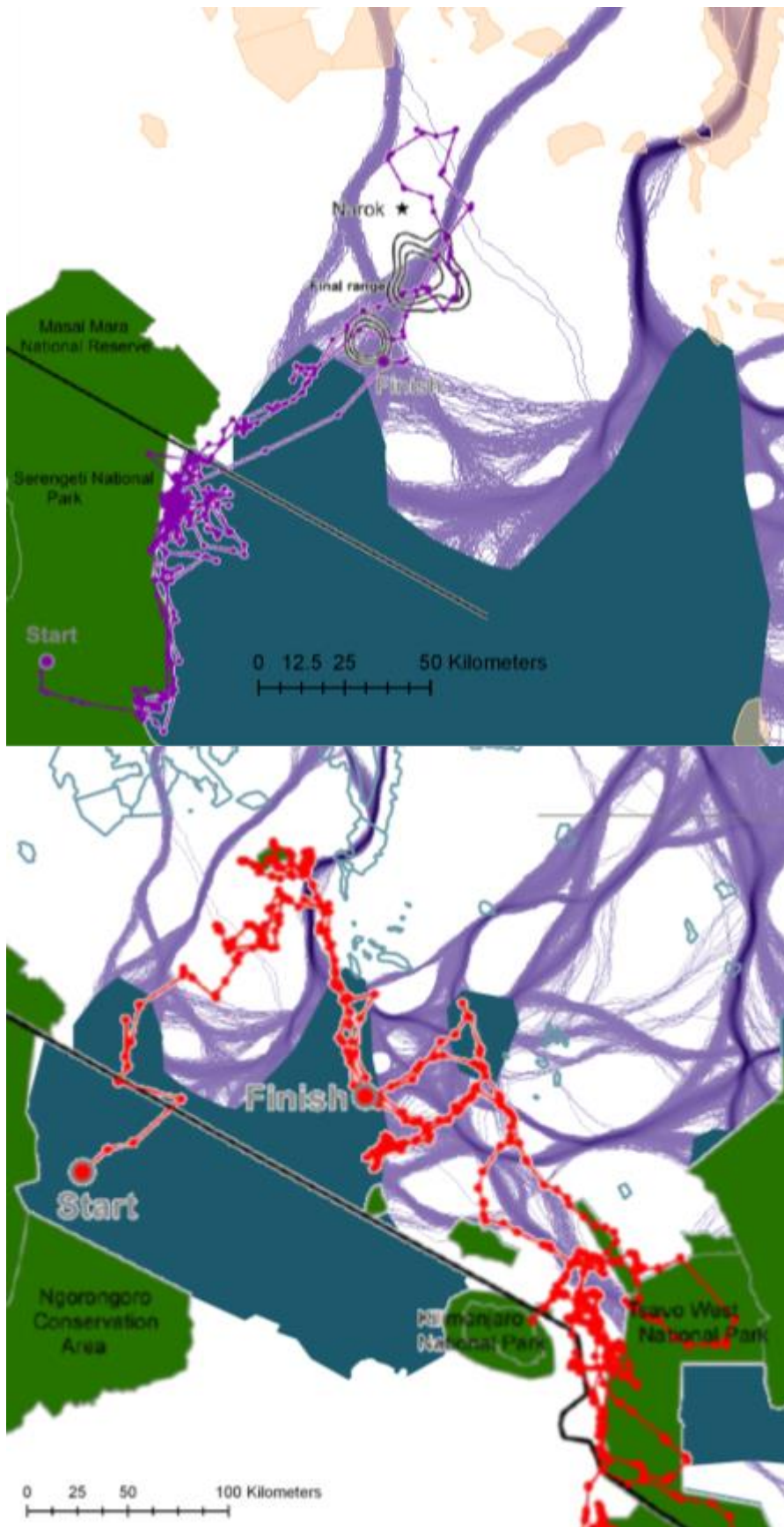


Figure 4.12. Movement pathways modelled for dispersal groups (using the full RSF model (i) and a 3000m moving window) between the Loliondo-Kajiado and Laikipia-Samburu range patches shown against observed wild dog movement pathways taken from Masenga *et al.* 2016

stages was in the amount of overall connectivity between the patches of wild dog resident range (Figure 4.6 & Figure 4.7). Dispersal groups were predicted to be able to move through a wider area than resident packs, with resident packs' potential movement corridors more concentrated in narrower areas.

4.4.2. Impact of Planned Linear Infrastructure Development

The planned location of LAPSSET overlaps extensively with the location of modelled movement pathways between remaining patches of wild dog resident range in Kenya (Figure 4.13). In western Kenya, one of the modelled movement pathways between the Laikipia-Samburu and the Omo-Mago populations runs alongside the planned location of the LAPPSET corridor (Figure 4.13). This may mean that this potential movement pathway may no longer be useable by the wild dogs or that there may be high levels of road and rail kill along this route.

In addition to the likely impact of LAPSSET on connectivity between wild dog populations, it is also noteworthy that two of Kenya's seven remaining patches of wild dog resident range are in the path of the LAPSSET corridor itself (Figure 4.13). This can be expected to have an important impact on the wild dogs in the Laikipia-Samburu and the Ijara populations, two of the largest resident population areas.

4.5. Discussion

These results suggest that it is possible that all known patches of resident wild dog range in Kenya are still connected. However some of the potential routes between patches, particularly in southern Kenya where human pressures are greatest, are narrow (Hypothesis A). Several of the predicted movement corridors would require animals to pass through areas of suboptimal habitat in order to move between populations and at least one of these links may already be blocked. The predicted connectivity levels for dispersal groups were substantially different to those of resident packs (Hypothesis B). The simulated pathways for dispersal groups covered a wider area than those of the resident packs, suggesting a higher probability that the pathways between range patches still exist. Several of the wild dog movement corridors identified here are in areas where the LAPSSET corridor and its associated building projects are planned (Hypothesis C). Two of Kenya's remaining wild dog populations can also be expected to be directly affected by LAPSSET.

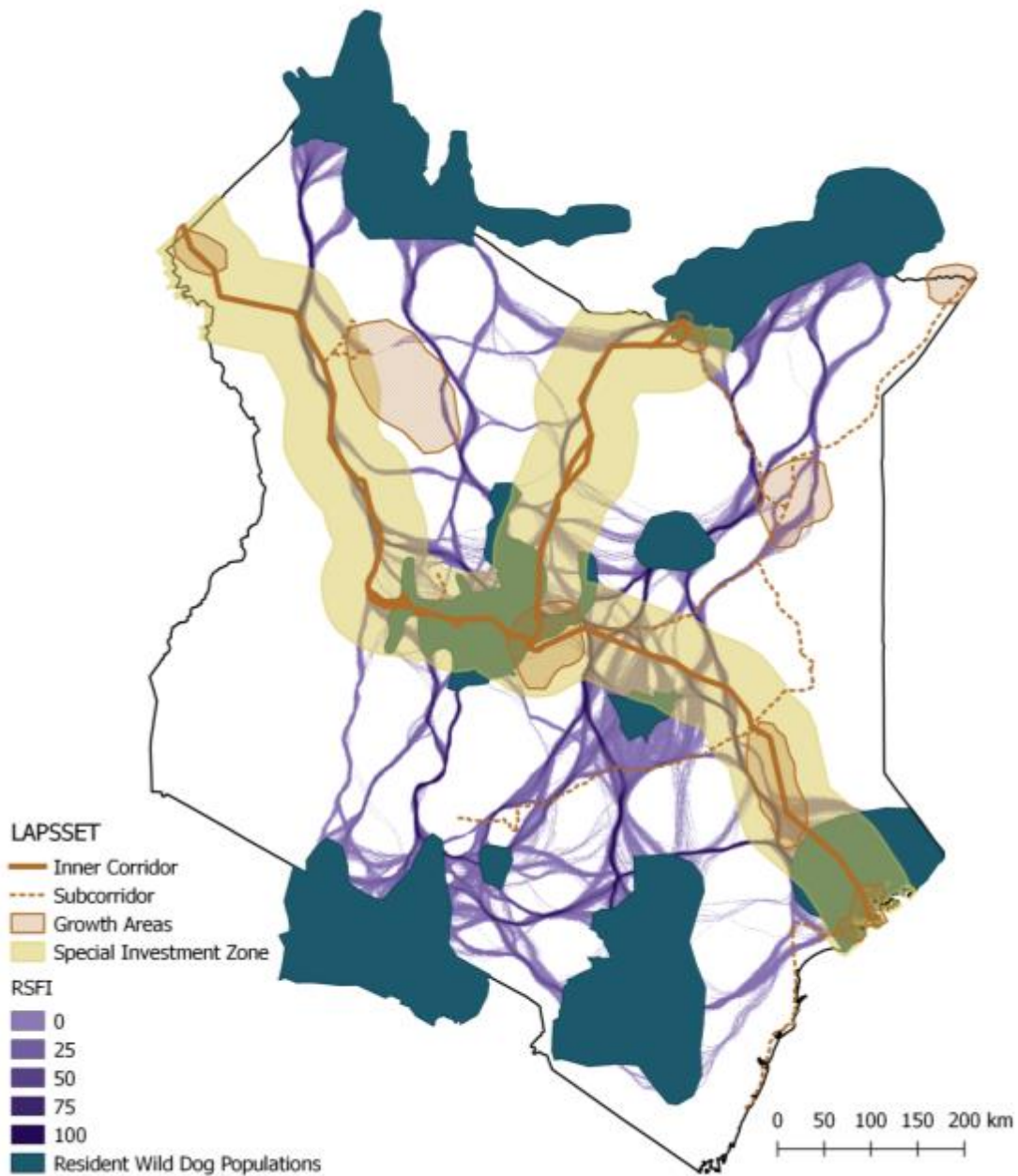


Figure 4.13. Location of LAPSSET corridor and associated development projects overlaid on the locations of patches of resident wild dog range and modelled movement pathways for dispersal groups (based on the full RSF model (i) and a 3000m moving window)

It should be highlighted that the potential movement pathways identified here are only predictions, and do not necessarily mean that these routes are still available for animals to use to move between populations. The comparisons of the connectivity maps produced by these models and the locations of collared wild dogs (Masenga *et al.*, 2016) suggest that these maps fit observed movement data relatively well. However, a wild dog which was originally collared from the Loliondo-Kajiado population in Tanzania, that was tracked moving north, despite initially following the modelled movement corridor, turned back and did not continue travelling northwards (Figure 4.12). It is possible that this is because of the relatively high human population densities in the area (Figure 4.11). Thus, although the connectivity analysis identified a possible linkage between the two populations it may well be that this corridor would require animals to pass through habitat that is too hostile and has in fact already been blocked. It is possible that certain habitat features, such as human population density, when they are above a certain threshold, form a complete movement barrier for wild dogs and animals will no longer be able to pass through an area. However, different wild dogs may also have different tolerances and while the collared wild dog from the Loliondo-Kajiado range did not successfully travel further north, it is possible other groups would.

The connectivity modelled here is based on data from individuals originating from only one of Kenya's remaining populations of wild dogs; therefore there may be aspects of their habitat selection preferences that are not common across different populations. For example, in the Laikipia-Samburu range patch the landscape is primarily *Acacia* bushland, meaning that roads are an easy way for wild dogs to move around their territories (Figure 4.14). It may be that in other habitats, which are more open and easier to travel through, that wild dogs may use roads less often and so this selection would be weaker. Northern Kenya has a lower density of roads than southern Kenya and so the inclusion of distance to roads within the model had a greater effect on the levels of projected connectivity in this area (Figure 4.6 & Figure 4.7). Even if individuals in parts of the country with few roads still show preferences for areas close to roads, the lack of roads in northern Kenya would be very unlikely to prevent wild dogs travelling through these areas. Nonetheless, it may be that the roads that are present would channel wild dog movement. Having lower densities of roads is likely to be beneficial for successful dispersal, as a preference for using areas close to roads would put animals at higher risk of being killed as a result of traffic collisions.



Figure 4.14. Wild dogs using a road to move between different parts of their territory

However, wild dogs across Africa have been shown to prefer areas close to roads (Woodroffe, 2010; Abrahms *et al.*, 2016) and the results presented in Chapter 3 suggest that resident packs and dispersal groups preferentially use areas close to roads. This preference was significantly stronger among dispersal groups than in individuals in other life stages (Chapter 3). Such use of linear features, such as roads, to facilitate movement has been noted in other species; for example, Tasmanian devils, *Sarcophilus harrisii*, and spotted-tail quolls, *Dasyurus maculatus*, have been found to select towards roads for both travelling and foraging (Andersen *et al.*, 2017). Wolves have also been found to make use of linear anthropogenic features to facilitate movement, making use of the compacted snow left in snowmobile trails to aid travel through areas of deep snow (Paquet *et al.*, 2010) and also to substantially increase their rate of movement through forested areas (Dickie *et al.*, 2017). The significantly higher selection for areas close to roads by wild dog dispersal groups could be because these areas are used by dispersing wild dogs as a relatively easy route across the landscape, thereby increasing their dispersal ability.

Whilst this study focussed on LAPSSET, a large infrastructure development project, it is not only the developments on this scale that will affect connectivity. Connectivity will likely be concurrently affected by other changes to the landscape,

such as the building of fences and changes in land-use, which this model does not account for. Even if some changes may not substantially reduce levels of connectivity when made in isolation, when several changes are experienced in concert they may have a more profound effect (Nellemann *et al.*, 2003). Future work on country-wide connectivity for wild dogs in Kenya should include genetic mapping of relatedness of different populations. This will give an indication of the recent levels of functional connectivity remaining between the country's populations (Tensen *et al.*, 2016). These data could then be analysed along with habitat selection data, such as those used here, to strengthen the mapping of remaining areas of connectivity between populations.

These results highlight the need to mitigate any potential negative impacts of LAPSSSET on this endangered species. The status of wild dogs across northern Kenya and into Somalia is currently classed as unknown (Figure 4.1; IUCN/SSC, 2007). Getting more information about the status of wild dogs in these areas will aid, not only future connectivity mapping, but also wider conservation planning. Continuing to collect data on the movement behaviours of dispersal groups is also likely to prove important, particularly as the LAPSSSET corridor develops. Monitoring dispersal behaviour in wild dogs is extremely challenging but collecting data from dispersal groups is likely to give the greatest insights to the impact of the LAPSSSET development on connectivity. Wild dogs from East Africa are relatively small, individuals collared as part of the research of the Kenya Rangelands Wild Dog and Cheetah Project (KRWDCCP) have a mean weight of 23kg (Woodroffe *et al.*, 2007c). This restricts the weight of the GPS collar it is possible to use and has meant that the only collars available have required project staff to physically locate collared individuals in order to download data from the GPS collar. This requirement has therefore presented a particular challenge when wanting to study the movement patterns of dispersal groups as, if the group travels a very long distance (for example to a different resident population), then it is difficult to keep track of them; particularly as dispersal groups can travel very large distances in short periods of time. In recent years however, miniaturised versions of satellite-GPS collars, which send GPS data through via satellite rather than requiring download over a radio link, have increasingly become available and are now small enough to be fitted to wild dogs. This technology will enable much more accurate and reliable monitoring of dispersal behaviour and will enable researchers to track dispersal behaviour on a much larger scale than has been possible previously. This will be particularly

important as the building work for the LAPSSET corridor continues, in order to determine any effects it may be having on dispersal routes.

In addition to the potential effects on dispersal corridors, two of Kenya's patches of wild dog resident range are likely to be directly affected by the LAPSSET development. The Ijara population is in the pathway of the corridor development and there is building underway for a large extension to the current port at Lamu and plans for the creation of a "resort city". This part of the LAPSSET development not only also has implications for wild dogs, it is also likely to negatively affect a critically endangered antelope species, the hirola, *Beatragus hunteri*, as this area is home to the only remaining hirola population (King, 2013). The Laikipia-Samburu population will be trisected by the LAPSSET corridor, in addition there are also plans for the construction of a "mega-dam" and a resort city close to Isiolo (LAPSSET Corridor Development Authority, 2015). The Laikipia-Samburu population is a particularly important one as it is the largest in Kenya (Kenya Wildlife Service, 2010) and, due to its position in the centre of the country, its persistence is also likely to be vital for maintaining connectivity between wild dog populations in the south of Kenya and those in Ethiopia.

Whilst monitoring the impacts of LAPSSET on connectivity is important, increased focus needs to be placed on ensuring mitigation measures are incorporated into development projects to minimise any deleterious impacts on wildlife. There are large areas of overlap between the dispersal corridors identified here and the locations of the LAPSSET corridor and its associated development projects (Figure 4.13). LAPSSET is planned to trisect the country (Figure 4.2), and is therefore likely to have pronounced negative effects on connectivity between northern and southern Kenya unless substantial mitigation techniques are incorporated. Ecotourism contributes a substantial amount to Kenya's GDP (World Travel & Tourism Council, 2017). LAPSSET incorporates the development of resort cities, aimed at increasing tourism revenue (LAPSSET Corridor Development Authority, 2015), protecting the wild species that tourists come to see is therefore vital for the success of these projects. The inner corridor of LAPSSET is planned to comprise an oil pipeline, a highway, a gas pipeline and a railway track in addition to the highway, with the inner corridor spanning between 500m and 10km (LAPSSET Corridor Development Authority 2015). In combination with the outer corridor, a 50km area on either side of the inner corridor, in which the development of farming, factories and industrial and management parks will be encouraged (LAPSSET Corridor Development

Authority, 2015); it is highly likely that these large-scale building and infrastructure projects will have extensive impacts on wildlife in their surrounding areas, including wild dogs. Although wild dogs select for areas close to roads, the LAPSSET highway and its associated infrastructure is highly unlikely to attract or benefit them in terms of landscape connectivity. As the main reason for building LAPSSET is to develop transport connections between the Kenyan coast, South Sudan and Ethiopia re-routing the development corridor is unlikely to be a viable option. In countries, including Canada, Spain and USA (Cain *et al.*, 2003; Mata *et al.*, 2008; Clevenger & Waltho, 2000), crossing structures have been built to enable the passage of wildlife across highways and other potential movement barriers such as railways. There are some such crossing structures already in existence in Kenya, such as an underpass constructed near Mount Kenya to facilitate elephant movement to and from the mountain, which has been used with some success by species including elephants, striped hyaenas, *Hyaena hyaena*, and caracals, *Caracal caracal* (Weeks, 2015; Nyaligu & Weeks, 2013). However, for such measures to prevent wildlife being killed on the roads, it is often necessary to construct fences around the road, in order to channel wildlife movements towards the crossing points, in order to ensure their efficacy (Clevenger & Waltho, 2000). A key consideration for such interventions in a country like Kenya, where many people live in rural communities reliant on livestock, which need to be regularly moved in search of water and grazing, is that their movements will also be disrupted by increases in fencing (East *et al.*, 2012). This means that any crossing points are likely to be used by both herders and wildlife – effectively funnelling people and wildlife into close contact. This has the potential to increase the risk of conflict between the groups. Increased human use of such crossing points may also decrease the likelihood of them being used by wildlife (Clevenger & Waltho, 2000). Such a pattern is seen in relation to water sources; where livestock densities are high near water sources, wildlife densities are depressed (de Leeuw *et al.*, 2001).

Although this study has focussed on Kenya, many of the challenges of balancing development projects and biodiversity conservation are also found elsewhere. Many countries in Africa and Asia are currently undergoing rapid economic growth and are constructing major infrastructure projects. Such projects are important for development and poverty alleviation. However, with considerable sections of their populations still dependent on natural resources, either directly or as a result of working in industries such as tourism, balancing these potentially opposing needs will be an important factor in future planning. Mitigation of the impacts of infrastructure

on wild species is possible; for example, in Canada, national parks have highways transecting them but have been able to safe-guard species through development of mitigation techniques such as under- and over- passes. As discussed above, there has already been some success with similar techniques in Kenya; the inclusion of such tools in infrastructure projects like LAPSSET may help to reduce the impact on wildlife.



Plate 6. A cheetah wearing a GPS collar

Chapter 5.

Going the Long Way Round: Energetic Effects of Increased Fencing on the Cheetah

5.1. Abstract

Although they may be built with the intention of conserving threatened species, wildlife fences reduce landscape connectivity and can negatively affect the movement patterns of wild species. For individuals in a wild population, an increase in fencing may mean they are no longer able to access all parts of the landscape, or that they will have to travel further to access some areas. Here the impacts of fencing on daily energetic expenditure by a wide-ranging, threatened species are investigated. A model to explore the effects of different fencing types on cheetah energy expenditure was developed, and parameterised using data collected from a GPS collared cheetah. Results showed that fence structure significantly affected the distance moved by cheetahs. Fences that were designed to be permeable to large carnivores had no effect on distance moved. However, less permeable fences caused the cheetah to move, on average, an additional 2.37 km before it was able to cross. This resulted in an estimated increase of 1059 kJ per fence encountered, equivalent to 12.0% of a cheetah's daily energetic expenditure. If all properties in the county were enclosed with this type of fence, then the model showed that cheetah energetic requirements would increase by as much as 14.8%. This study shows that fences can have substantial impacts on energetic budgets; should fencing become sufficiently widespread, animals may no longer be able to meet their daily energy requirements which may reduce their probability of survival and reduce reproductive success. This indicates the mechanism by which fences may ultimately affect population size of large carnivores.

5.2. Introduction

5.2.1. Fences

In recent years, there has been increased pressure on governments and land owners to make use of large-scale fencing interventions (Durant *et al.*, 2015b). Whilst some of these fences are developed with conservation in mind, e.g. the fencing of protected area boundaries, they may also be erected for other reasons such as border fencing and as part of wider infrastructure plans (Durant *et al.*, 2015b). This increase, particularly with respect to the use of fences in conservation, is in marked contrast to the wider focus within conservation on maintaining ecosystem connectivity (Crooks & Sanjayan, 2006). Fences do not necessarily act as complete movement barriers for all species that interact with them (Cozzi *et al.*, 2013); depending on their structure and the species in question, fences can range from being entirely permeable to being total barriers to movement (Slotow, 2012). Nonetheless, if fences form enough of a barrier to prevent animals from moving easily across a landscape there may be harmful long-term population effects (Hanski, 1997).

Fences have long been used by conservation practitioners as a method intended to safeguard biodiversity (Hayward & Somers, 2012). Creating barriers between biodiverse areas and the factors that threaten them, such as land-use change, human encroachment or unsustainable exploitation, can be an important way of preventing or minimising biodiversity loss (Hayward & Kerley, 2009). Fences have been used across the globe in order to mitigate a wide range of threats; they have been employed in disease control, exclusion of invasive species, protected area boundary delineation, prevention of road traffic collisions and to address human-wildlife conflict (Hayward & Somers, 2012; Woodroffe *et al.*, 2014). Conservation fencing, by restricting movement, is usually used to control unwanted interactions; for example, between invasive and native species or between wildlife and local communities (Hayward & Kerley, 2009).

Whilst conservation fences are used in an attempt to protect wildlife species, not all fences that have an impact on wild species are erected with the aim of aiding conservation (Newmark, 2008). Fences are used for a wide variety of purposes; these include as boundary markers by property owners, to contain livestock or around infrastructure (Evans & Adams, 2016). Landscape fences may affect animal

movement regardless of whether that was the original objective (Løvschal *et al.*, 2017). Fencing of property boundaries contributes to fragmentation of habitat and may also affect species movements, for example increases in fencing in the Greater Mara ecosystem is thought to threaten the annual wildebeest migration (Løvschal *et al.*, 2017). Fencing around roads and railways can exacerbate the barrier effects of the infrastructure; for example the Ulaanbaatar-Beijing railway in Mongolia is fenced to prevent collisions between trains and livestock but has had serious impacts on the movement patterns of wild ungulates in the ecosystem, including the Mongolian gazelle and Asiatic wild ass (Ito *et al.*, 2017). The impacts of landscape fences on endangered wildlife populations are as important to establish and mitigate as the impacts of conservation fences.

For a manager considering building a conservation fence, an important first step is to determine the overall aim (Durant *et al.*, 2015b). Fencing is often used as a method of reducing contact between humans, and their property, and wildlife (Woodroffe *et al.*, 2014; Kioko *et al.*, 2008; Durant *et al.*, 2015b). Minimising encounters aims to protect wildlife from poaching, prevent crop-raiding or livestock depredation and to protect both humans and wildlife from potentially fatal encounters (Woodroffe *et al.*, 2014). In deciding whether to construct all types of fencing, important factors to consider include not only the effect the presence of fences is likely to have on the species targeted by the fence, but also on non-target species (Hayward & Kerley, 2009; Slotow, 2012). This is particularly the case where the target species coexists with other species that are at high extinction risk. For example, it may be desired to restrict the movement of elephants in order to reduce crop raiding, but there may be no need to restrict the movements of carnivores through agricultural crops. This would mean that rather than building an impermeable fence, it may be more appropriate to design the fence so that carnivores can pass underneath it whilst still limiting elephant movement. However, even where there is extensive planning there could be unforeseen impacts. For example, in some areas African wild dogs have developed hunting techniques exploiting fencing to increase their hunting success rate (Davies-Mostert *et al.*, 2013). This behavioural adaptation can result in over-hunting of prey populations (Davies-Mostert *et al.*, 2013). In some areas this has led to conflict with landowners, who may suffer financially from loss of game species and increased fence repair costs (Lindsey *et al.*, 2012). If such costs are perceived to be too high they may lead to predators being removed from reserves (Woodroffe *et al.*, 2014). Where fences are expected, or found, to have negative impacts on other species it

may be possible to mitigate these impacts by altering the design of the fence, however these alterations must be balanced against any loss of efficacy.

Large carnivore species tend to be wide-ranging and are therefore particularly likely to be threatened by factors associated with a loss of connectivity resulting from increased fencing (Ripple *et al.*, 2014). However, human-wildlife conflict has also been identified as one of the most important threats to the persistence of many carnivore species (Ray *et al.*, 2005; Di Minin *et al.*, 2016). As a result, there have been calls in the literature to fence remaining populations to ensure their long-term persistence (Packer *et al.*, 2013a). In one study, African lions were found to be closer to their populations' estimated carrying capacity inside fenced reserves than unfenced reserves (Packer *et al.*, 2013a, 2013b). The findings of this study were contested as there were several small fenced reserves which had populations that were significantly above their estimated carrying capacity that had a large effect on the overall findings. In addition, whilst having a population at carrying capacity may be desirable, arguably a more important goal is to have a functioning population of adequate size to be self-sustaining. A population below carrying capacity which comprises several hundred individuals is likely to be of greater conservation significance than several populations that are close to their theoretical carrying capacity but which number only a handful of animals (Creel *et al.*, 2013).

5.2.2. Energetics

The balance of energy intake and energy expenditure by an organism is one of the most fundamental components of biology. All living organisms must ultimately have levels of energy intake that equal or exceed their energy expenditure in order to survive (Gorman *et al.*, 1998; Halsey, 2016). The trade-off between body size, energy requirements and food type shapes species' evolutionary trajectory (Carbone *et al.*, 1999). How species are able to balance this trade-off is a central aspect of how they are able to persist in an environment (Carbone *et al.*, 2007). Energetics is the ultimate driver of an individual animal's behaviour and ecology therefore if its environment changes it is likely to alter the animal's energy balance (Halsey, 2016). For example, if changes to its habitat mean the animal has to expend more energy in order to find food it may have to compensate by spending more time foraging or by resting for longer periods to conserve energy. Ultimately, this shift in energy budgets may affect the animal's reproductive potential and/or probability of survival (Perrigo, 1987; Wilson *et al.*, 2012; Wirsing *et al.*, 2002). This

will have cascading population level impacts such that, at the point when daily energy needs for sustenance and reproduction can no longer be met, populations will decline until extinction.

Fences have the potential to affect animals' energetic balance in several ways. Increases in the number of fences an animal encounters may restrict the animal's access to parts of the landscape; if those areas contain important food resources this may reduce the animal's potential energy intake. Fences are not always impermeable barriers and so animals may still be able to cross them, however if there are few potential crossing points, the animal may have to expend additional energy in order to reach them. It is possible that fences may reduce animals' potential energy intake, whilst also increasing their energetic expenditure; putting wider population persistence at risk.

5.2.3. Cheetah

The cheetah is among the widest-ranging of all large carnivore species and as such populations require large contiguous wildlife-friendly areas to persist (Durant *et al.*, 2017). Adults have been recorded as having home ranges of over 3000 sq km (Marker *et al.*, 2008). Cheetahs also live at very low population densities: recorded densities are rarely more than 20 individuals per 1000 sq km (Durant *et al.*, 2017) and have been recorded as being as low as 0.2 per 1000 sq km (Belbachir *et al.*, 2015). Areas of contiguous, carnivore-friendly land of at least 10,000 sq km are typically needed to sustain viable populations (IUCN/SSC, 2007, 2012, 2015); this means that few protected areas are large enough to support viable cheetah populations.

An increase in the amount of fencing on private land is likely to have the greatest impacts on populations of wide-ranging species. It is of particular concern for the cheetah, as the most recent estimate is that 77% of the species' remaining range is outside officially protected areas (Durant *et al.*, 2017). This, in combination with the species' wide-ranging nature, leaves them particularly vulnerable to the effects of increased fencing. As few protected areas are large enough to sustain viable cheetah populations on their own, cheetahs living in protected areas are likely to be reliant on being able to range outside of reserve boundaries (Maddox, 2002). If areas of private land are fenced, it may limit individuals' abilities to exploit the resources found in those areas, and therefore negatively impact the cheetahs' ability to adequately provision themselves and/or their offspring.

Scantlebury *et al.* (2014) quantified cheetah energetics and found that cheetahs' daily movement patterns were the main cause of energy expenditure. Hunting was not a major source of energy expenditure – this is due to the stalk and ambush hunting technique used by cheetahs, which requires only occasional, short bursts of energy (Scantlebury *et al.*, 2014). If fences affect cheetah movement patterns then, because moving across their home ranges comprises a large proportion of a cheetah's Daily Energetic Expenditure (DEE), fences may have an important impact on cheetahs' energy budgets as a result.

This study models the potential effects of different fence designs on cheetah movement patterns and the resultant effect on DEE. The model is parameterised using data from a cheetah GPS collared in the human-dominated landscape of Laikipia County, Kenya.

5.2.4. Hypothesis and Predictions

Hypothesis A: Fence structure has a significant impact on animal movement patterns

Prediction A.1: Fences that are designed to be permeable to animal movement will have less of an impact on movement patterns than fences that are designed to be impermeable

Hypothesis B: Impermeable fences impact on animal daily energetic expenditure

Prediction B.1: Impermeable fences will increase cheetah daily energetic expenditure due to extra travel demands

5.3. Methods

5.3.1. Study site

Laikipia County in northern Kenya is home to a key part of the world's second largest cheetah population (Durant *et al.*, 2017), as such it is of great conservation significance. The county comprises a patchwork of different land-use types, including commercial livestock farming, traditional pastoralism and private wildlife sanctuaries (Ulrich *et al.*, 2012). Over the past fifty years the county's human population has grown rapidly, from 66,506 in 1969 to 399,227 in 2009 (Kenya National Bureau of Statistics, 1969, 2009) putting increased pressure on the county's remaining natural resources. Nonetheless Laikipia remains an important

wildlife area and has the second highest wildlife densities in Kenya (Kinnaird & O'Brien, 2012).

Wildlife conservation is one of the management goals for some properties in Laikipia. Many of these properties have ecotourism businesses which provide a key source of income (Evans & Adams, 2016), with most also incorporating livestock ranching as well. These properties, where the primary land-use is ranching & wildlife or wildlife only (hereafter referred to as “wildlife areas”), are generally larger than other properties in the county, (wildlife areas mean area: 61.30 sq km, range: 0.03 – 386.05 sq km; other areas mean area: 25.23 sq km, range: 0.00 – 295. sq km). Much of the county’s wildlife is concentrated in the wildlife areas.

In recent decades some landowners in Laikipia have erected or reinforced fences along their property boundaries for conservation purposes. Kenya Wildlife Service’s rhino conservation strategy requires impermeable fencing structures around rhino sanctuaries, to increase security and help safeguard populations (Kenya Wildlife Service, 2012). This has meant that those property owners who wanted to reintroduce rhinos have been required to build fences. These fences, in addition to protecting the rhinos, may impede the movement of other wildlife species. However, in order to mitigate effects on other species, the landowners often use permeable fence designs and/or purposefully incorporate gaps into the structure of the fence in order to allow other species to move through (Dupuis-Désormeaux *et al.*, 2016).

A large proportion of properties in Laikipia do not have conservation as a central aim of their management strategy. This means that in addition to conservation fences, the landscape also has fences that have been built for other reasons; these include delineating property boundaries and preventing other people accessing the property (Evans & Adams, 2016; Yurco, 2017). Depending on the design of these fences, they may also impact on wildlife movement patterns.

5.3.2. Impact of Fence Structure on Movement Patterns

In order to evaluate the effects of fencing on the distance moved by cheetahs, movement data were collected from one of three cheetahs that were GPS-collared in Laikipia in 2014/2015. The cheetahs were each fitted with GPS collars (Figure 5.1; Sirtrack Pinnacle LITE G5C-275 GPS Iridium Collar) which collected hourly GPS locations. The three cheetahs fitted with GPS collars were from three



Figure 5.1. Fitting a cheetah with a GPS collar (photo by Stefanie Strebel)

separate social groups: a female with two young dependent cubs, a territorial male with one coalition partner and a non-territorial male with two coalition partners. The movement data presented here are from the non-territorial male (Figure 5.3); data from the other collared cheetahs were not included as they had very restricted home ranges due to their behavioural states. The non-territorial male (hereafter referred to as the cheetah) was collared for a period of 5 months during which time it travelled more than 870km.

GPS locations recorded by the collar with a Dilution of Precision (DoP) of 5 or more were removed from the dataset. DoP gives a measure of the accuracy of GPS locations in relation to the spatial configuration of satellites (Langley, 1999). Movement data were then mapped using QGIS (version 2.14.1; QGIS Development Team, 2012) and step length (the straight line distance between a location and the subsequent location; Figure 5.2) and turn angle (the degree of direction change between two steps) were calculated using the *movement.pathmetrics* tool in the *Geospatial Modelling Environment* (version 0.7.3.0; Beyer, 2010).



Figure 5.3. The non-territorial male cheetah after being fitted with a GPS collar

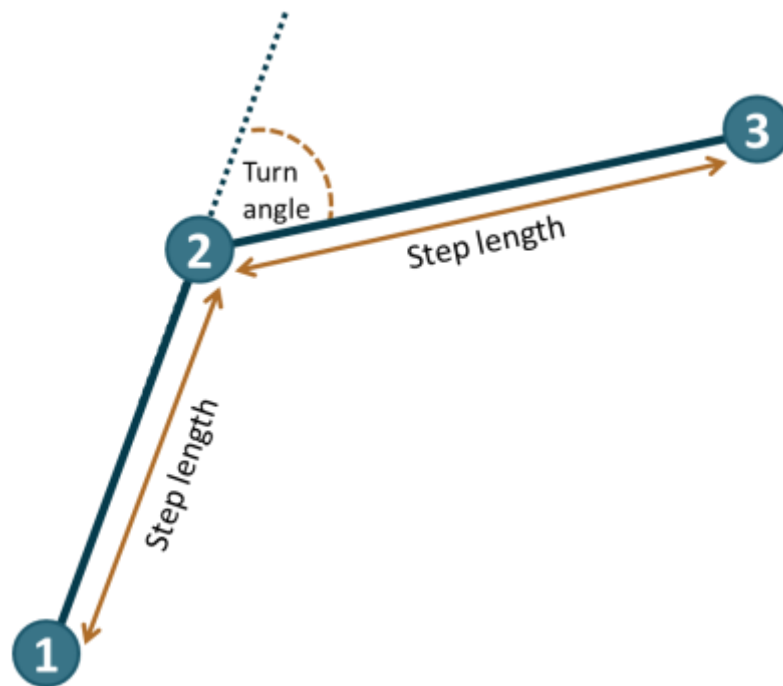


Figure 5.2. Diagram illustrating step length and turn angle. Points 1,2 & 3 represent location data from GPS collars, step lengths are the straight line distance between subsequent locations, turn angle is the degree of direction change between steps.

The cheetah's mean daily distance moved was calculated by summing all the step lengths for each 24h period.

The cheetah's movement track was overlaid on a map of property boundaries, and occasions when the cheetah crossed a property boundary were identified. Property boundaries were categorised into three types according to the presence or type of fencing present as described in Table 5.1. Any boundaries that did not fit into these categories, or where the current status of any fences was not known, were not included in the analysis. Boundaries where there were additional potential movement barriers, such as roads and rivers, were also excluded from the analysis as these may have also affected the cheetah's crossing probability.

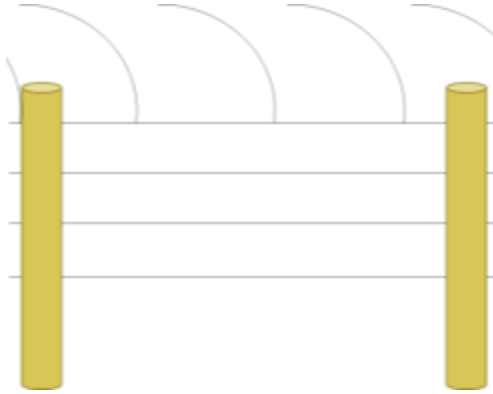
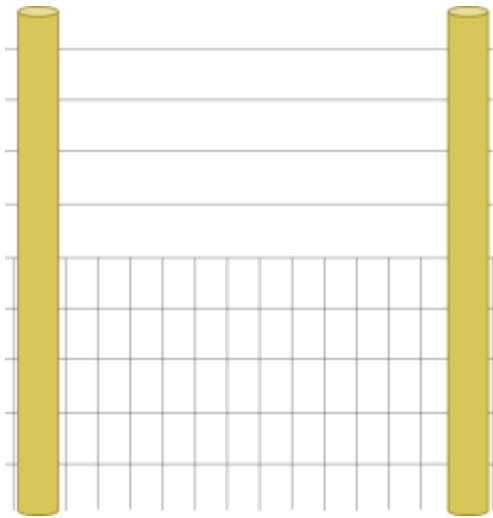
To evaluate if the boundary type had an effect on distance travelled, the distance moved by the cheetah each time it crossed a property boundary was calculated. As the cheetah approached a property boundary, the GPS location either closest to the boundary or the last GPS location before a significant change in direction (defined as a turn angle of more than 60° which resulted in the following pathway segment(s) running approximately perpendicular to the boundary line) was taken as the starting point for the interaction with the boundary. The end point was defined as the nearest location on the other side of the boundary to the starting point (Figure 5.4). Only occasions when the cheetah successfully crossed the boundary were included in the analysis. In addition, GPS locations were only recorded once per hour, therefore only relatively large detours could be detected. This means that estimates from these data of the impact of fences on distance travelled are likely to be conservative, as shorter detours would have been missed. To calculate the additional distance travelled, the straight-line distance between the start and end points of the interaction with the boundary was then subtracted from the length of the route taken by the cheetah.

The additional distances travelled were then compared across boundary types and tested for significance by a Kruskal-Wallis test using the *kruskal* function in the *agricolae* package in *R* (De Mendiburu, 2014; R Core Team, 2016).

5.3.3. Modelling the Effect of Increased Fencing Levels on DEE

To calculate the amount of additional energy used when crossing fences, the relationship between distance moved and energy expenditure, described by Scantlebury *et al.* (2014), was used.

Table 5.1. Descriptions and diagrams of property boundary classifications

Boundary Type	Description	Diagram
No Fence	Unfenced property boundary	
Type 1 Fence	Wire strand fences, less than 1m in height and raised from the ground. Sometimes electrified, usually targeted at restricting elephant movement.	
Type 2 Fence	Fences made from wire mesh or closely aligned wire strands, more than 1m high. Intended to prevent movement of all medium and large bodied species except through designated fence gaps. Usually electrified.	

Scantlebury *et al.* (2014) calculated that distance travelled was related to cheetah DEE by the equation:

$$DEE (kj) = 447 \times \text{distance (km)} + 7103$$

The mean additional energy expenditure was calculated using the mean extra distance travelled for each boundary type.

To evaluate the potential impact on cheetah DEE if all property boundaries were to be fenced, movement pathways were simulated across Laikipia. Random start points were generated using the *Random Points* tool in *QGIS*. The model was run twice overall, first using 10,000 start points spread across all properties in the county irrespective of land-use type (9864 sq km), and second using 5,000 start

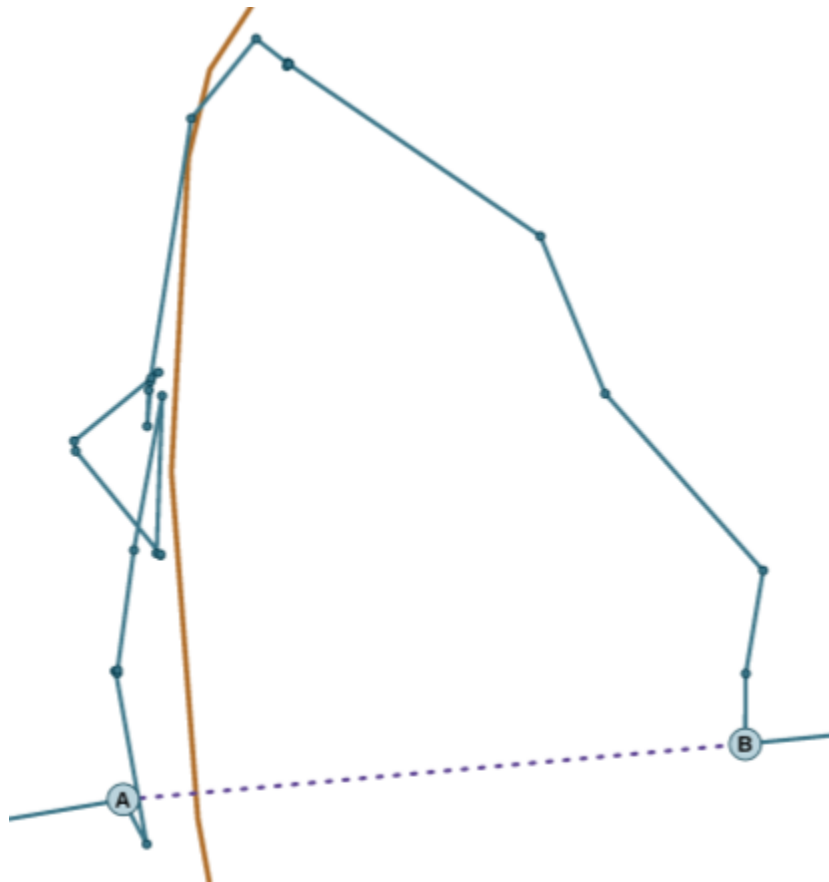


Figure 5.4. Cheetah movement track near a fence line. Brown line shows the fence. Points A and B are the start and end points respectively of the interaction. Small points are GPS locations and the blue line is the track assumed to have been taken by the cheetah, which was compared to the straight-line distance shown as a purple dotted line.

points in wildlife areas (3336 sq km). As wildlife areas tend to be larger, if individual cheetahs primarily used wildlife only areas they would be expected to cross boundaries less frequently than if they used all land-use types, which would result in a smaller impact on DEE.

For each start point 10 movement pathways were simulated. Each simulated movement pathway was 24 steps in length, equating to 24 hours of movement. The simulated movement pathways were initially parameterised using the movement metrics from the cheetah's GPS collar data which were used to determine the most appropriate distributions to use for step length and turn angle. The observed step lengths had a gamma distribution (Figure 5.6); the shape and scale parameters were extracted from the data which were then used to parameterise the step length distributions of the simulated pathways. The observed turn angle distribution showed that the frequency of angles were similar across the range except for a peak in frequency around 0°. In order to simulate this distribution, a uniform distribution was used for the turn angles -180° to -10° and 10° to 180°. A separate

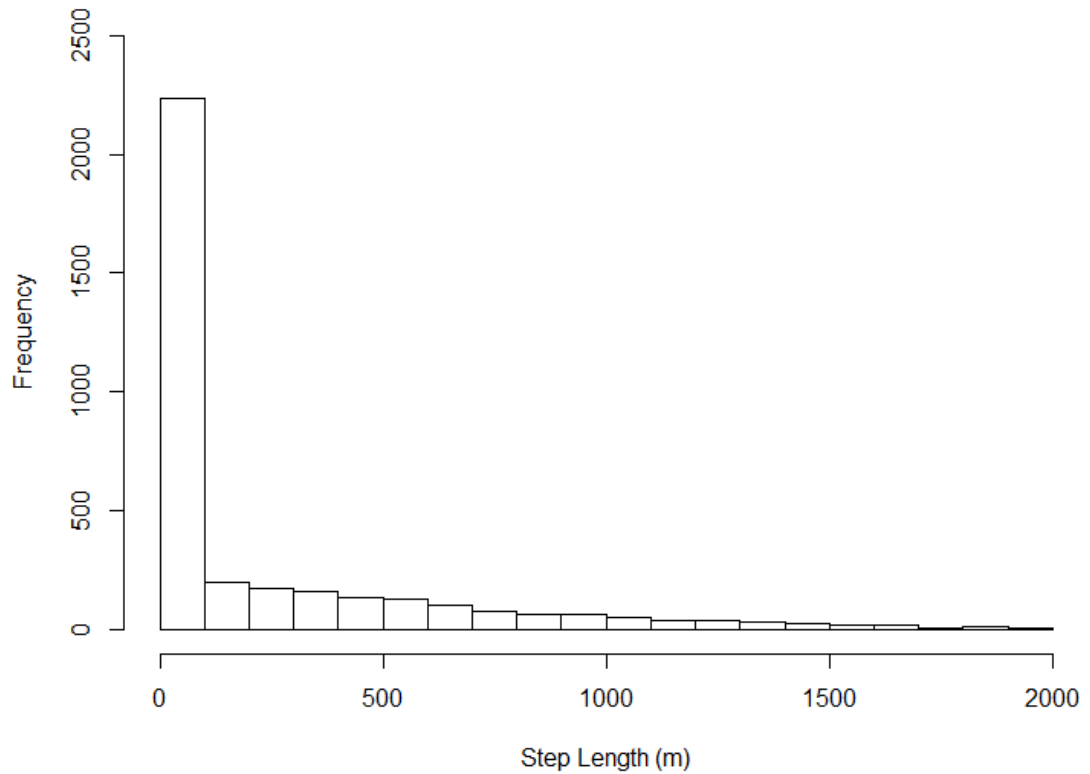


Figure 5.6. Frequency of step lengths from cheetah GPS collar data

uniform distribution was created, for -10° to 10° with a higher number of points and then the two distributions combined to simulate the shape of the observed turn angle distribution (Figure 5.5). The goodness of fit for the generated step length and turn angle distributions was compared with the distributions of the GPS collar

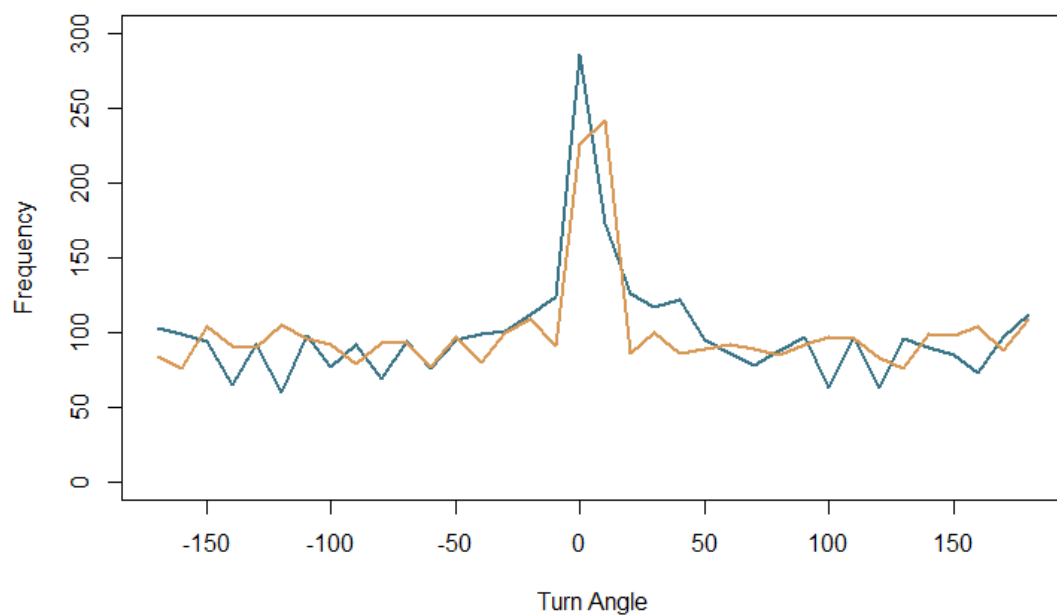


Figure 5.5. Turn angles extracted from the cheetah's GPS collar data (blue line) compared with the generated turn angle distribution (brown line)

data using Chi-square tests which showed that the simulated data were similar to the observed data (Step Length: $\chi^2 = 450$, $df = 420$, $p\text{-value} = 0.1505$; Turn Angle: $\chi^2 = 12008000$, $df = 12004000$, $p\text{-value} = 0.25$). The simulated pathways were then created using step lengths and turn angles randomly selected from the generated step length and turn angle distributions.

Simulated movement pathways were overlaid onto the property boundary layer and the number of times each pathway crossed a property boundary was counted. This gave a frequency at which a cheetah could be expected come into contact with a fence. This frequency was then multiplied by the calculated energetic cost of crossing a fence to give the projected increase in energy requirements.

A cut-off point for the maximum number of fences a cheetah could be expected to cross each day was calculated, based on the cheetah's mean daily distance travelled. This cut-off was used to prevent outliers, where movement pathways crossed an extremely large number of fences, having a disproportionate effect on the overall estimate of energy expenditure. The cut-off point was set to the number of fences which, if the cheetah crossed them, would require the cheetah to move three times its mean daily distance moved. Where a pathway crossed more than the cut-off number of boundaries, the additional boundaries were disregarded.

In order to determine the sensitivity of the model to differences in step length, the model was then rerun with varying parameters for the step length distribution

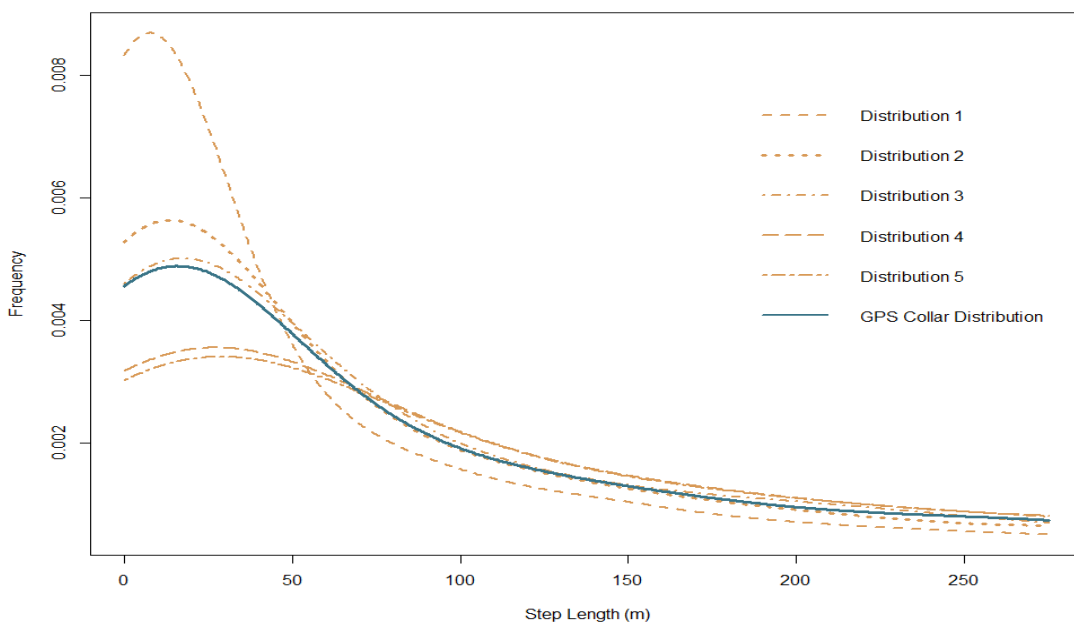


Figure 5.7. Step length distributions across the five sensitivity simulations with varying shape parameters compared to the distribution with parameters extracted from the cheetah GPS collar data

(Figure 5.7). This was done by varying the shape parameter of the gamma distribution. The step length distribution fitted to the GPS collar data had a shape parameter value of 0.36, and so the model was rerun using shape parameters of 0.25 (Distribution 1), 0.30 (Distribution 2), 0.35 (Distribution 3), 0.40 (Distribution 4) and 0.45 (Distribution 5) to evaluate how assuming longer and shorter step lengths affected the results of the simulations.

5.4. Results

5.4.1. Impact of Fence Structure on Movement Patterns

The cheetah's GPS collar recorded 3595 locations over 151 days (mean step length: 241.95m, range: 0.00m - 2702.86m) with a mean daily distance travelled of 5.80km (range: 0.12km - 13.58km). During these 151 days, there were 72 occasions when the cheetah crossed a property boundary; of these 41 were excluded due to the presence of roads and other potential movement barriers, meaning 31 boundary crossings were used in the analysis.

Only one of the fence types was found to significantly increase the distance travelled by the collared cheetah (Table 5.2). Type 1 fencing (the most permeable) did not have a significant impact on distance travelled compared to boundaries with no fences (Table 5.2). Type 2 fences caused the cheetah to significantly increase the distance (Table 5.2), with a mean additional travel distance of 2.37 km per fence

Table 5.2. Number of encounters by the cheetah with different fence types and the resulting effects on distance moved.

Post-hoc test: T-student = 3.67 at $p = 0.001$; variables in same group = no significant difference, different groups = significant difference

Boundary Type	Number of Encounters	Mean Additional Distance Moved (km)	Range of Additional Distance Moved (km)	Kruskal-Wallis Post-Hoc Test	
				Mean Rank	Group
No Fence	18	0.006	0 – 0.104	13.78	A
Type 1 Fence	6	0.000	0 – 0.000	13.00	A
Type 2 Fence	7	2.374	0 – 8.595	24.29	B

(Table 5.2). One notable occasion of the cheetah interacting with a fence is shown in Figure 5.8. In this case the cheetah crossed a fence and then moved back and forth numerous times, appearing to be trying to find a way to cross the fence again.

5.4.2. Modelling the Effect of Increased Fencing Levels on DEE

The mean additional distance moved to cross a Type 2 fence would increase the individual's energy expenditure. Using the parameters estimated by Scantlebury *et al.* (2014), each fence crossing would equate to a mean increase of 1059 kJ; which is equal to 12.0% of average cheetah DEE. If all of the 72 boundaries crossed by the collared cheetah across the 151 days of movement data had been type 2 fences then this would equate to a total increase of 76,248 kJ or 5.7% of its total energy expenditure.

When the model was run using movement parameters based on data from the cheetah GPS collar, a large percentage of the simulated 24 hour movement pathways were found to cross at least one property boundary. As the mean daily distance moved was 5.80 km, the cut-off point for the maximum number of fences a cheetah could be expected to cross was set at 5. If the cheetah crossed 5 fences it

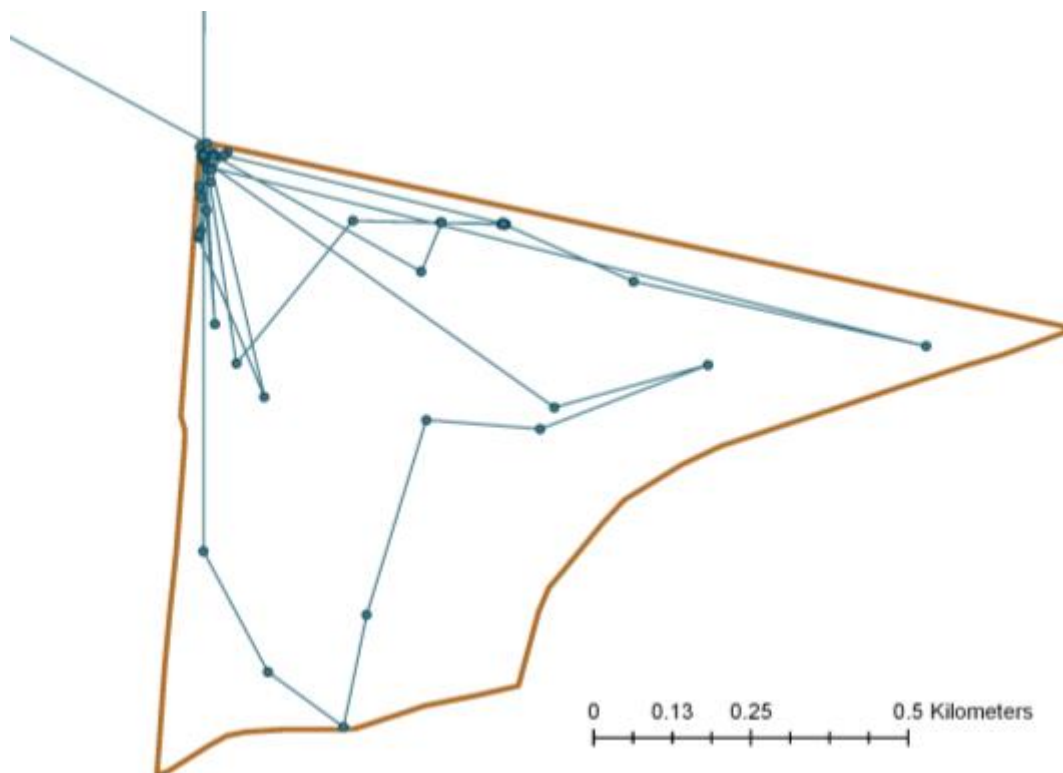


Figure 5.8. Map of the GPS collared cheetah's movements in an area with a type 2 fence. The orange line shows the position of the fence, blue dots are GPS collar locations and the blue line shows the steps between GPS locations.

would be equivalent to moving an additional 11.87km, therefore making the distance moved that day, three times the mean daily distance moved.

Of the simulated paths that began at random start points across all the properties in Laikipia, 48.0% crossed at least one boundary. Only 15.0% were projected to only cross one boundary, 33.0% of paths encountered multiple boundaries. For the simulated paths that began at random start points within wildlife areas 36.1% crossed at least one boundary. Again, a relatively small proportion of these pathways were expected to only encounter one boundary (11.5%), 24.6% crossed multiple boundaries (Table 5.3).

The projected change in an individual’s energetic expenditure was calculated using these parameters, assuming that all the property boundaries in Laikipia were changed to Type 2 fences. If an animal encountered fences at the rates estimated by the simulations, then its energy expenditure would be expected to increase by 10.9% in wildlife areas and 14.8% across the county - the equivalent of up to 54.2 extra days per year of normal daily energy expenditure (Table 5.4).

Table 5.3. Percentage of simulated pathways encountering different numbers of boundaries with start points randomly generated in either all properties in Laikipia or wildlife areas only

Property Type	Number of Boundaries Crossed by Simulated Movement Pathways					
	None	One	Two	Three	Four	Five or More
All Properties	52.0	15.0	11.9	7.5	5.5	8.1
Wildlife Areas	63.9	11.5	9.4	5.5	4.0	5.7

When the model was rerun with varying parameters for step length, shorter step lengths resulted in shorter overall path lengths and a lower proportion of paths encountering property boundaries. Nonetheless, even the simulated pathways using the distribution with the shortest mean step length (Distribution 1; mean: 169.0m) still showed an increase in DEE of 11.1% for those beginning across the county, and 7.9% for those starting in wildlife areas. The simulated pathways using the distribution with the longest mean step length (Distribution 5; mean 303.4m) showed a much larger increase in DEE of 18.1% across the county or 13.5% in wildlife areas.

Table 5.4. Differences in energy expenditure for different step length distributions

	Mean Step Length (m)	Property Type	Difference in Energy Expenditure (%)	Equivalent Number of Days' Energetic Expenditure per Year
GPS Collar Distribution	241.3	All	14.8	54.2
		Wildlife	10.9	39.7
Distribution 1 shape = 0.25	169.0	All	11.1	40.5
		Wildlife	7.9	28.8
Distribution 2 shape = 0.30	218.4	All	12.8	46.6
		Wildlife	9.3	33.8
Distribution 3 shape = 0.35	236.0	All	14.6	53.2
		Wildlife	10.9	39.6
Distribution 4 shape = 0.40	284.9	All	16.3	59.4
		Wildlife	12.1	44.2
Distribution 5 shape = 0.45	303.3	All	18.1	66.0
		Wildlife	13.5	49.2

5.5. Discussion

The results presented here showed a significant impact of fence structure on the movement patterns of the collared cheetah, suggesting that impermeable boundary fences have a marked impact on animal movement patterns. Fences that were designed to be permeable to animal movement were not associated with a significant increase in the distance travelled by the cheetah (Hypothesis A). The distance moved when crossing a fence that was designed to be impermeable to animal movement was calculated to be equivalent to 12.0% of cheetah daily energetic expenditure (Hypothesis B). If all of the property boundaries in Laikipia County were fenced using this type of fence then results from simulations suggest that this could result in a large increase in cheetah DEE, of up to 14.8% per year.

If a large proportion of the boundaries in Laikipia had Type 2 fencing then it is likely that this would place substantial additional energetic demands on the cheetah population. The simulated movement pathways which had start points across all of Laikipia encountered at least one property boundary on 48% of days, and those starting in wildlife areas on 35.4%. These encounters were modelled to result in a potential increase in DEE of 14.8% and 10.9% respectively.

The simulation results suggest increases in DEE that are substantially higher than the estimated 5.7% increase based on observations of the 72 boundaries crossed by the collared cheetah across 151 days of data. There may be several factors which have influenced these differences. Firstly, only successful boundary crossings were included in this analysis, incidents where the cheetah encountered a Type 2 fence but did not cross it were not included. This was because where a cheetah encountered but did not cross a boundary it was not possible to determine, (A) if the cheetah was actually trying to cross and (B) if it was, there was no base line for comparison and so additional distance travelled in order to cross the boundary could not be calculated. However, for the simulated pathways, every encounter with a boundary was assumed to result in a successful crossing. Secondly, the collared cheetah rarely left wildlife areas (3002 locations in wildlife areas vs 593 elsewhere) whereas, although one set of simulations used only start points in wildlife areas, the simulated movement pathways were not restricted to these areas and so some pathways moved out into other land-uses. The simulations were not restricted to wildlife only areas because, although the collared cheetah rarely ventured outside of these areas, other members of the cheetah

population do make use of them (Pers. Obs.). Finally, the amount of time taken to cross boundaries may have affected the results. The maximum number of boundaries used for the calculations was 5, equivalent to the cheetah needing to triple its mean daily travel distance in order to cross them all. However, these calculations only took distance into account, not time. Thus it may be, when a cheetah has to make substantial diversions in practice, it runs out of time before it is able to cross this many barriers each day.

It should be noted that several of the crossings of the Type 2 fences did not occur at purposefully constructed crossing points. These fences are designed to restrict the movements of all terrestrial wildlife species and so the cheetah was likely crossing the fences in areas where the fences had been damaged and there were holes large enough for the cheetah to pass through (Figure 5.9). Therefore the permeability of such fences, and the distance animals have to travel to traverse them, is likely to be highly dependent on the level of fence maintenance. If Type 2 fences were perfectly maintained, then the permeability of these fences would decrease further and the distance travelled by an animal to cross would increase, thereby further exacerbating the fences' impact on energetic expenditure. In addition, as discussed above, the results presented here only take into account successful crossings. This could have an important impact if the area of land on the other side of the fence was one of high quality habitat, that the cheetah was therefore unable to access, thus limiting its ability to balance its increased energy expenditure.

Fencing might prompt an additional increase in energetic costs by increasing predator and competitor density and/or reduce access to competition refuges, thereby increasing the risk of kleptoparasitism. Scantlebury *et al.* (2014) showed that cheetahs were energetically resilient to kleptoparasitism, with a loss of 25% of



Figure 5.9. Photograph of a hole found in a Type 2 Fence (photo: Rosie Woodroffe)

kills resulting in a 12% increase in daily energy expenditure. However, an increase in fencing, which increases foraging travel while reducing access to competition refuges for cheetahs, may increase both kleptoparasitism rates and travel distances, which may prove to be unsustainable. Hyaenas and lions usually live at higher population densities inside protected areas, to which Laikipia's wildlife areas are analogous, than they do in community lands with higher human densities (Dolrenry *et al.*, 2014; Bohm & Höner, 2014); lion population densities are particularly high in fenced reserves (Packer *et al.*, 2013b). An increase in fencing may result in cheetahs encountering lions and hyaenas more often, thereby increasing the risk of kleptoparasitism of cheetah kills and putting individuals at higher risk of predation. Alternatively, cheetahs may respond by avoiding some of the areas with higher lion and hyaena density (Durant, 2000), which are likely to be the areas with higher prey densities and lower human densities.

This study has evaluated the potential impacts of fencing on animal movement patterns and energetics using cheetahs in Laikipia County, Kenya as a case study. It is likely that these results would be applicable both to other carnivore species, and to other human-dominated landscapes. An important finding is that the type of fencing is key to the impact it is likely to have on movement patterns. In this case, fences that are targeted at restricting the movements of rhinos seem to be successful at not impacting the movement patterns of a non-target species. However, the results presented here are based on the movement patterns of only one individual which, although its ranging patterns in terms of overall distance covered were broadly similar to studies elsewhere, may not be typical. However, this approach, based on step length and turn angle, can be easily adapted to a more representative dataset as it becomes available. The general principle, that fences can incur additional travel costs, and that this will have impacts on energetic expenditure still stands, although the exact impact may change depending on more data, and on the local ecological and environmental circumstances.

Within Kenya there have been increases in the number of properties being fenced, including in important wildlife areas such as the Mara ecosystem (Evans & Adams, 2016; Løvschal *et al.*, 2017), thus this study provides a timely insight into how such fencing might impact populations. As fences have been shown to affect different species to different extents, with some species observed to be better at crossing fences than others (Cozzi *et al.*, 2013), it is likely that fences will affect individual species differently and therefore may change species distribution within a habitat.

This can carry through to ecosystem effects where some species are so negatively affected by increases in fencing within their landscape that their carrying capacity is reduced or even that populations collapse as a result (Boone & Hobbs, 2004; Jaeger & Fahrig, 2004; Whyte, 1988). This can particularly be the case where fencing prevents animals from accessing important resources such as water or seasonal food sources (Berry, 1997; Hayward & Somers, 2012; Whyte, 1988). Whilst this study suggests that some fences may not have a detectable effect on non-target species, other fences have substantial impacts. It also adds to the concerns that have been raised elsewhere about the impacts of fencing areas in an attempt to prevent movements of all wildlife species. By restricting movements of species, particularly wide-ranging ones, it may render populations non-viable.

The energetics-based approach used here is not only applicable to the impact of fences but also to other potential movement barriers, and could be used to increase the efficacy of mitigation interventions. By incorporating an energetics-based approach to the design of potential movement barriers such as fences and roads, it may be possible to calculate an optimal density of crossing points to enable the passage of threatened species. Using a hypothetical example, if a maximum acceptable increase in DEE was estimated to be 10%, then for a species with a DEE of 10,000kj which was estimated to expend 500kj per kilometre of travel, having a fence gap at least every 2km would keep additional daily energy expenditure incurred by travel to fence gaps to within 10%. Using such an approach could not only be used to determine the required density of fence gaps but also for mitigation structures for other linear movement barriers for example under- or over-passes for roads and railways.

Fences are often erected alongside highways in an attempt to reduce roadkill and to channel animals towards purpose-built crossing structures (Clevenger *et al.*, 2001; Clevenger & Waltho, 2000; Olsson & Widen, 2008). The efficacy of crossing structures has been widely investigated with respect to their design and the characteristics of their surrounding habitat (Cain *et al.*, 2003; Clevenger & Waltho, 2005, 2000; Foster & Humphrey, 1995), as well as looking at the impact of crossing structures on animal movement behaviour (Olsson & Widen, 2008). Incorporating an evaluation of the impacts of movement barriers and the mitigation projects associated with them on animals' energetic expenditure is likely to increase understanding of how animals and populations are affected by these structures, and could then feed into more efficient future planning.



Plate 7. An African wild dog

Chapter 6.

The Effect of Wildlife Fences on African Wild Dog Movement Patterns and Demography

6.1. Abstract

Fences restrict animal movement across a landscape, which may have important implications for the long-term survival of wildlife populations. The African wild dog is an extremely wide-ranging species and likely to be among the most affected by a loss of landscape connectivity as a result of fencing. Laikipia County in northern Kenya is a globally important stronghold for the species, however new wildlife fences are increasingly being built in the area. Wildlife fences are considered an important tool in the conservation of many species, including threatened species such as black and white rhinoceros. Whilst it is generally acknowledged that fences may have important impacts on connectivity and animal movement patterns, there are scant studies which have been able to show direct demographic effects on populations caused by the presence of fences. Using a long-term dataset from a free-ranging wild dog population, the effect of fences' structure and design on the ability of animals to cross them was evaluated. The efficacy of purpose-built gaps, which are intended to maintain connectivity, was also investigated and examples of how wildlife fences have impacted wild dog demography within the study population are presented. This study suggests that the design of a fence has important demographic implications, with the least permeable of the fences evaluated having clear negative impacts on wild dog packs living in the area. These results also suggest that by restricting the movement of packs, there may have been instances where wildlife fences have contributed to instances of human-carnivore conflict. Based on these findings, careful evaluation should be given to the necessity of erecting fences. Where fencing is unavoidable, projects should use the most permeable fencing structures possible, to minimise impacts on wide-ranging wildlife. Ecological impact assessments should be undertaken for all large scale fencing interventions.

6.2. Introduction

6.2.1. Fences

Fencing is a key tool in conservation which has been widely used across the globe (Hayward & Somers, 2012). Some regions have made greater use of fences than others; for example fences have been used extensively in Australia and New Zealand to limit the effects of invasive species in protected areas (Hayward & Kerley, 2009). Across Africa there have been differing attitudes towards fencing resulting in regional differences in the extent of use of fences in conservation contexts. Historically, southern Africa has tended to make the greatest use of fences (Hayward & Kerley, 2009). However, in recent years there has been a push towards an increased use of fencing in other regions as well (Durant *et al.*, 2015b; Gadd, 2012).

Fences are often used in an attempt to reduce the incidence of human-wildlife conflict (Woodroffe *et al.*, 2014). Across Africa there are many local communities for whom agriculture and livestock farming are their major sources of income (World Bank, 2007). Communities close to areas with high densities of wildlife can experience serious negative impacts of wildlife, for example elephants may raid crop fields or large carnivores may attack and kill livestock (Balmford & Whitten, 2003; Evans & Adams, 2016; Woodroffe *et al.*, 2005b). The people most at risk from these types of conflict are often among the most vulnerable and marginalised communities (Balmford & Whitten, 2003), and even relatively low levels of conflict may have devastating impacts on the households concerned. Fences have been used in many areas with the intention of reducing contact between local communities and wildlife in order to reduce conflict. In such areas, fences are typically built around areas with high wildlife densities, reducing the ability of wild animals to venture into community lands where conflict may occur (Somers & Hayward, 2012). The efficacy of this approach has been questioned, with evidence that in some circumstances fences can increase conflict rather than reduce it (Gadd, 2012). Where fences are used to try to reduce conflict, a high level of maintenance is vital to ensure that fences remain an impermeable barrier, however this has high financial and logistical implications (Kesch *et al.*, 2014).

Fences have also been used as a tool to try to reduce incidents of illegal hunting (Woodroffe *et al.*, 2014). This is through a combination of keeping wildlife in certain

areas where they can be more closely monitored and protected, and attempting to prevent potential hunters from accessing those areas. However, although the reaction to an increase in illegal hunting can be to increase fencing, there is evidence that the efficacy of such a strategy may be low; for example, fencing can act as a readily-available and cheap supply of wire that can be repurposed to make snares for bush-meat hunting (Becker *et al.*, 2013; Gadd, 2012). In addition, whilst it is certainly possible to build fences that prevent wildlife movements, it is almost impossible to build and maintain a fence to a sufficient standard so as to prevent determined humans from crossing it (Durant *et al.*, 2015b).

For conservation purposes, using fences has been recommended only as a last resort (Woodroffe *et al.*, 2014), yet most fences are not built with conservation as a central goal. Fences erected for other reasons, such as boundary demarcation, can also have important effects on the wildlife found in a region (Trouwborst *et al.*, 2016). The reduction of permeability across fenced boundaries for native wildlife has been observed, for example across Eurasia and in the border region between the USA and Mexico (McCallum *et al.*, 2014). The serious negative effects on local wildlife resulting from these fences are reflected in the warnings surrounding the ecological effects of the proposed large scale fencing across Europe in response to the refugee crisis (Linnell *et al.*, 2016) or the proposed US-Mexico border wall (Owens, 2016). Any new fence is likely to impact the wildlife populations in its immediate area because fences act as movement barriers (Linnell *et al.*, 2016). This can have long-term consequences for wildlife populations by reducing the level of connectivity across the landscape (Harris *et al.*, 2009).

6.2.2. Connectivity

The risks of landscape-scale connectivity loss are well known (Epps *et al.*, 2005; Løvschal *et al.*, 2017) and habitat loss and fragmentation are recognised as the leading threats to global biodiversity. Movement barriers, such as fences, are an important cause of fragmentation (Clevenger & Waltho, 2000). With respect to the direct effects of fences on populations of wildlife, there are many reports in the literature of animal mortalities as a direct result of individuals coming into contact with fences (Gadd, 2012); the differential ability of species to cross various movement barriers has also received some attention (Cozzi *et al.*, 2013). However, whilst there are numerous examples where fences have restricted access to vital resources, thereby negatively affecting wild populations, the impact of movement

barriers on individual animal movements, and how that affects intraspecific interactions, are poorly understood. Fence structure is likely to have a significant impact on how easily animals are able to cross them (see Chapter 5), but even fences which animals can traverse could have impacts on the wild populations.

In an attempt to mitigate the impact fences have on landscape connectivity, purpose-built gaps are sometimes included in the structure of a fence (Dupuis-Désormeaux *et al.*, 2016). These gaps are usually built in such a way as to permit the passage of some species through the fence, whilst still preventing the movement of other species, such as rhino (Dupuis-Désormeaux *et al.*, 2016). Whilst the presence of such gaps may mean that the fences are more permeable, if there are only a small number of gaps built into the fence then animals may have to move a considerable additional distance in order to cross. The potential energetic impacts of increasing the distance animals have to travel in order to traverse a fence and move across a landscape are explored in Chapter 5. Fence gaps may also have important impacts on the movement of wildlife species as they are likely to funnel wildlife into certain areas (Little *et al.*, 2002), particularly if there are only a small number of gaps built into the fence. This then may impact on species distributions across a landscape (Dupuis-Desormeaux *et al.*, 2016).

Wildlife mobility is particularly important in dryland ecosystems as in these arid landscapes resources are limited and highly variable both temporally and spatially. Historically, people and wildlife have relied on being able to move across arid landscapes in order to access resources when they become available, however movement barriers such as fences make this increasingly difficult. Durant *et al.* (2015) identified six key areas where the scientific knowledge of the effects of fencing in drylands ecosystems was lacking. This study investigates some of the impacts of fencing, focussing on research areas identified by Durant *et al.* (2015) including the effects of fencing on connectivity and the importance of connectivity to the goals of fenced reserves and ecosystem function, in particular relating to how fences affect wildlife movements.

6.2.3. African Wild Dogs

The African wild dog is an extremely wide-ranging species, currently classified by the IUCN Red List as Endangered (Fuller & Kat, 1990; Woodroffe & Sillero-Zubiri, 2012). The species is threatened by habitat loss and fragmentation; it is estimated

to have been extirpated from 93% of its former range (IUCN/SSC, 2015, 2012, 2007).

Fencing has the potential to affect wild dogs in a number of ways. Due to their wide-ranging nature, wild dogs need access to large, contiguous areas of wildlife-friendly habitat in order to persist in an area. Increases in fencing are therefore likely to negatively affect wild dogs because where fences are built to be impermeable, they will effectively split the landscape into smaller fragments and prevent wild dogs moving through all of the habitat that was once available to them. Where there are increases in fencing wild dogs may suffer from increased interspecific competition and predation. Wild dogs are vulnerable to the effects of competition and predation by other larger predators such as lions and hyaenas (Creel & Creel, 1996; Mills & Gorman, 1997). Due to their much smaller body size, wild dogs cannot compete directly with these larger predators and so rely on being able to move into areas where the densities of lions and hyaenas are lower (Broekhuis *et al.*, 2013; Swanson *et al.*, 2014). Lions and hyaenas are both found at higher densities within protected areas than in unprotected areas (Dolrenry *et al.*, 2014; Bohm & Höner, 2014) and lions are found at particularly high densities in fenced reserves (Packer *et al.*, 2013a). Wild dogs are therefore likely to be dependent on being able to move across the extent of their landscapes in order to access all of the resources they need, while avoiding their primary competitors, lions and spotted hyaenas (Broekhuis *et al.*, 2013; Swanson *et al.*, 2014); an ability which may be jeopardised by the erection of fences.

This study explores the impacts of different fence designs on animal movement using long-term GPS and VHF collar datasets from a free-ranging population of endangered African wild dogs in Laikipia, Kenya. The following hypotheses are investigated:

6.2.4. Hypotheses and Predictions

Hypothesis A: Fence structure will affect wild dog movements

Prediction A.1: Wild dogs' ability to cross a fence line will be influenced by the design of the fence

Hypothesis B: Purpose-built fence gaps are used by wild dogs to move in and out of fenced properties

Prediction B.1: Wild dogs rely on purpose-built gaps to cross low permeability fences

Prediction B.2: Fence gaps affect wild dog spatial distribution

6.3. Methods

6.3.1. Study Area

The study area falls within Laikipia County in northern Kenya. It is a dryland landscape with land-uses including traditional pastoralism, commercial livestock ranching, subsistence agriculture, large-scale farming, and tourism (Ulrich *et al.*, 2012). Laikipia supports the second highest densities of wildlife found in Kenya, with only the Maasai Mara having higher densities (Kinnaird & O'Brien, 2012). The landscape is divided into privately and community owned properties which range in size from less than 1 sq km to 386 sq km. As well as having high densities of wildlife, Laikipia is an important area for some of Kenya's most threatened species, including the African wild dog. Although historically present, wild dogs disappeared from Laikipia in the 1980s (Woodroffe, 2011). The area was naturally recolonised by wild dogs in the late 1990s, with the first den for the new resident population in 2001 (Woodroffe, 2011). Since then the population has grown dramatically to become one of the largest in the world, making it of global conservation significance.

The amount of fencing in Laikipia has increased in recent decades; many of the properties in Laikipia are fenced to demarcate their boundaries (Evans & Adams, 2016; Yurco, 2017) but there are also large-scale fencing projects like the West Laikipia Fence (Evans & Adams, 2016). In addition, in Kenya there are management guidelines that properties which have rhino on their land should be fenced in order to better protect the animals (Kenya Wildlife Service, 2012). Fencing is also used across Laikipia to try to reduce human-wildlife conflict; for which there is support within some local pastoralist communities (Blair & Meredith, 2017).

This study focuses on the effects of the fences of two of the most important wildlife properties in Laikipia, referred to here as Property A and Property B. These properties employ three types of fencing which are described in Figure 6.1.

Property A is approximately 225 sq km in size and is split into two sections – on the western side is the main ranch which is approximately 78% of the property's total area. This section supports a wide variety of wildlife and is also where the property's ranching and businesses are based. This main ranch (area approximately 175 sq km) is fenced with a Type A1 fence (Figure 6.1a), 55.9 km in length, which is an electrified fence intended to restrict the movement of megaherbivores. The main ranch fence has five purpose-built gaps to enable the passage of most wildlife species; although the gaps are designed in such a way as to prevent rhinos moving off the property (see Figure 6.2 for an example fence gap). The eastern side of the property (hereafter the east ranch) is a private reserve and is set aside for wildlife (area approximately 50 sq km). It is separated from the main ranch by a public road and is surrounded by a Type A2 fence (Figure 6.1b), 31.9 km in length. This fence is also electrified but is intended as a barrier to medium and large bodied species as well as megaherbivores. When first erected, the east ranch fence had no gaps built into it; however, in 2013 a fence gap was added between the east and main ranches to enable the passage of wildlife between the two (Figure 6.2). However, using the gap requires wildlife to cross the public road which separates the two sides of the property. Of the properties that border Property A, those to the west and east are wildlife conservancies; the properties to the north and south are cattle ranches.

Property B is approximately 340 sq km in size and has a Type B fence (Figure 6.1c). The fence is 141.6 km in length, and is a large electrified fence which is designed to restrict the movement of medium and large bodied mammals. It was erected in 2006, at which time three gaps were built into it which are clustered in the north-western corner to allow the passage of wildlife in and out of the property (Figure 6.2). Of the properties that border Property B, those to the north are wildlife conservancies; the properties to the south, west and east are a mixture of wheat farms and community land.

6.3.2. Wild Dog Movement Data

GPS collars were used to investigate the effects of fencing on wild dog movement behaviour. Wild dogs were immobilised and collared as described in Woodroffe (2010). This study uses data collected between 2004 and 2017. During this time 27 wild dogs from 15 packs were fitted with GPS collars (Televilt & Vectronic Aerospace). Collars were programmed to record the wild dog's location between 6

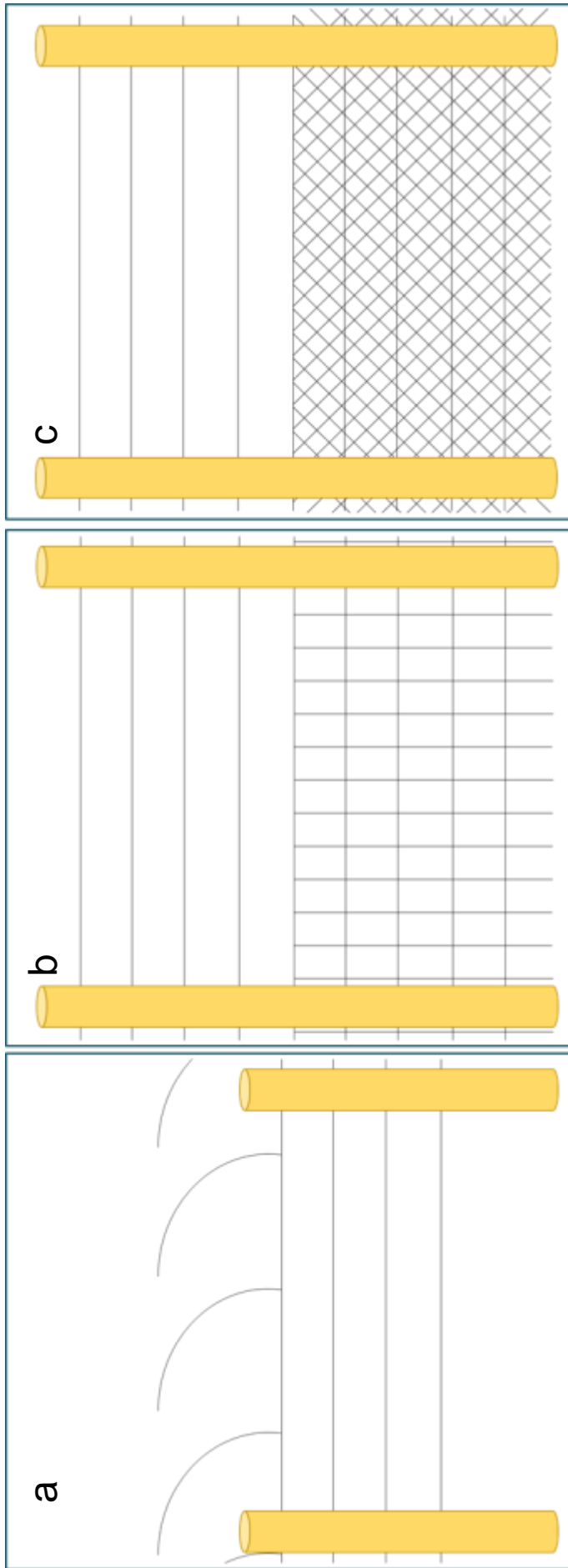


Figure 6.1. Diagrams showing different fence types. Panel a shows a Type A1 fence which surrounds Property A's main ranch. Panel b shows a Type A2 fence which surrounds Property A's east ranch. Panel c shows a Type B fence which surrounds Property B.

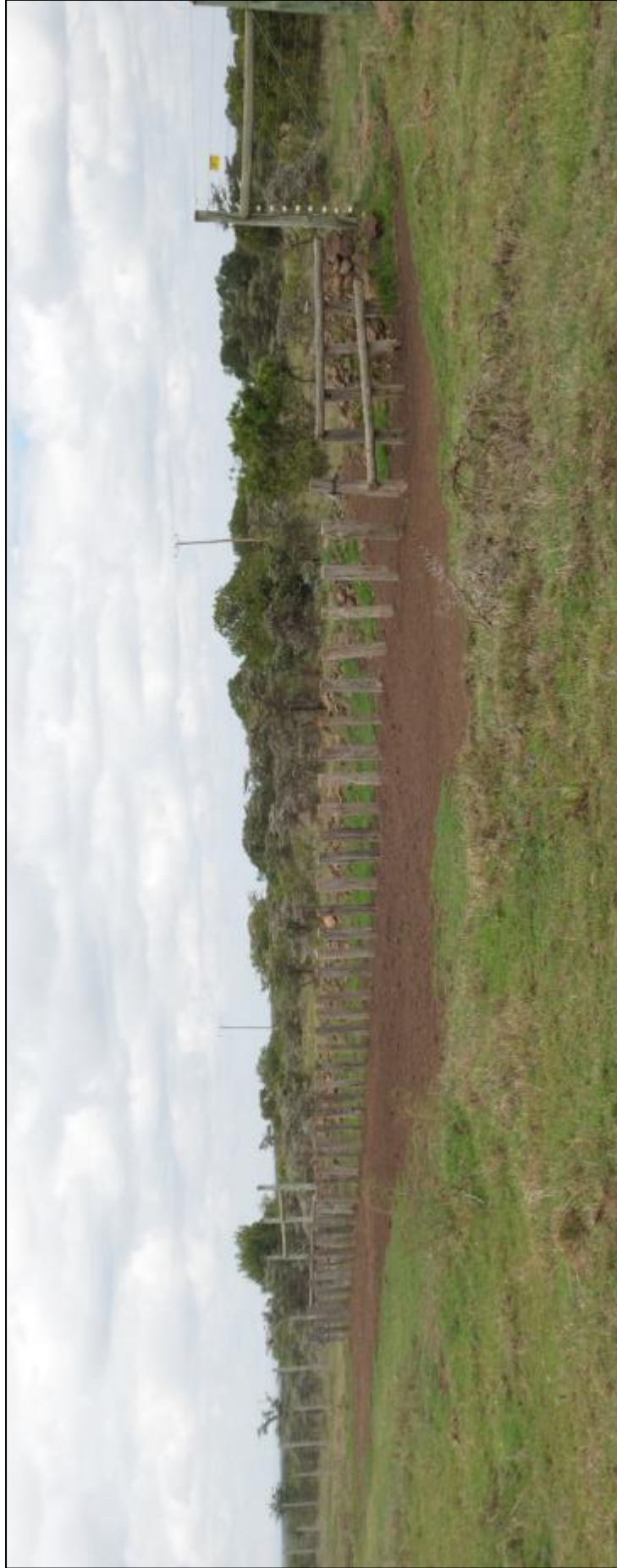


Figure 6.2. Example of a fence gap (from Property B) designed to restrict rhino movement but allow other species to cross the fence line

and 13 times per day. Although some packs had multiple individuals that were collared, they were collared at different times so no pack had two individuals fitted with GPS collars concurrently. Wild dogs are a highly crepuscular species (Woodroffe *et al.*, 2017), most of their activity and movements occur at dawn and dusk and so the collars were programmed to collect highest resolution data at these times. Of the collared wild dogs, 13 individuals from 9 packs interacted with at least one of the fences surrounding Properties A and B during the time they were fitted with GPS collars.

6.3.3. *The Effect of Fence Structure on Wild Dog Movement*

Wild dog GPS locations were plotted using QGIS (QGIS Development Team, 2012) and the step lengths (defined as the straight-line distance between a GPS location and the subsequent location, Figure 6.3) for each wild dog's movement pathway were calculated using the *movement.pathmetrics* tool in *Geospatial Modelling Environment* (Beyer, 2010). The timings at which locations were recorded varied across the years; the shortest time period varied in length from 30 minutes to 120 minutes. For each wild dog, the mean step length for the shortest time interval between GPS locations was calculated, there was no correlation between the length of time and mean step length for that time period (Pearson's product-moment correlation: $t = 0.80$, $df = 11$, $p = 0.44$). Buffers were drawn around each fence for each wild dog; the buffer width used was equal to that individual's shortest time period, mean step length (range: 0.42 – 2.02 km; mean step length across all 13 individuals: 1.06 km).

The number of times that each wild dog successfully crossed a fence was counted. An individual was considered to have crossed a fence when a GPS location was recorded on one side of a fence and the subsequent location was on the other side of the fence. Each record was checked to ensure it was a true crossing event and could not be a result of the individual circumnavigating the fence (Figure 6.4). The number of steps within each wild dog's fence line buffer was also counted. To calculate the percentage of successful crossings, the number of fence crossings was divided by the number of steps within the fence line buffer. This was done for every wild dog at each of the fences that it encountered (Figure 6.5).

Simulated fence lines were created in order to generate a baseline success rate for fence crossings, i.e. the expected crossing rate if each fence did not present a movement barrier. Three fences were simulated which were located close to the

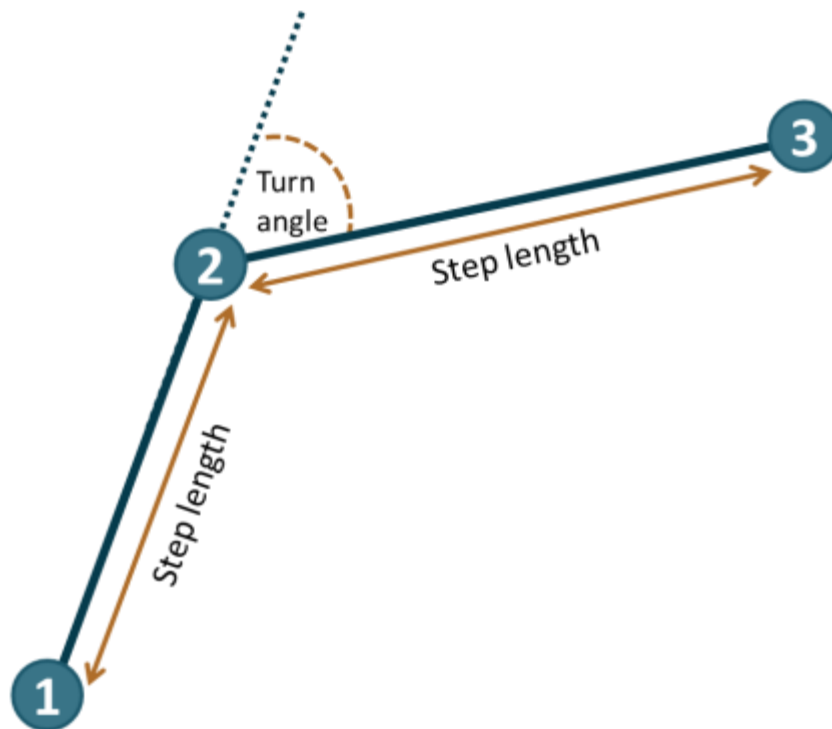


Figure 6.3. Diagram showing what is meant by step length. Dark blue circles represent GPS locations recorded by a GPS collar. Black lines are straight lines drawn between locations representing "steps".

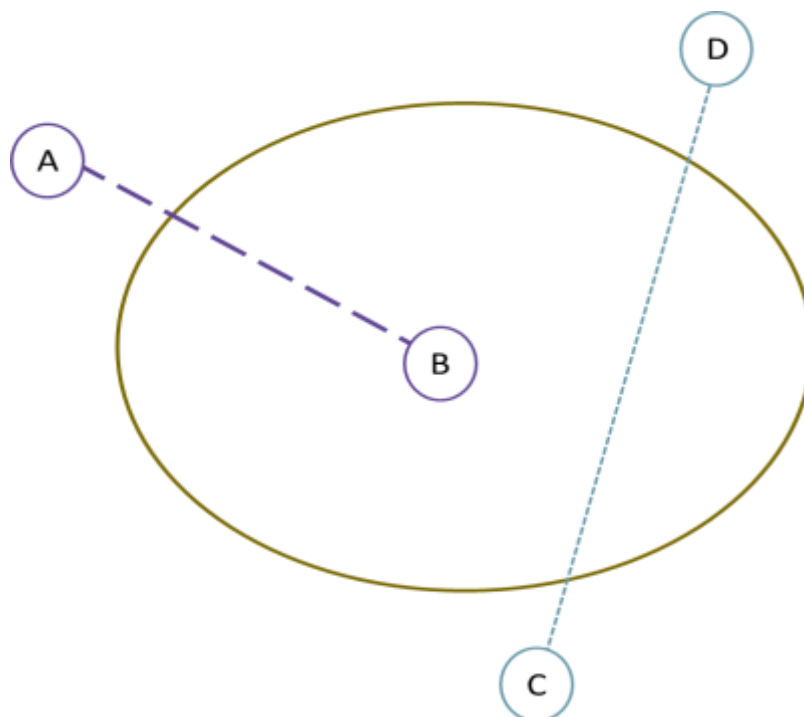


Figure 6.4. A GPS collared individual was considered to have crossed a fence when a location and its subsequent location were on opposite sides of the fence as shown by the purple dashed line between points A and B. The blue line would not have been counted as a crossing event as locations C and D are both on the same side of the fence and the individual is likely to have gone around the fence rather than crossing it.

real fences; one for the main ranch on Property A, one for the east ranch on Property A, and one for Property B. Fences were simulated by randomly generating two points at least 10km apart and joining them with a line resulting in simulated fences which were randomly orientated in areas close, and analogous, to the real fences but where no fences, or other potential movement barrier (e.g., rivers, roads) actually existed. The same process as described above for the real fences was followed to establish a baseline measurement of crossing success.

To analyse the effect of fence structure on wild dog fence crossing success these data were analysed using a generalised linear mixed model (GLMM) with binomial distribution. Fence crossing success used as a binary response variable (crossed successfully vs failed to cross) was compared with fence type (Type A1: Property A main ranch; Type A2: Property A east ranch; Type B: Property B; or Simulated) with individual wild dog identity as a random variable.

6.3.4. Use of Purpose-Built Fence Gaps by Wild Dogs

To determine whether wild dogs use fence gaps to cross low permeability fences, the proportion of successful crossings which occurred in the vicinity of the gaps was calculated. Steps which crossed the fence and had at least part of their length

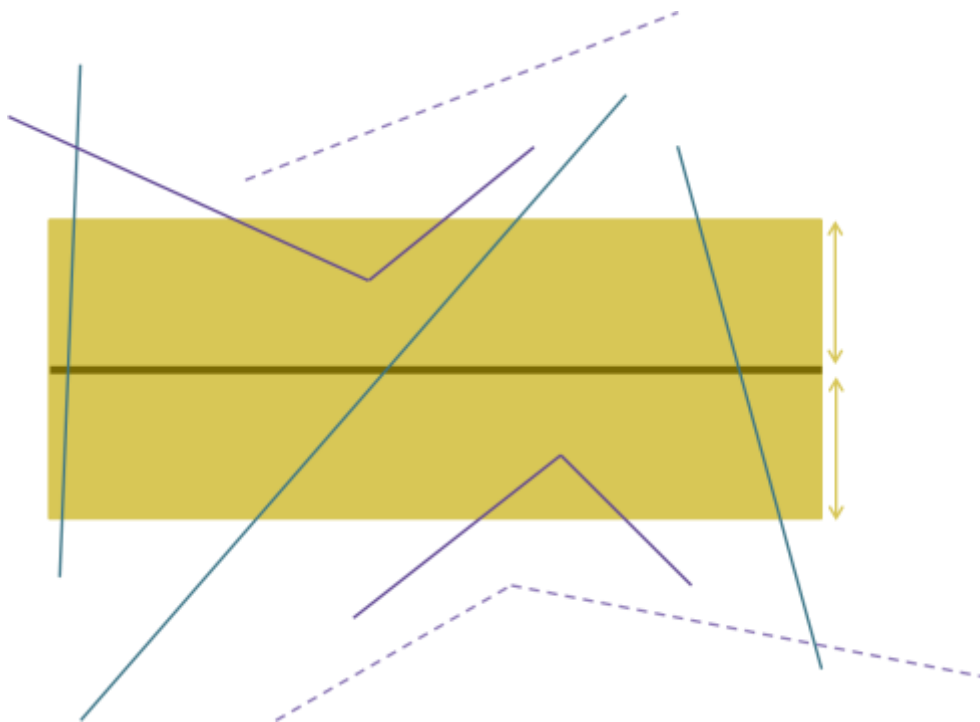


Figure 6.5. Deriving the fence crossing success ratio. Dark brown line represents the fence, with the yellow shading showing the buffer distance, equal to the individual wild dog's mean step length (yellow arrows). Blue lines show successful crosses, purple solid lines are steps within the buffer and purple dashed lines are outside of the buffer distance and so not used in the analysis.

within 1 km of a fence gap location (hereafter referred to as the fence gap buffer) were assumed to have made use of the gap. A buffer distance of 1 km was chosen as it was equivalent to the mean step length 1.06 km for the 13 wild dogs, as calculated above. The number of crossings in the fence gap buffer was then compared with the expected number of crossings using a Chi-squared test. The length of fence within the gap buffer was substantially shorter than the length of the rest of the fence so a 2x1 contingency table was used; the expected number of crossings was calculated as the total number of fence crossings multiplied by the proportion of the fence which fell within the gap buffer.

For properties where wild dogs were found to use fence gaps to cross low permeability fences, the impact of the fence gaps on the spatial distribution of wild dog locations was investigated. In order to capture the effects of the gaps on the wild dogs' distribution, beyond their immediate passage through the gaps, a 10km wide buffer was created around the property's fence line and wild dog locations within this buffer used for the analysis. Data from denning wild dog packs were not included in the analysis because during denning periods wild dog movement patterns are atypically restricted. Using only locations recorded at 13:00 (n=304 from 3 individuals), when the wild dogs were likely to be resting and therefore not actually in the process of travelling through the fence gaps, the distance from each location to the nearest gap was calculated. An equal number (n=304) of random points, were generated within the 10km buffer for comparison, and the distance from each of these random points to their nearest gap was also calculated. The distances between the wild dog locations and the fence gaps were compared with those of the random points using a Welch two sample t-test.

6.3.5. Effects of Fences on Wild Dog Demography

To provide insight into the impacts of fences on wild dog demography, examples of interactions between wild dogs and fences in Laikipia are reported. The wild dog population of Laikipia has been continually monitored since 2001. Each study pack had at least one individual fitted with a VHF or GPS collar and they were regularly tracked and observed. The frequency that packs were visited varied due to logistical constraints; however packs were usually checked at least once every 1-4 weeks. During observations, data were collected about pack size and behaviour, as well as about the status of the individual pack members, resulting in a long-term demographic dataset (Woodroffe, 2010). Although observed interactions with

fences are rare, since 2001 several incidents have been observed which have had tangible impacts on wild dog movement and pack dynamics. These are collated and described to provide context for the quantitative results.

6.4. Results

6.4.1. The Effect of Fence Structure on Wild Dog Movement

The percentage of wild dog steps which resulted in fence crossings varied significantly with fence type. When analysing the number of steps (n=1234) within the wild dogs' step length buffers around the simulated fence lines, 17.8% of steps resulted in a crossing. The crossing frequency of the Property A main ranch fence was calculated to be 18.0% and was not significantly different from the success rate of the simulated fences (Table 6.1; Type A1 fence). The east ranch fence had a crossing success of 13.7%, significantly lower than the crossing rate for the simulated fences (Table 6.1; Type A2 fence). However, it was the Property B fence that presented the greatest movement barrier, in this case only 2.9% of the steps within the buffer area resulted in a successful crossing of the fence (Table 6.1; Type B fence).

Table 6.1. Results of GLMM of fence structure on wild dog fence crossing ability

Variable		Coefficient	Standard Error	P-value	Sig
Fence type	Simulated				
	Type A1	0.059	0.09	0.52	ns
	Type A2	-0.36	0.12	0.003	**
	Type B	-2.10	0.17	<0.001	***
Dog ID					ns

6.4.2. Use of Purpose-Built Fence Gaps by Wild Dogs

As discussed above, two of the fences investigated (Property A's east ranch fence – and Property B's fence) were found to be significant movement barriers; the extent to which wild dogs use the fence gaps built into these fences was therefore evaluated.

The east ranch fence (Type A2) is 31.9 km in length with 2 gaps, therefore 12.6% of the fence is within 1 km of a gap. Of the successful crossings of the east ranch fence 16.1% were in the vicinity of one of the gaps. The number of crossings per km within the fence gap buffer was 29, which was not significantly different from that expected at random, which was calculated to be 22.21 ($p = 0.34$; Table 6.2).

Table 6.2. Use of purpose-built fence gaps by wild dogs. The expected number of crossings was calculated as the total number of fence crossings multiplied by the proportion of the fence line which fell within the fence gap buffer

Fence	Crossings in fence gap buffer	Expected number of crossings	χ^2	P	Sig
Type A2	29	22.21	0.90	0.34	ns
Type B	32	2.20	25.97	<0.001	***

The proportion of successful crossings of the Property B fence that were in the vicinity of one of the fence gaps was significantly higher than would be expected by chance. The Property B fence is 141.6 km in length and has 3 gaps, 4.2% of the fence is within the fence gap buffer. Of the successful crossings of the Property B fence, 61.5% were within 1 km of a fence gap. The number of crossings within the buffer was significantly higher, at 32, than the calculated expected number of crossings if dogs were crossing at random, which was 2.2 ($p < 0.001$; Table 6.2). This may, however, be an underestimate of how reliant the wild dogs were on the gaps to cross the fence. As can be seen in Figure 6.6, nearly all successful fence crossings are clustered in the north-western corner of the property, despite not all of them falling within the 1km fence gap buffer.

As Property B was the only fence where a significantly greater than expected number of fence crossings were found close to fence gaps, the effect of fence gaps on wild dog spatial distribution was only investigated in relation to this fence. The fence gaps affected wild dog spatial distribution around Property B. Wild dog locations were an average distance of 13.52 km from the fence gaps, in contrast to an average 16.66km distance from randomly generated points within the 10 km buffer ($t = -5.07$, $p < 0.001$). See Table 6.3 for t-test results for each individual.

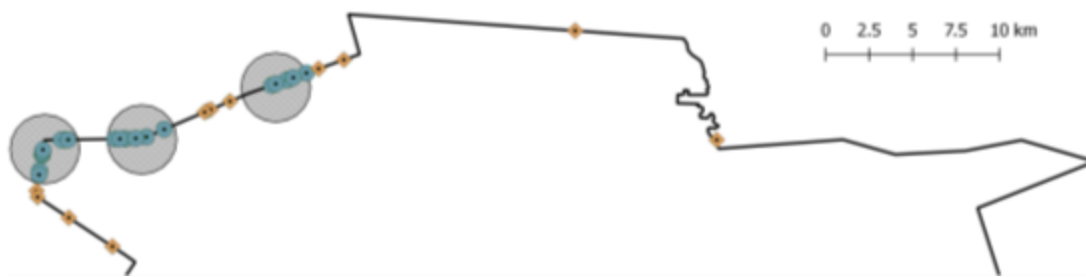


Figure 6.6. Northern fence line of Property B showing locations where steps from GPS collared wild dog tracks successfully crossed the fence. The fence is shown by the black line with tracks shaded areas denoting the 1000m buffer around each fence gap. Blue circles show locations of successful crossings within the buffer distance, orange diamonds show locations of successful crossings outside the buffer distance.

Table 6.3. t-test results for the distance of midday locations from purpose-built fence gaps for each collared wild dog using on Property B.

Individual	Mean distance from fence gap (km)	t value	P value	sig
Simulated locations	16.66			
WDF130	6.52	-13.60	<0.001	***
WDM97	10.20	-7.21	<0.001	***
WDM118	14.14	-3.46	<0.001	***

6.4.3. Effects of Fences on Wild Dog Demography

Since 2001, 19 encounters between wild dogs and fences have been recorded which have had negative impacts on pack dynamics and demography. Property A has been part of the territory of a large number of packs over the course of the study (Figure 6.7) but there have been no deleterious effects recorded in relation to the main ranch (Type A1) fence (Table 6.4). Instead there have been repeated on-the-ground observations of wild dogs easily crossing the fence by passing underneath the wires.

The east ranch fence, which was successfully crossed significantly less often (Table 6.1), has been associated with some negative effects, mostly related to wild dogs being killed on the main road which runs along one side of the east ranch fence

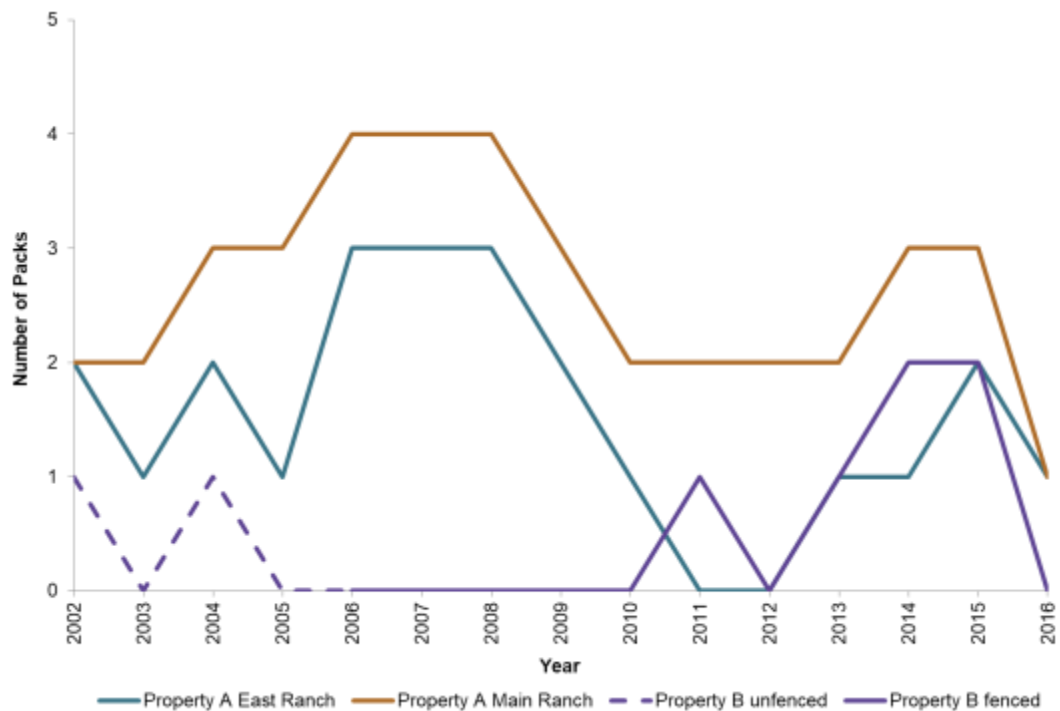


Figure 6.7. Number of packs with each property as part of their territory each year

(Table 6.4). Laikipia has approximately 542.7km of main roads; the stretch of road next to the east ranch fence is approximately 13.6km in length. Whilst it is not possible to definitely attribute the cause of these mortalities to the presence of the fence, since 2001, 11 road killed wild dogs have been recorded in the study area, of which 4 were on this stretch of road.

Property B has had the fewest years where it had resident packs (Figure 6.7) but there have been 15 negative encounters recorded between wild dog packs and this fence (Table 6.4).

6.4.3.1. Observed Encounters between Wild Dogs and Fences

The recorded harmful encounters observed between wild dogs and fences within the study area are summarised in Table 6.4 and more detailed accounts are given below:

One of the packs normally resident on Property A’s east ranch went on an excursion to the east of their territory, the reason for which was unknown. Landowners then reported seeing 20 wild dogs split by a game fence running between two properties near Mount Kenya. Reports continued over the next four months, although the number of dogs seen declined from 20 to 8, when the pack split apart. The alpha

Table 6.4. Number of different types of impacts observed in relation to fences during the course of the study

Type of incident	Number of times observed	Fences involved
Dispersal group split	2	Property B
Pack separation	2	Property B + other
Roadkill	4	East Ranch
Livestock depredation	>10	Property B
Pack extinction	1	Property B

female returned to the pack’s core territory on the east ranch but some of the pack remained near Mount Kenya (Figure 6.8).

Two wild dogs, which were fitted with VHF collars, dispersed from their natal pack’s territory in the north of Laikipia. The wild dogs travelled south and separated while close to the property B fence. One of the collared dogs entered Property B, while the other continued south. It is very unusual for single sex dispersal groups to



Figure 6.8. Locations of VHF collared wild dogs separated by a game fence. Green dots and lines are before the pack was separated, blue dots and lines show the alpha female's locations when she returned to her previous territory after denning. Yellow dots and lines show the locations of the rest of the pack which remained

separate, suggesting that this was a result of the individuals becoming stuck on opposite sides of the Property B fence.

A pack of wild dogs (hereafter PB pack) whose territory was centred on Property B became separated by the fence near a river with 3 or 4 individuals on the conservancy side of the fence and 13 individuals on the outside. During the time the pack was separated there were several reports of sheep and goats being killed by the wild dogs on community land outside the conservancy and the pack was threatened with being poisoned. After several weeks the conservancy was able to cut part of the fence in order to reunite the pack, after which there were no more depredation reports.

On a subsequent occasion the PB pack was seen resting near the fence soon after the death of the pack's alpha female. Also present was a lone, unrelated young female from a nearby pack was observed on the other side of the fence, calling and looking towards the PB pack (Figure 6.9). The PB pack had no unrelated female members which could take the place of the deceased alpha female. Packs in this situation often leave their territories in search of new females. Soon after the encounter with the unrelated female, the PB pack left Property B and moved south into community areas where there were several reports of livestock depredation. The alpha male died during this time; the rest of the pack split and were lost to monitoring. After the encounter the young female returned to her natal pack, soon afterwards the alpha male of this pack was killed in retaliation for the pack's livestock depredation. It is unknown what happened to the rest of the pack, including the young female, however it is likely that they were also killed. If the young female had not been separated from the PB pack by the fence, she would not have been with the BA pack when it was attacked by the local community and so may have survived and become the reproductive female of the PB pack.

6.5. Discussion

The results presented here show that fences can have a significant impact on wild dog movement and demography. The least permeable fence evaluated (Type B) had significantly lower numbers of successful crossings than would be expected if the fence was completely permeable, suggesting an important effect of fence structure on wild dog movements (Hypothesis A). The analysis also showed that wild dogs were heavily reliant on the presence of purpose-built gaps to cross the relatively impermeable Property B fence (Hypothesis B). The fence gaps had a



Figure 6.9. The PB pack separated by the Property B fence from a potential new alpha female. Panel a shows the pack resting next to the fence. Panel b shows the alpha male looking through the fence and panel c shows the young female from the BA pack on the other side (the blurred lines in panel c are the wires of the fence). (photos by Stefanie Strebel)

significant effect on wild dog spatial distribution, with daytime resting locations clustered close to the gaps. The impacts of the less permeable fences (Types A2 and B) on wild dogs' movement patterns and spatial distribution had important effects on the population's demographic processes. Effects including permanent social group separations, human-wildlife conflict and wild dog mortalities have all been observed in association with fences.

These results show that some fences within the landscape have had important effects on one of the endangered species living there. The observed reduction in connectivity is likely to have had important long-term impacts on the wild dog population, as well as having likely contributed to conflict with local communities. This could affect the community's long-term perception of living with wild dogs in addition to the direct retaliatory killings of individual animals that has resulted. As well as showing the long-term impacts on landscape connectivity, these results elucidate the mechanisms by which wild dog demography is affected by living with fences.

The movement behaviour and crossing ability of wild dogs strongly suggest that the design of fence structures and the inclusion of fence gaps are vital for maintaining landscape connectivity. Fence A1 had little impact on wild dog crossing ability, whereas fence B was relatively impermeable. A large percentage (61.5%) of the crossings of fence B were within 1 km of a fence gap however, due to the relatively coarse measure used, it is likely that this is an underestimate (Figure 6.6). The importance of the fence gaps is also supported by the wild dogs' GPS collar locations being significantly closer to the gaps than would be expected by chance, suggesting that gaps are not only vital for enabling movement, but also channel wild dogs into specific areas.

As fence gaps appear to channel wild dog movement and affect spatial distribution, careful consideration should be given to both their location and the number incorporated into a fence. A specified aim of fence around Property B is to prevent medium and large bodied wildlife from moving out of the property and onto community land in order to try to reduce conflict with local communities. This means that the locations of the fence gaps are not random and are focussed in areas of good habitat, further away from human settlements. The gaps therefore seems to be successful in channelling movement of species into certain areas and away from local communities, as the wild dogs tended to stay in areas close to the gaps. However, because the gaps are in close proximity to each other there are

long stretches of the fence which are almost completely impermeable. This has then caused problems when individuals or packs have left the property and then moved away from the gaps and have become stuck on the “wrong” side of the fence.

As documented in Table 6.4, it is likely that the Property B fence has led to cases of livestock depredation by wild dogs. The African wild dog is an obligate social species; resident packs have an extremely strong group bond – even when an individual from the pack is severely injured the rest of the pack will continue to provision that individual rather than abandon them (Courchamp & Macdonald, 2001). Therefore it is unsurprising that, when the PB pack was split by the fence, the two halves remained close to each other over many days rather than permanently separating. The result was that the large number of individuals on the outside of the fence were left in an area with little wild prey, where they were reported attacking livestock. This indicates the implications that fence gaps may have for local communities living close to a reserve, particularly where reducing human wildlife conflict is a central aim of the fence. There is an inescapable contradiction between erecting a barrier to separate wildlife from local communities and then building a hole into it. Instances of wild dogs being effectively stuck on the “wrong” side of a fence may have directly led to human-wild dog conflict and resulted in the death of several wild dogs, and contributed to the loss of entire packs, in the area. Although not widely commented on within the literature, the issue of what to do when animals become trapped on the wrong side of a fence is an important one. Animals that are found on the wrong side have to be returned if the fence is to be effective; this is likely to require intervention because, as seen in this study, animals often do not find their way back through on their own (Sinclair, 2008; Krebs *et al.*, 2001).

These results also suggest that not all fences have measurable negative effects on wild dogs; depending on their structure, fences may have little or no apparent effects on wild dog demography. For example, the fence around the main ranch of Property A (Type A1) was found to be highly permeable to wild dogs; these findings suggest that this style of fencing does not present a significant movement barrier for wild dogs. The relative permeability of the main ranch fence is also reflected by the lack of observations of its impact on wild dog demography. This is despite Property A being closer to the centre of the study area and being more commonly used by study packs.

The Property A east ranch fence (Type A2) was found to have reduced permeability (13.7%) compared to the simulated fences. The main structure of this fence is more similar to that of the Property B fence than to the main ranch fence (Type A1). Fence A2 is a tall, electrified fence which reaches down to/below ground level with relatively small wire mesh. It is thought that the reason for the much higher levels of permeability in this fence than Property B's fence may reflect its state of repair. Fences are expensive and difficult to maintain (Hayward & Kerley, 2009); this fence is substantially older than the fence around Property B and over the years this fence has been observed to have holes in it which are likely to be used by medium and large carnivores such as wild dogs to traverse the fence (Figure 6.10). This higher level of overall permeability also likely explains the relatively low levels of fence gap use that was observed. Despite its relative permeability, the east ranch fence may have had demographic consequences for the wild dog population, as there have been several wild dogs killed by vehicle collisions on the road which runs along the one side of the fence (Table 6.4). It is not possible to definitively say that these fatalities were a direct result of the fence, as wild dogs are susceptible to being killed on roads regardless of the presence of fences (Woodroffe & Ginsberg, 1999). However, there have been reports of individuals from another threatened species, the cheetah, being chased along this road by vehicles whilst attempting to cross the fence between the road and the east ranch (Woodroffe Pers. Com; Pers. Obs.).

In some reserves in southern Africa wild dogs have been observed to use fences to increase their hunting success rates and to enable them to catch larger prey (Davies-Mostert *et al.*, 2013). By chasing prey animals towards fences, packs increase their chance of capture because the prey's possible escape routes are reduced. Due to the method used to evaluate the ability of wild dogs to cross the fences, if packs were employing this hunting strategy it could provide a possible



Figure 6.10. Hole in Property A's East Ranch fence (photo by Rosie Woodroffe)

reason for the high numbers of wild dog locations found close to fences but that did not result in successful crossings. However, this behaviour has not been seen during on-the-ground observations of any packs in Laikipia and has not been reported by landowners or conservancy managers. Causing large prey animals to run into fences often causes substantial damage to the fence, meaning that it would be expected that conservancy managers would quickly become aware of this behaviour if it was occurring because it would lead to an increase in fence maintenance costs (Lindsey *et al.*, 2005b). It would also be expected that if packs were using the fences in this way that similar behaviour would be seen with the east ranch fence – this fence is of a similar height to the Property B fence and would likely be difficult for a fleeing prey animal to go over, under or through; however no such evidence was found.

Fences can be important for the successful conservation of threatened species, however it is vital to consider the short and medium term effects on wildlife populations in their design (Durant *et al.*, 2015b). The African wild dog is one of the most threatened canid species in the world with an estimated global population of fewer than 6600 individuals (Woodroffe & Sillero-Zubiri, 2012). The results here strongly suggest that some fences have important impacts on wild dog demography and movement patterns. The Laikipia wild dog population is of global significance, being one of the largest remaining wild dog populations. This in turn means that the impacts of the fences described here arguably have global conservation impacts. Where fencing is considered essential, preference should be given to the building of more permeable fences, such as the Type A1 fence found around the Property A main ranch; this fence has been shown to have minimal effects on wild dog movement patterns, and it is therefore likely to also have minimal impacts on other similarly sized species. Where it is considered a necessity for a less permeable fence to be erected careful consideration should be given, not only to the longer term techniques for mitigating connectivity loss, but also to planning how to react if social groups of any species become separated by the fence so that rapid mitigation is possible.

These results show the importance of careful consideration that must be given to the type of structure employed when erecting fences, and what the possible unintended consequences of a fence might be. Fences are widely recognised as causing landscape fragmentation and reducing connectivity and have been cited as a cause of the loss of many large terrestrial mammal migrations (Harris *et al.*, 2009).

This has led to the Convention on Migratory Species developing guidelines on addressing the impact of fences and other linear movement barriers on migratory species (Wingard *et al.*, 2014). The evidence presented here suggests that it is possible to successfully target fences to certain groups of species, such as rhinos, without negatively impacting landscape connectivity for other species. However, whilst these permeable fences do not appear to affect connectivity for wild dogs, and likely also other similarly sized species, they are likely to affect other non-target species. For example, whilst targeted primarily at preventing rhino movement and channelling elephant movement, these fences are also likely to affect the movement behaviour of other, non-target, megaherbivores such as giraffes, *Giraffa camelopardalis*. These results provide important information on the impact of fences on connectivity as set out by the framework provided by Durant *et al.* (2015). This new information highlights the importance of conducting full environmental impact assessments before new fences are erected, as recommended by Durant *et al.* (2015). These results show that impermeable fences have a significant effect on long-term connectivity levels across a landscape for wide-ranging species; and that this results in notable short-term impacts on the population.



Plate 8. A lactating alpha female African wild dog with cattle being herded past her den

Chapter 7.

General Discussion

This thesis has explored how humans alter landscape connectivity for wildlife, using two wide-ranging endangered species as case studies. In this final chapter, I shall briefly summarise my findings and then discuss their wider relevance to the theory and practice of wildlife conservation.

In Chapter 3, African wild dogs were found to avoid areas of high human density but to favour areas close to roads and rivers. Wild dogs' second order (home range) habitat selection differed from their third order (within home range) selection; whilst the direction of selection (i.e. towards or away from landscape features) remained broadly consistent, the magnitude of selection varied significantly between orders. Habitat selection also varied across life stages, with dispersal groups found in areas of highest human impact and resident-denning packs found in areas furthest from human disturbance.

Chapter 4 explored connectivity between the known remaining populations of wild dogs in Kenya. Models predicted greater connectivity between populations when using data from dispersal groups than when using data from resident packs. However, connectivity is threatened by planned infrastructure development projects, particularly the Lamu Port – South Sudan – Ethiopia Transport corridor (LAPSSET). LAPSSET is also likely to directly affect two of Kenya's seven resident wild dog populations.

The impacts of fencing on wild dogs and cheetahs were explored in Chapter 5 and Chapter 6. Fence structure proved to be important to the effects that fences had on both species. The most permeable fence structure investigated had no measurable effect on either cheetah or wild dog movement patterns, however, less permeable fences had substantial impacts. A GPS collared cheetah crossing fences intended to be impermeable moved significantly further than would be expected if the boundaries were unfenced, which was equivalent to an increase of 12.0% of the cheetah's daily energetic expenditure for each fence encountered. If all property boundaries within Laikipia were to be converted to this type of fence then simulations suggest that cheetah energetic expenditure could increase by up to 14.8%.

The effects of fences on wild dog movement ecology and demography were evaluated in Chapter 6. The least permeable fences were found to have significant impacts on wild dogs' ability to cross the structure, with individuals being reliant on purpose-built fence gaps to cross the fence. These gaps changed the spatial distribution of animals in the fenced reserve with collared individuals found significantly closer to the gaps than would be expected by chance. Impermeable fences were also observed to have important impacts on the demography of the wild dog population of Laikipia. Fences were associated with pack separations, human-wild dog conflict and have been implicated in the deaths of individual wild dogs and pack extinctions.

These results have important implications for the conservation of cheetahs and African wild dogs in Kenya. Many of these findings and methodologies are also likely to also be widely applicable to other species living in human-dominated landscapes. In the rest of this chapter I will discuss the wider conservation implications of this thesis.

7.1. Implications for Conservation of Wide-Ranging Species

7.1.1. Conservation Implications for African Wild Dogs

African wild dogs are currently categorised as Endangered by the IUCN Red List; among the greatest threats to their long-term persistence are habitat loss and fragmentation (Woodroffe & Sillero-Zubiri, 2012). Whilst the remaining range of the species has been mapped, a key knowledge gap has existed regarding the extent to which the different patches of resident range remain connected. Establishing levels of landscape connectivity and ascertaining the locations of potential movement corridors were key requirements identified as part of the East Africa Regional Action Plan for the Conservation of Cheetahs and African Wild Dogs (IUCN/SSC, 2007) and the Kenya Conservation and Management Strategy for Cheetahs and Wild Dogs (Kenya Wildlife Service, 2010). In particular, one of the targets in both the Regional Action Plan and the National Conservation and Management Strategy is:

“Target 4.3: Explicit information provided to the management authorities to support identification and prioritisation of corridor and dispersal areas for improved connectivity of cheetah and wild dog ranges”

The target has two activities associated with it:

“Activity 4.3.1: Determine the spatial extent of corridor and dispersal areas between resident, possible and unknown ranges”

“Activity 4.3.2: Determine threats, habitat quality, and the extent of suitable habitat in and surrounding corridors and dispersal areas”

The wild dog entry in the IUCN Red List also specifies connectivity as a key area where further research is needed (Woodroffe & Sillero-Zubiri, 2012), specifically:

“Determining the landscape features which facilitate (or prevent) wild dog movement over long distances and hence promote (or block) landscape connectivity.”

The connectivity maps developed in Chapter 4 are the first empirically based connectivity maps developed for wild dogs in East Africa. These maps predict the locations of the key movement corridors and dispersal areas across Kenya, as required by Activities 4.3.1 and 4.3.2. Evaluating the impacts of fences on wild dog movement behaviour in Chapter 6 elucidated the effects of these important landscape features as identified by the Red List as a key concern. This information can then be used for planning conservation activities, for land-use planning, and for assessing the environmental impact of development activities.

7.1.2. Conservation Implications for Cheetahs

These findings likewise have implications for cheetah conservation. Most directly, this research showed that fencing has damaging effects on this endangered species. These effects were not, as expected, because fences blocked access to resources, but because cheetahs regularly crossed fences intended to be impermeable, expending time and energy as they did so. This finding is important for assessing the impacts of fencing – whether or not it is constructed for conservation purposes – on this and other endangered species.

In addition to this direct impact of these findings, the collaring efforts involved establishing the first cheetah monitoring in the area. Data from these GPS collars have shown that individuals traverse far more properties than realised by local landowners. This work has contributed data about population densities to a recent study of cheetah distribution and status (Durant *et al.*, 2017) and has revealed that cheetah density in the area is markedly lower than assumed by local conservationists and landowners.

Finally, my analyses of connectivity for wild dogs can be interpreted, with caution, to infer possible movement corridors for cheetahs.

7.1.3. Conservation Implications for Wide-Ranging Species

Although the effects of landscape features on cheetahs and wild dogs were studied separately there were some similarities observed. With respect to fences, both species were found to have similar reactions to different fence structures. For example, when encountering the most permeable fence type evaluated, both wild dogs and cheetahs did not exhibit any measurable effects on their crossing rates or distance moved (Chapter 5 & Chapter 6). Less permeable fences affected both species; reducing the crossing rate for wild dogs and causing cheetahs to move significantly further before being able to successfully cross. Similarities between cheetahs and wild dogs in their barrier crossing ability were also reported by Cozzi *et al.* (2013).

Although habitat selection by cheetahs was not directly evaluated due to a small dataset, it was observed that the GPS collared cheetah rarely strayed from wildlife areas with only 16.5% of recorded locations outside of such areas (Chapter 5). It is possible that cheetahs may have a similar aversion to areas of higher human density as that exhibited by wild dogs (Chapter 3). This would fit with findings elsewhere, which suggest that cheetahs avoid areas of high human population densities (Ahmadi *et al.* 2017) and that higher human population densities increase extinction risk for both cheetahs and wild dogs (Woodroffe 2000). Future research into cheetah habitat selection with respect to anthropogenic landscape features will be important for informing future land-use planning.

Whilst there are numerous similarities in the conservation requirements for cheetahs and wild dogs, there are also some differences, a key one of which is the reaction of the two species to roads. Wild dogs select for areas close to roads (Woodroffe 2010; Chapter 3) and may use them to move around their landscape, whereas roads can be a barrier to cheetah movement (Moqanaki & Cushman, 2017). Roads are a conservation concern for both species as roadkill is an important cause of mortality across both wild dog and cheetah populations. For example in Iran, the last remaining population of the Asiatic cheetah experiences high levels of roadkill; wild dog preference for areas close to roads exacerbate the threat (Hunter *et al.* 2007; Woodroffe, Davies-Mostert, *et al.* 2007).

The connectivity maps generated in this thesis may also have relevance to other species in the region. It is likely that connectivity modelled using data from other species will vary slightly from those produced for wild dogs, as different species will have somewhat different habitat selection preferences. However, some aspects of habitat selection exhibited by wild dogs, for example avoidance of areas of high human population density, are likely to be common to other species also. One aspect of wild dog selection models that may not be observed in other species is the selection of areas close to roads; therefore it may be that the sensitivity analysis conducted which did not include roads in the model may be more widely applicable.

A finding that is likely to be applicable to other species is that cheetahs and wild dogs were able to cross areas of fences that were intended to completely block animal movement. Whilst many of the occasions that wild dogs crossed the least permeable fence entailed using purpose-built gaps, this was not always the case. The cheetah also crossed impermeable stretches of fence without using purpose-built gaps. However, doing so caused problems for both species, including causing additional energy expenditure and demographic effects such as splitting up social groups. It is likely that similar impacts will affect other species that come into contact with such fences. These impacts may negatively affect the likelihood of some species persisting in the landscape. The effects that fences have on the movement ecology and demography of wildlife are likely to be of particular importance as the amount of fencing across landscapes increase.

7.1.4. Landscape Connectivity in Kenya

In Kenya the human population has grown rapidly over recent decades, increasing from 9.5 million people in 1965 to 47.2 million in 2015 (UN DESA, 2017); this trend is still continuing, with an estimated annual population growth rate of 2.49% (UN DESA, 2017). This means that, in the coming years, there are likely to be further impacts of Kenya's human population on the country's remaining wild spaces, and therefore on its wildlife. Kenya has a relatively high multidimensional poverty index; this is a measure of the multiple deprivations that people face encompassing indicators across education level, health, and standard of living (Jahan, 2016). Development and poverty alleviation projects are therefore a high priority for the country (Ndung'u *et al.*, 2011). However, the impact that these projects may have on Kenya's wildlife is also an important concern, not least because wildlife tourism contributes a substantial amount to Kenya's GDP (World Travel & Tourism Council,

2017). This is important as it means that the wildlife that tourists pay to see, not only contributes a substantial amount to tax revenues, but also provides development and employment opportunities that will likely disappear if wildlife and wild spaces are not adequately conserved. LAPSSET is an extensive infrastructure project, and it is not realistic to expect building to be halted, however it may be possible to incorporate tools to help mitigate the negative impacts that LAPSSET and other infrastructure development projects may have on wild species and habitat connectivity. Doing so will mean the tourism sector can be maintained whilst also improving the country's infrastructure and addressing Kenya's urgent development needs. It is also important to look beyond the impact of individual infrastructure development projects, as focussing only on individual projects may underestimate the long-term effects of the overall infrastructure network (Nellemann *et al.*, 2003). Major infrastructure development projects, such as LAPSSET, are not happening in isolation. Other projects, such as laying tarmac on previously unpaved roads, may also have an important effect which, taken in concert across the country, could have much greater combined effects on wildlife than otherwise anticipated (Nellemann *et al.*, 2003). This work suggests that LAPSSET and other development projects may have serious consequences for wildlife connectivity. However it has also developed a novel methodology, using an energetics-based approach to use to determine the spacing of crossing-points needed to maintain connectivity.

Kenya's Environmental and Management Co-ordination Act (EMCA; *ACT NO 8 OF 1999*) is the key piece of legislature that regulates environmental management and conservation in the country. It sets out the legal framework which determines whether an Environmental Impact Assessment (EIA) may need to be conducted in advance of, for example, a change of land-use or the construction of a new building project. The second schedule of the EMCA specifies the types of projects which require EIAs, these include major roads and railways. The regulations do not specifically reference fences, although they do refer to (1a) an activity out of character with its surrounding and (1b) any structure of a scale not in keeping with its surrounding; which could be interpreted to encompass fences. Some fence-building projects, such as the West Laikipia Fence have undergone an EIA before construction (Thiane, 2007). In light of the impacts that large-scale boundary fences have been shown to have, it may be appropriate to consider whether an expansion of the EIA requirements to specifically encompass all boundary fences on properties above a certain size may be appropriate.

7.2. Habitat Selection and Connectivity

Maintaining habitat connectivity may help mitigate the effects of habitat loss and fragmentation on wild populations (Crooks & Sanjayan, 2006). Different species have different dispersal abilities which make them more or less able to traverse areas of suboptimal habitat in order to reach new habitat patches (Santini *et al.*, 2013). There is increasing recognition that an individual's behavioural state impacts their habitat selection; however, despite this, there is still a relative paucity of studies that explicitly incorporate life stage in connectivity analyses (Abrahms *et al.*, 2017; Tobin *et al.*, 2010; Roever *et al.*, 2014). The results presented in Chapter 3 showed that habitat selection by wild dogs differed between orders of selection and across different life stages, with dispersal groups most likely to be found in areas with higher anthropogenic impacts. These results, which are based upon a long-term dataset of individually known, free-ranging wild dogs support the initial findings from elsewhere (Abrahms *et al.*, 2017; Jackson *et al.*, 2016; Masenga *et al.*, 2016). In addition, the finding that dispersal groups have differing habitat requirements has been found across a variety of species. Within the *Carnivora*, similar patterns have been found when comparing dispersing and resident African lions (Elliot *et al.*, 2014b) and Iberian lynx (Gastón *et al.*, 2016). In both of these species dispersers were found to be more willing to tolerate areas of suboptimal habitat. These findings have important implications for connectivity mapping. As discussed in Chapter 4, the predicted connectivity levels for wild dogs differed substantially between life stages. This is important because it is not realistic to expect authorities to prevent development from occurring across all potential movement corridors for all species. Decisions on which areas to prioritise should be based on the best evidence possible, and the best evidence possible is likely to be based on data from individuals that are most likely to make use of such corridors.

Both resident and dispersing wild dogs selected areas close to roads (Chapter 3), leading to a prediction that roads may be associated with likely movement pathways between populations (Chapter 4). Roads are generally considered to reduce, rather than promote, landscape connectivity (Forman & Alexander, 1998). This is because many species avoid areas close to roads, which can act as an almost complete movement barrier for some species (Shepard *et al.*, 2008). Studies have also found that wolves use linear features such as roads; travelling along such features enables them to move further and faster as well as improving their hunting opportunities (Dickie *et al.*, 2017). It may be that wild dogs in the Laikipia population

use roads in a similar way as they are often observed hunting along roads (Pers. Obs.). Whilst wolves use some roads, they have been shown to avoid higher-use roads (Whittington *et al.*, 2004). The effect of traffic level on habitat selection of wild dogs was not investigated in these analyses and would be a useful subject for further study. It could be that traffic levels, as currently experienced in Laikipia, do not have a major impact on wild dog use of roads; however at higher levels of traffic there could be a tipping point where wild dogs begin to avoid roads. A similar phenomenon is found with cougars, which show evidence of using dirt roads to facilitate movement but avoiding paved roads (Dickson *et al.*, 2005). It may be that if roads in Laikipia begin to have higher traffic volumes and/or become paved that wild dogs will also begin to show some signs of avoidance or decreased usage. Wild dogs are prone to being killed on roads (as discussed in Chapter 3) and so as the number of paved and/or busy roads increases they are likely to be negatively affected. Although some roads may positively affect wild dog dispersal within local areas, it seems unlikely that roads will have a positive impact on large-scale connectivity due to the risks involved with travelling along them. Roads are built between towns, so may channel wild dogs into unsuitable areas of the landscape; however, the biggest risk will be from the mortality risk associated with roads. This is particularly relevant to the suggestion that roads may aid long distance dispersal – travelling along a road has an inevitable mortality risk for wild dogs as they may be hit by vehicles also travelling along the road. If wild dogs spend a long time on the road, for example while making a long-distance dispersal, the overall probability that they will be hit by a vehicle is likely to increase. If roads do act as movement channels, it is likely to be associated with a high mortality risk.

Human population density had an important influence on levels of landscape connectivity for wild dogs, with wild dogs preferring areas with lower density. For many species, human settlements and areas of high human population density tend to reduce landscape connectivity (Joshi *et al.*, 2013; Rabinowitz & Zeller, 2010; Singleton *et al.*, 2004). Although some species of carnivore can survive, or even thrive, in such environments (Fedriani *et al.*, 2001; Yirga *et al.*, 2013), the majority of species avoid human settlements (Joshi *et al.*, 2013; Rabinowitz & Zeller, 2010). However, wild dog dispersal groups were found to be more willing to tolerate higher levels of anthropogenic influence and are therefore expected to move across a wider proportion of the landscape. As dispersers in a variety of species have been found to have a greater ability to tolerate suboptimal habitats than residents and/or adults, this pattern, where connectivity mapping based on data from adults predicts

lower connectivity than that based on dispersers, is likely to hold true across other species. As dispersers are the most likely to move between populations, connectivity maps based on dispersal data are likely to give the most accurate estimate of levels of connectivity remaining in a system. It may mean that areas that were previously thought to be redundant for conservation may still have some value for connectivity. It may also mean that less needs to be done to restore modified habitat to make it part of an effective corridor.

Whilst maintaining connectivity between remnant habitat patches is a key tool in landscape level conservation, it is highly unlikely that all potential movement corridors can be or will be conserved, particularly where there is a need for infrastructure development. Corridors between habitat patches, particularly where the distance between them is large, are unlikely to be used by animals very often. It is therefore unlikely to be feasible to prevent, or even delay, development projects in order to maintain the ability for animals to occasionally pass through an area. Possibly a more effective, and realistic, focus will be to concentrate on the inclusion of mitigation tools, and careful land-use planning, to try to maintain as high a level of connectivity as possible, whilst acknowledging that development is going to happen regardless.

7.3. Fences

Fences can have substantial impacts on the movement ecology of wildlife found in their vicinity and even fences that do not represent a complete movement barrier may have important negative effects on wildlife (Chapter 5 & Chapter 6). Increases in fencing are likely to have important impacts on landscape connectivity and so incorporating fences into connectivity modelling is likely to substantially improve accuracy. However, whilst collecting data on fence locations is possible over relatively small areas, it is difficult to do so over large areas, such as the whole of Kenya, as there are no centralised databases of fence locations. Satellite remote sensing is generally unable to pick up fences; even where fences can be detected, it is unlikely to be in sufficient detail to determine the fence's structure and therefore the extent to which it may be a movement barrier. It is for these reasons that fences were not included in the habitat selection and connectivity models presented in this thesis. Increases in fencing may have serious impacts on connectivity, even in areas where land-uses remain wildlife-friendly, thus fencing policy should be an explicit part of future land-use planning. For example, requiring land owners to

notify land-use planning and wildlife authorities before building new fences so that environmental impacts can be assessed and databases on their locations can be maintained. Also, a full environmental impact assessment should be conducted before the erection of new fences, or the reinforcement of existing ones.

These findings have elucidated some of the mechanisms by which wildlife may be affected by living in proximity to fences. Studies that evaluate the impacts of fences on wild populations often focus on long-term effects arising from decreased connectivity leading to impacts on genetic diversity, or a lack of access to important resources. This work has shown the short-term impacts on animals which are also likely to be important in the long-term, resulting from the changes in individuals' movement ecology and energetic expenditures caused by the presence of fences. This is particularly important as the fences evaluated here were not completely impermeable and many of the negative impacts of the fences (for example, increasing the distance moved by the cheetah or splitting wild dog social groups) were associated with the fences being semi-permeable. This is an important point as the incorporation of purpose-built gaps in the fence can be recommended as a way of mitigating their impacts on wild species, and yet in this case the semi-permeability of the fence due to the presence of the gaps has been shown to have some negative impacts. Maintaining landscape connectivity is of high importance, and erecting impermeable fences is to be avoided wherever possible as the long-term impacts of a total loss of connectivity is likely to be more severe than the problems caused by semi-permeable fencing related here. However, these results showed that not all fence designs had measurable negative effects on cheetahs and wild dogs, and these fences were still successful in their aim of preventing rhinos from moving out of the conservancies. Using such designs wherever feasible is likely to be preferable to building impermeable fences with a small number of gaps.

Fences are often recommended, and used, as a method of reducing human-wildlife conflict, with the idea being that by separating people, their livestock and their crops from wildlife that there should be fewer losses on both sides (Hayward & Kerley, 2009). In Chapter 6, the impact of fencing on human-wild dog conflict was discussed, with the fence around Property B being implicated in several incidents of livestock depredation by wild dog packs. This is of particular importance as in the study system, cheetahs and wild dogs are not causes of substantial levels of human-wildlife conflict (Woodroffe *et al.*, 2007b), yet they are negatively affected by the conservation intervention designed to reduce it. However, it is difficult to

determine what the net effect of the fence is – although the fence likely caused some incidents of livestock depredation, it is possible that the overall level of depredation was nonetheless lower than if the fence did not exist. When evaluating the impact of the fence on human-wildlife conflict it is important to look at the wider picture as there are several other predator species also living on Property B which could also cause conflict; for example, even if the level of human-wild dog conflict had been increased by the presence of the fence, the overall level of human-carnivore conflict could be lower if there had been a substantial reduction in the level of livestock depredation by lions and other predators.

Fence gaps were found to be effective in channelling wild dog movement into certain areas of the landscape away from human settlement. However the small number and clustered spatial distribution of these gaps meant that packs risked being split and/or stuck on the “wrong” side of the fence. Having a greater number of gaps dispersed throughout the length of the fence may have made it easier for wild dogs that were stuck outside the conservancy to find their way back in; it would of course also mean that wild dogs and other predators would be able to leave the conservancy more easily as well. This again comes back to the problem discussed in the previous paragraph of whether the level of conflict related to the fence was higher or lower than it would have been without it. Rather than relying on small gaps, it may be appropriate to incorporate larger lengths of more permeable fence types into the main fence; these should be located in areas to channel animal movements away from human settlements, but may reduce the probability of animals being stuck on the wrong side of the fence as they would have greater opportunities to cross back to the “right” side.

The impacts of the presence of fences on animals’ daily energy balance is a relatively unstudied aspect of the effects of fencing; but based on the results from Chapter 5, is likely to be an important one. It is likely to be of particular importance for wide-ranging species as a large proportion of their daily energetic expenditure is often already spent on their daily movement patterns (Halsey, 2016). The cumulative effect for animals attempting to cross several barriers as they move through the landscape may add up to effectively an impermeable barrier (Nellemann *et al.*, 2003). As seen in Chapter 5, in simulations where all boundaries in Laikipia were fenced, the energetic costs to the animal were substantial. When developing policies for land-use planning, incorporating regulations on the fencing of property, and other, boundaries and the inclusion of mitigation tools including fence gaps and

underpasses may be appropriate, particularly in marginal systems where resources are limited such as drylands (Durant *et al.*, 2015b). Using information about animals' energetic budgets and the potential costs of moving additional distances to cross fences and other types of infrastructure, as suggested in Chapter 5, could be an effective way of determining the required frequency of passageways such as fence gaps or over- and underpasses.

7.4. Conclusions

Wildlife conservation needs to be at the centre of future land-use and development planning. This is likely to be important in the face of future increases in infrastructure, land division, fencing and climate change. Wide-ranging species such as cheetahs and wild dogs are at risk of being negatively affected by such threats but, as charismatic and economically important species, are well placed to garner political support for changes to planning regulations and to influence future land-use planning. Overall, these results have highlighted the importance of maintaining landscape connectivity for successful conservation, but also of evaluating the impacts of conservation interventions, such as fences, on species that are affected by them.



Plate 8. A cheetah wearing a GPS collar

Appendix 1.

Appendix 1 Table 1. List of GPS collared study animals

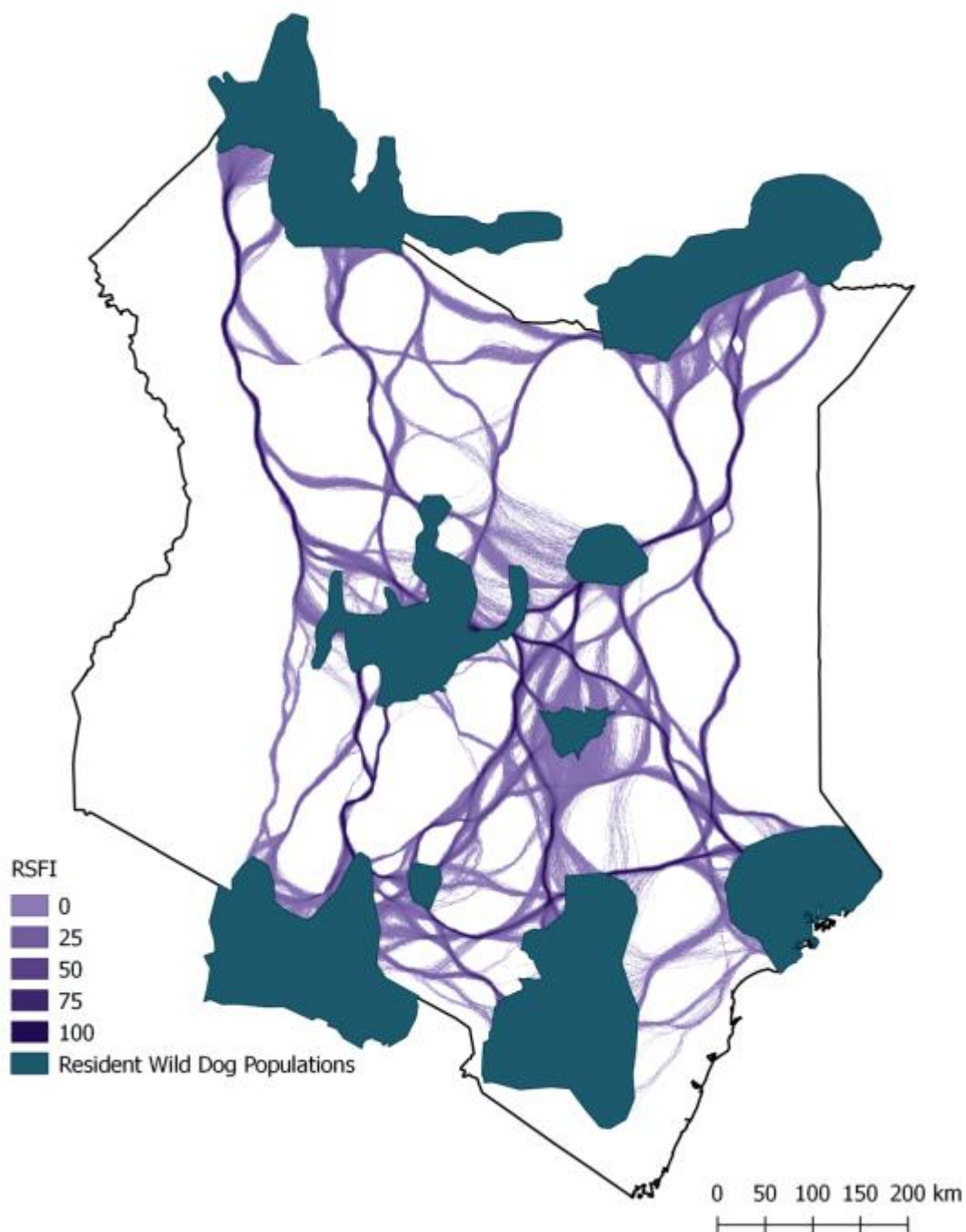
Species	Animal ID	Collar Type	Chapters Data Used In	Why Collar Dataset Ended	Did Monitoring of Individual Continue After Collar Dataset?
Wild dog	WDF25	Televilt	6	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDF96	Vectronics	3, 4, 6	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDF105	Vectronics	3, 4	Lost to monitoring during dispersal	No
Wild dog	WDF109	Vectronics	3, 4	Died (during dispersal)	NA
Wild dog	WDF120	Vectronics	3, 4, 6	Collar fell off (individual part of resident pack at time)	Yes – individual part of monitored study pack
Wild dog	WDF123	Vectronics	3, 4	Collar removed (individual part of resident pack at time)	Yes – individual part of monitored study pack
Wild dog	WDF126	Vectronics	3, 4, 6	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDF130	Vectronics	3, 4, 6	Collar fell off during dispersal	Intermittently – lost to monitoring after 5 months of dispersal. Returned to study area without collar, intermittent sightings since.
Wild dog	WDF137	Vectronics	3, 4, 6	Died (during dispersal)	NA
Wild dog	WDM30	Televilt	6	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDM64	Televilt	6	Collar removed	Yes – individual part of monitored study pack
Wild dog	WDM91	Vectronics	3, 4	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack

Wild dog	WDM97	Vectronics	6	Died (individual part of resident pack at time)	NA
Wild dog	WDM111	Vectronics	3, 4, 6	Lost to monitoring (individual part of resident pack at time)	No – had established new home range in Mt Kenya National Park & not possible to continue monitoring
Wild dog	WDM112	Vectronics	3, 4	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDM115	Vectronics	3, 4	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDM118	Vectronics	3, 4, 6	Died (individual part of resident pack at time)	NA
Wild dog	WDM119	Vectronics	3, 4	Collar removed (individual part of resident pack at time)	Yes – individual part of monitored study pack
Wild dog	WDM131	Vectronics	3, 4	Battery expired, collar changed to VHF	Yes – individual part of monitored study pack
Wild dog	WDM132	Vectronics	6	Died (individual part of resident-denning pack at time)	NA
Wild dog	WDM133	Vectronics	3, 4	Lost to monitoring (individual part of resident-denning pack at time)	No
Wild dog	WDM135	Vectronics	3, 4	Died	NA
Wild dog	WDM136	Vectronics	3, 4, 6	End of study	Yes
Cheetah	Tenai	Sirtrack	5	Lost to monitoring (presumed dead as social group subsequently sighted without him)	No

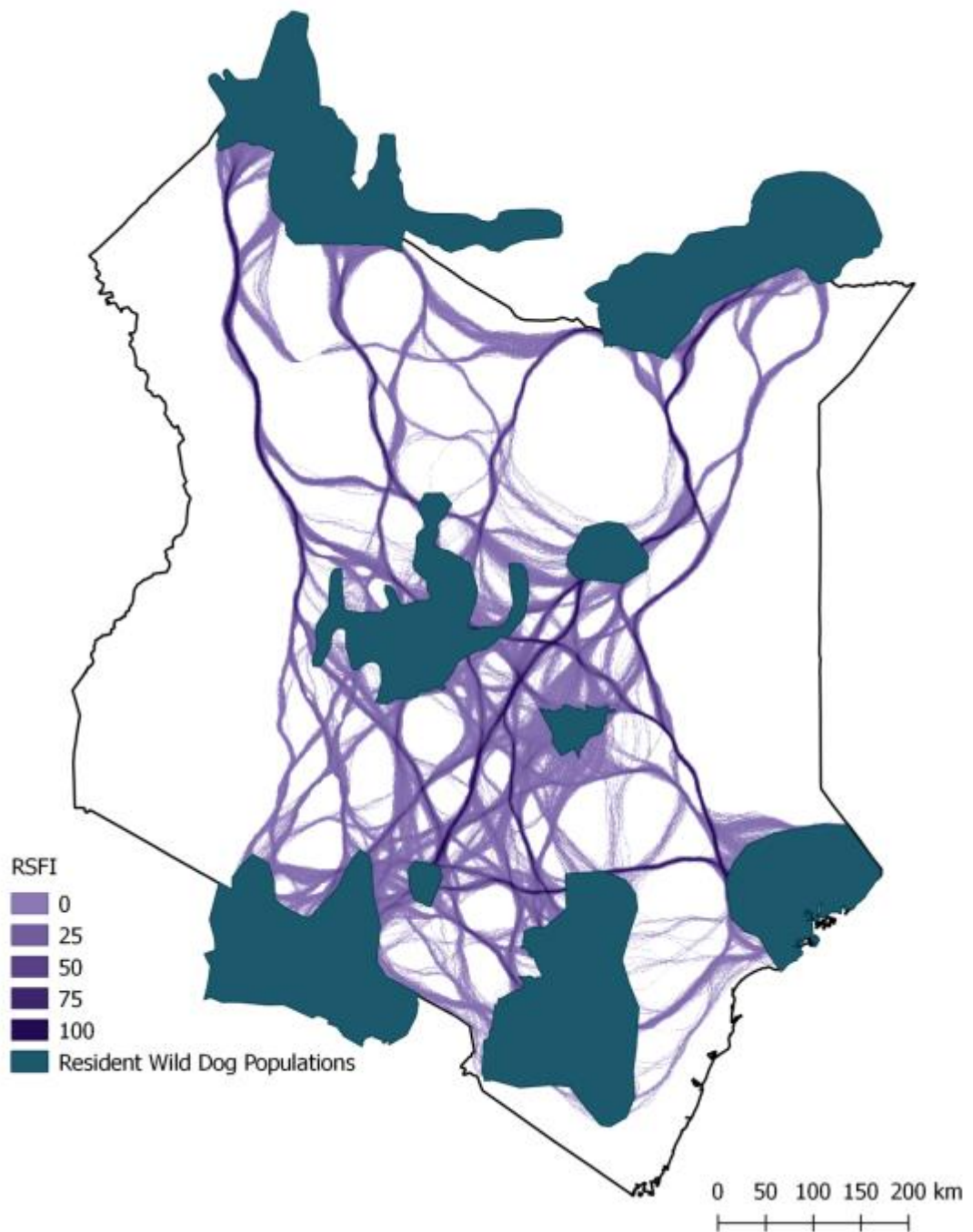
Data from Televilt collars were not used in wild dog habitat selection (Chapter 3) or connectivity (Chapter 4) analyses because collars did not record DoP (GPS accuracy) data and so accuracy of locations could not be determined. WDM132 was also not included in these analyses due to a small dataset and unusual behaviour observed.

Individuals were not included in analyses for Chapter 6 if they did not encounter fences.

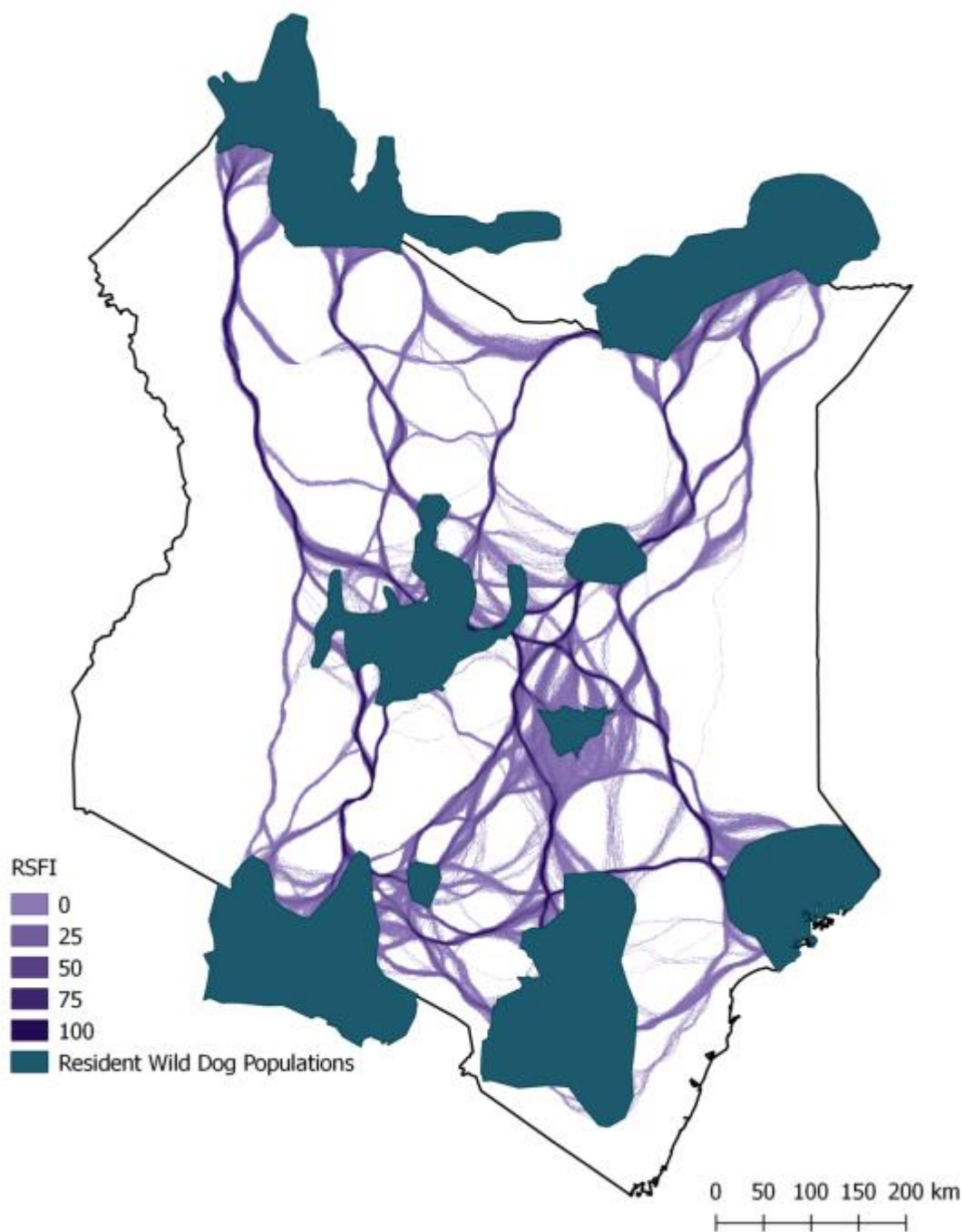
Appendix 2.



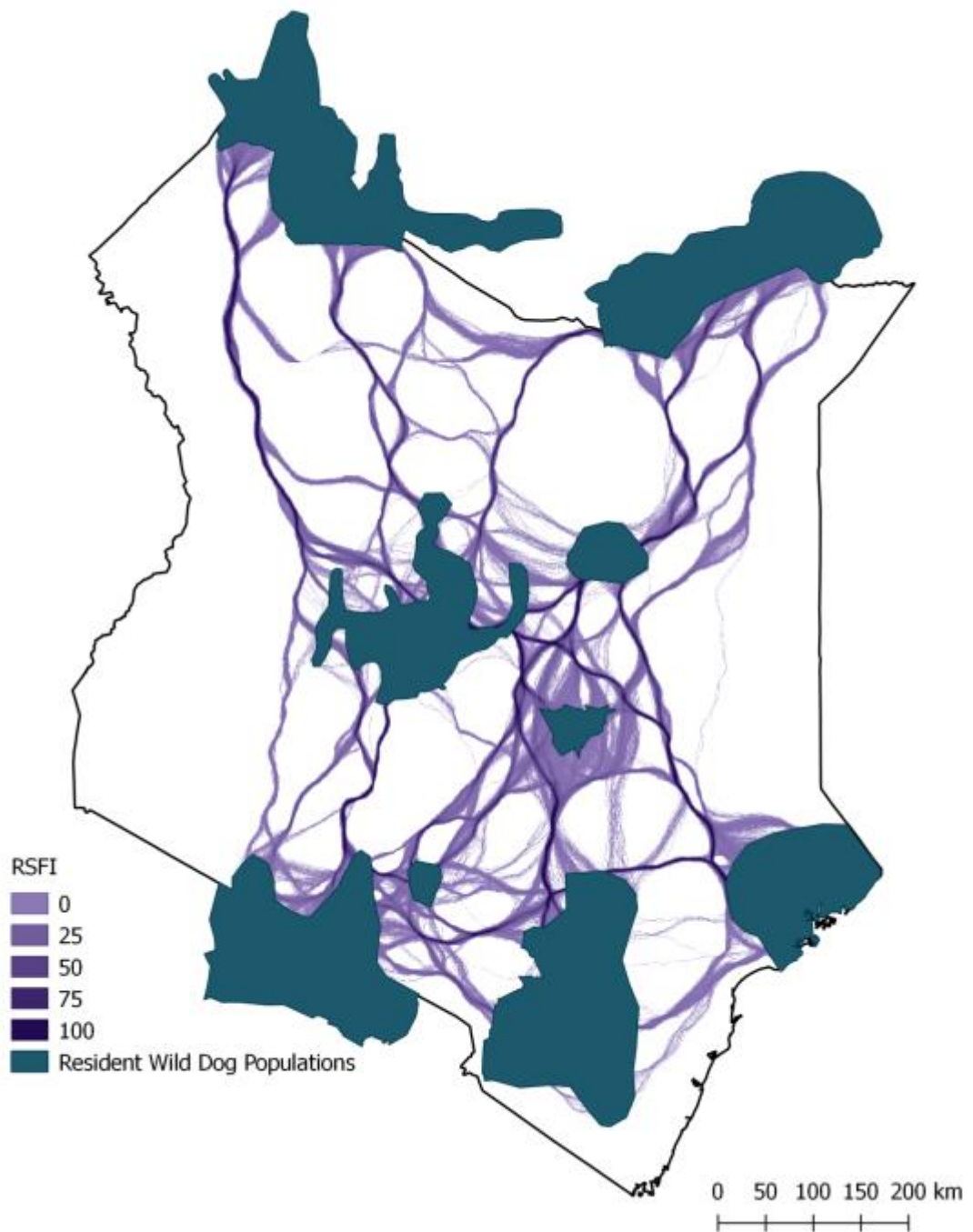
Appendix 2 Figure 1. Connectivity map based on the RSF model not including distance to rivers (iii) using GPS data from dispersal groups and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



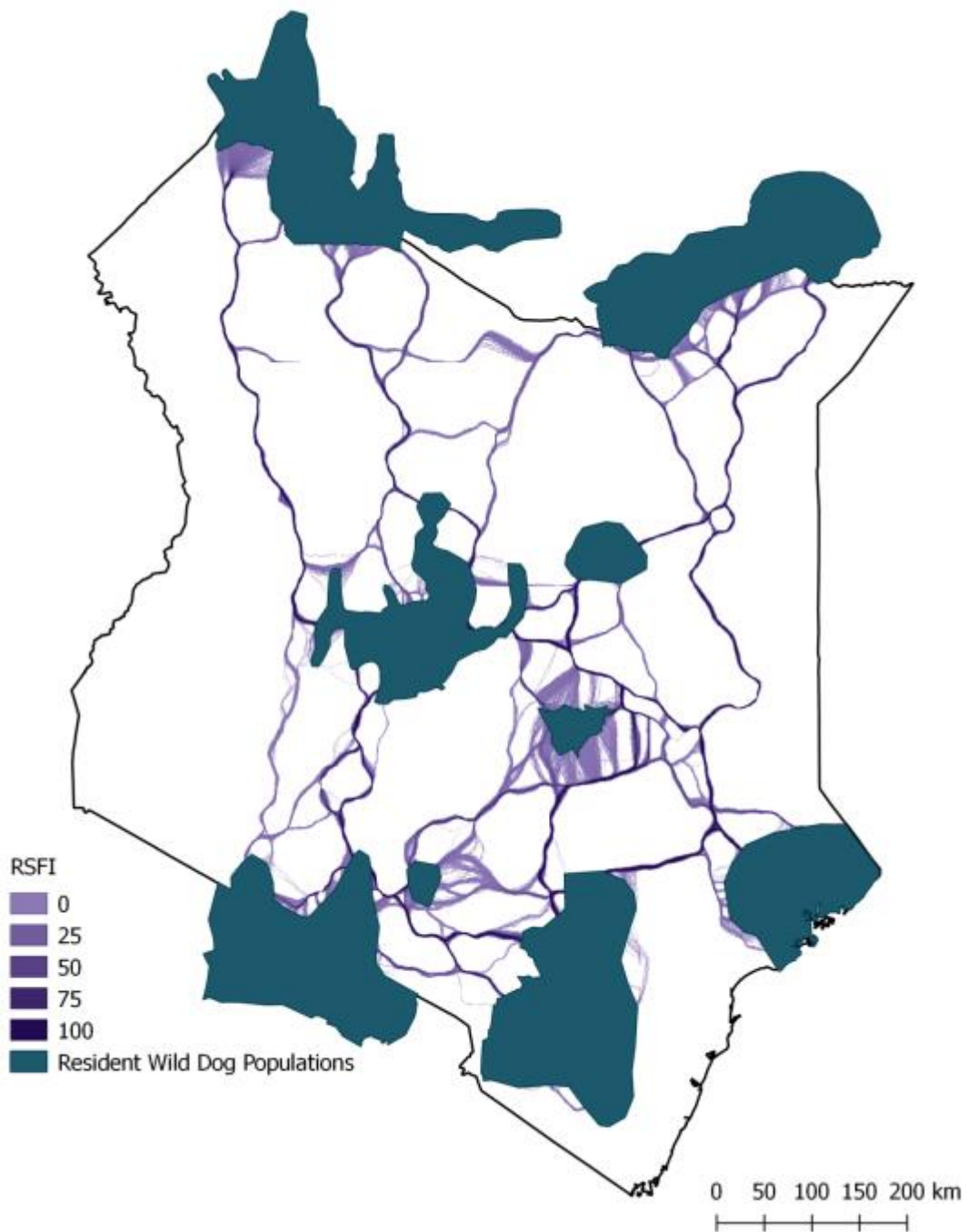
Appendix 2 Figure 2. Connectivity map based on the RSF model not including human population density (iv) using GPS data from dispersal groups and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



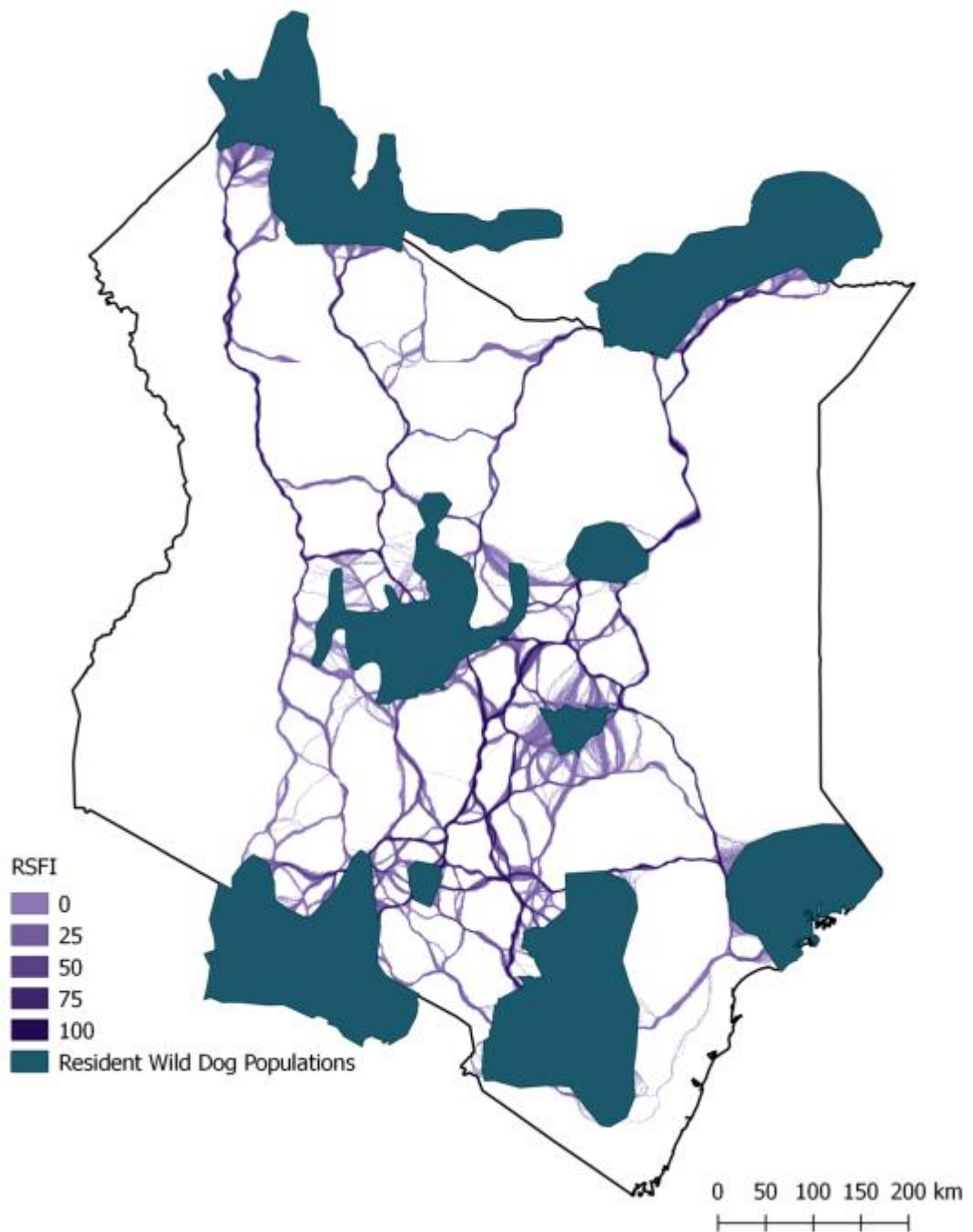
Appendix 2 Figure 3. Connectivity map based on the RSF model not including percentage tree cover (v) using GPS data from dispersal groups and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



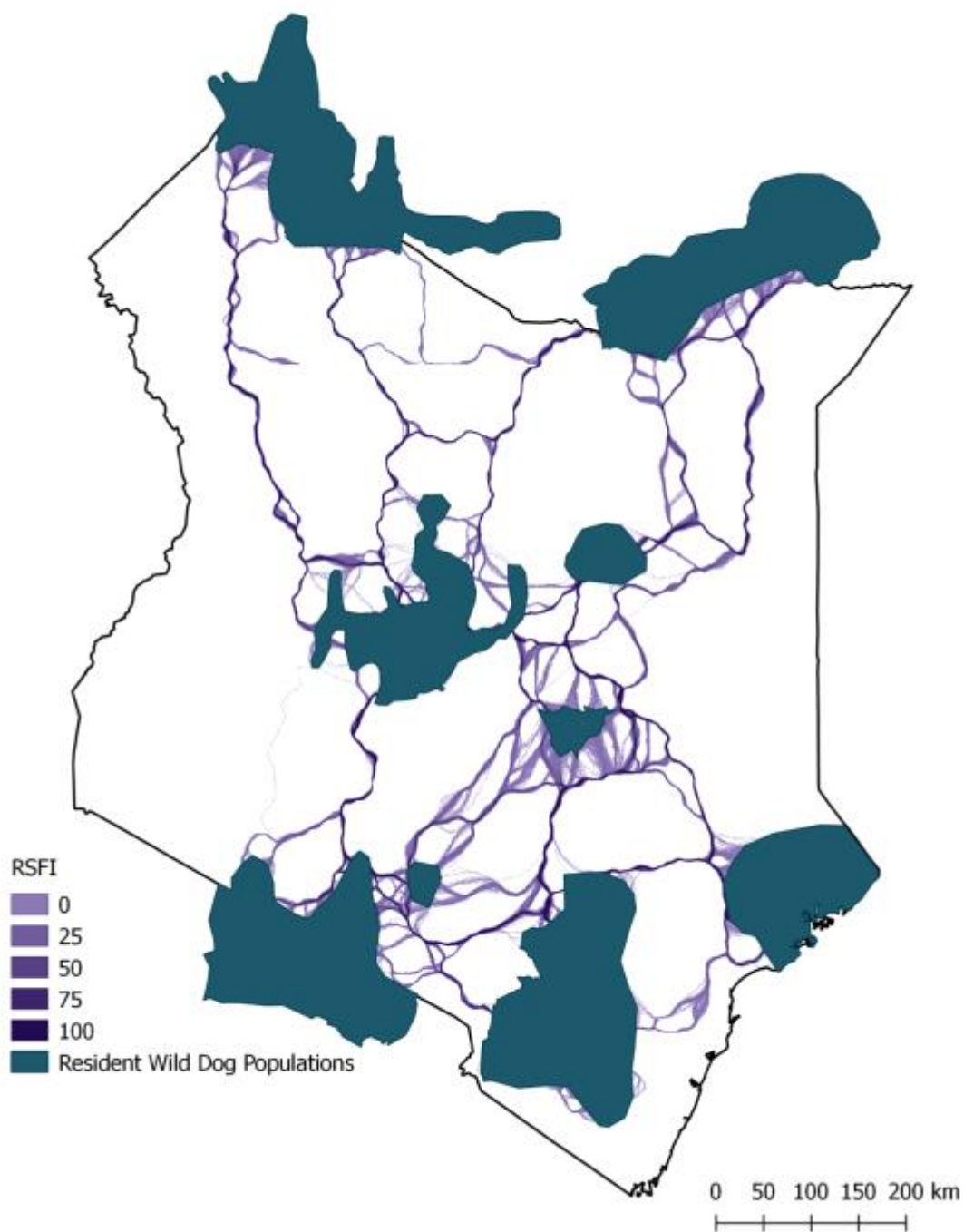
Appendix 2 Figure 4. Connectivity map based on the RSF model not including terrain ruggedness index (v_i) using GPS data from dispersal groups and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



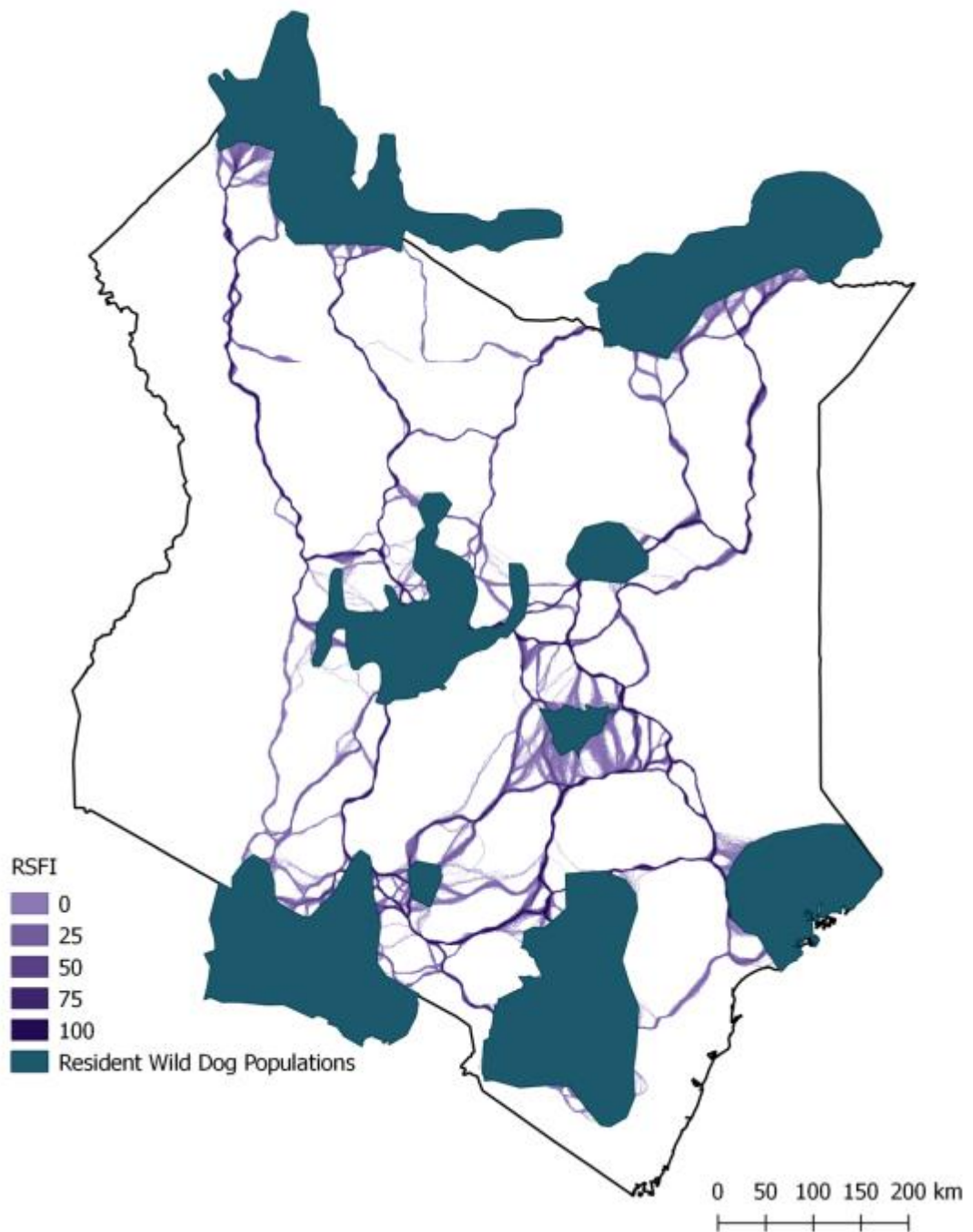
Appendix 2 Figure 5. Connectivity map based on the RSF model not including distance to rivers (iii) using GPS data from resident packs and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



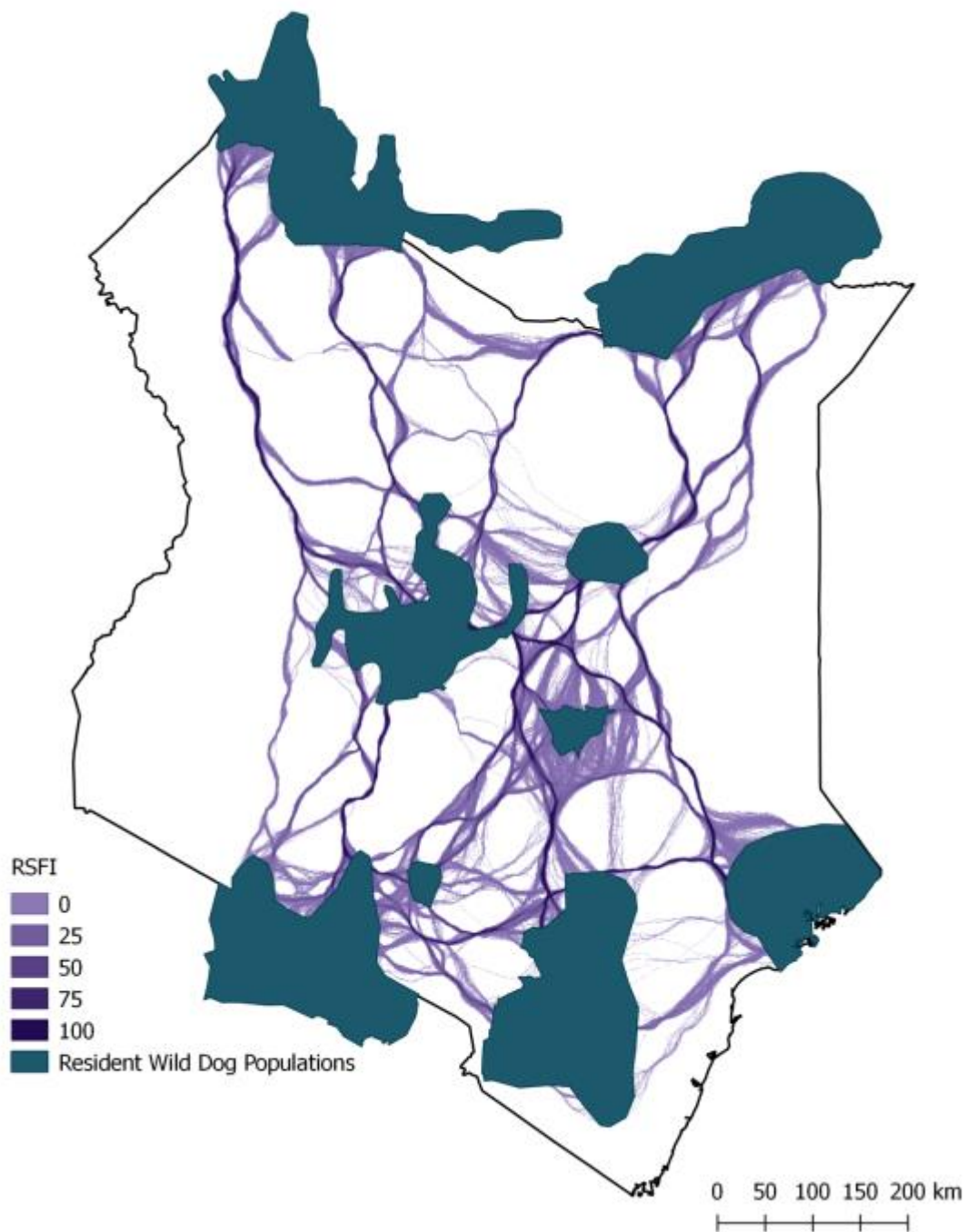
Appendix 2 Figure 6. Connectivity map based on the RSF model not including human population density (iv) using GPS data from resident packs and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



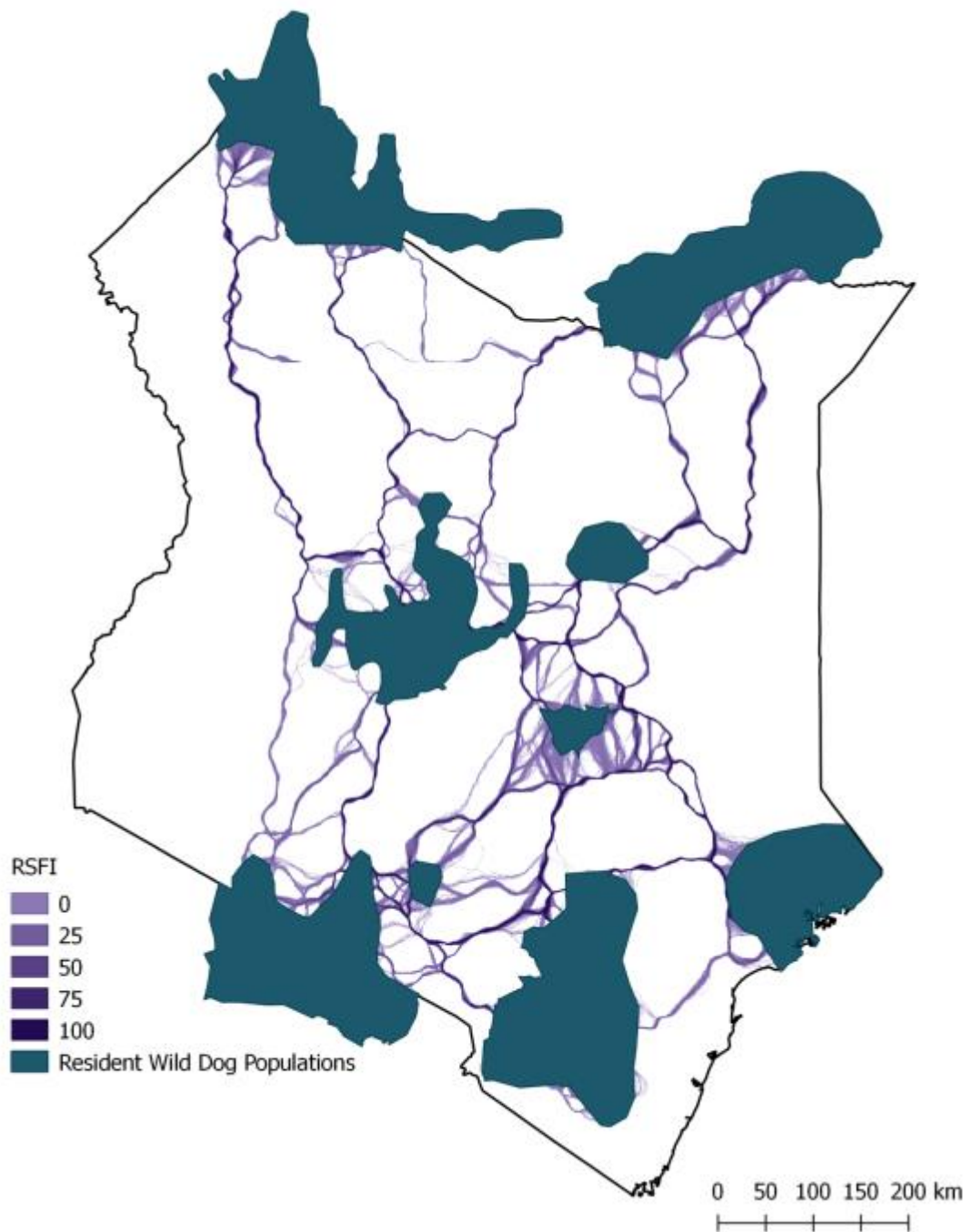
Appendix 2 Figure 7. Connectivity map based on the RSF model not including percentage tree cover (v) using GPS data from resident packs and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



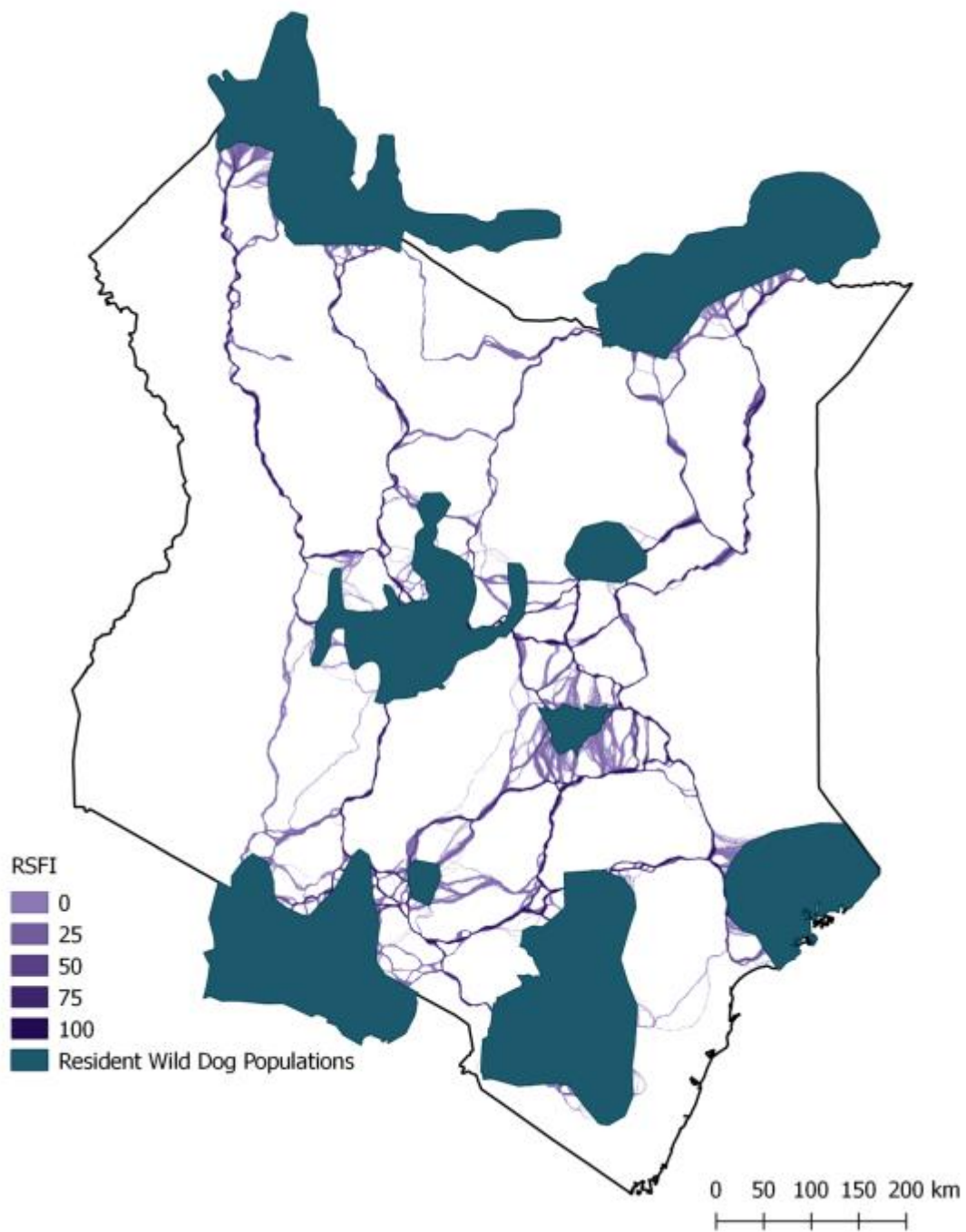
Appendix 2 Figure 8. Connectivity map based on the RSF model not including terrain ruggedness index (v_i) using GPS data from resident packs and a 3000m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



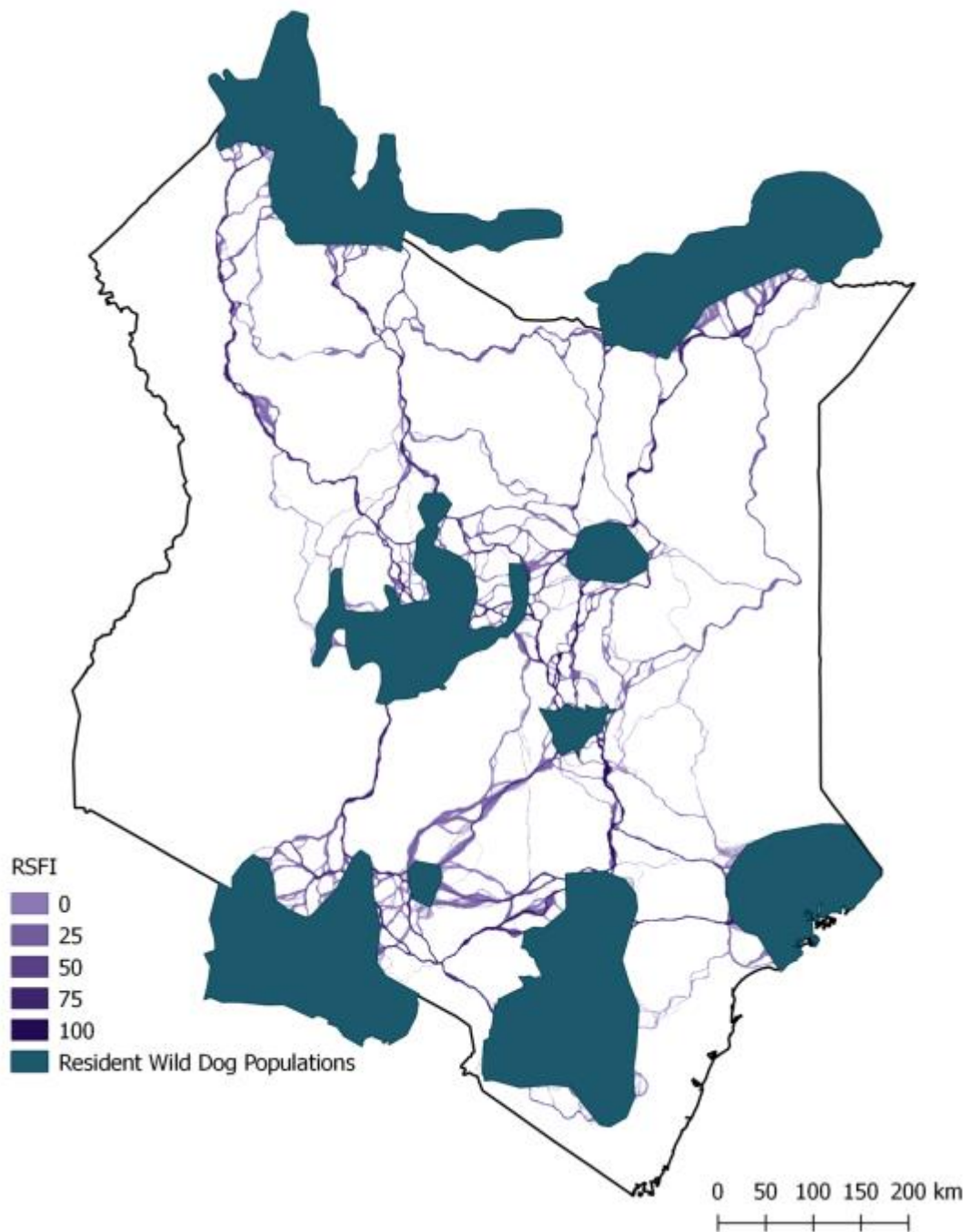
Appendix 2 Figure 9. Connectivity map based on the full RSF model (i) using GPS data from dispersal groups and a 1500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



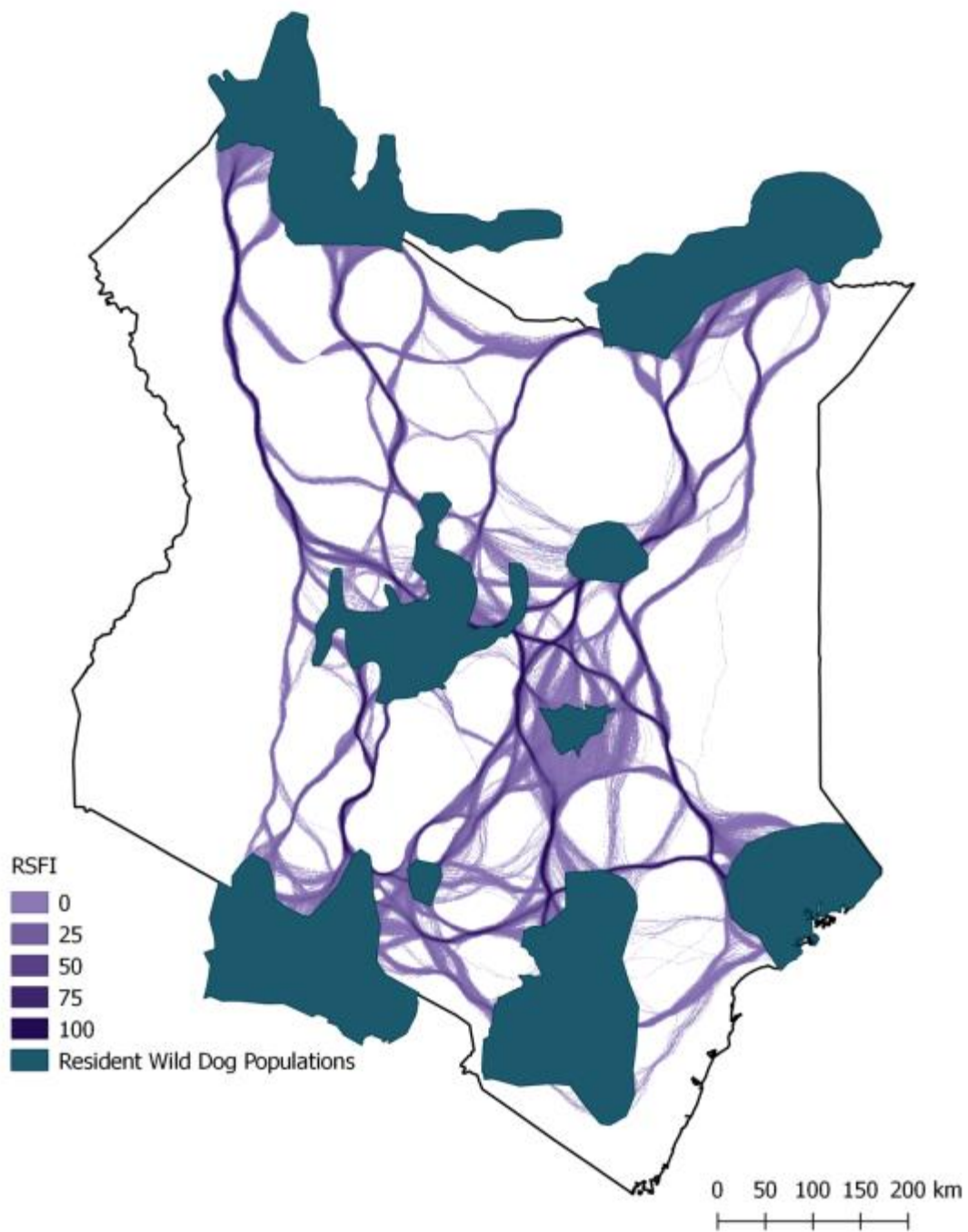
Appendix 2 Figure 10. Connectivity map based on the RSF model not including distance to roads (ii) using GPS data from dispersal groups and a 1500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



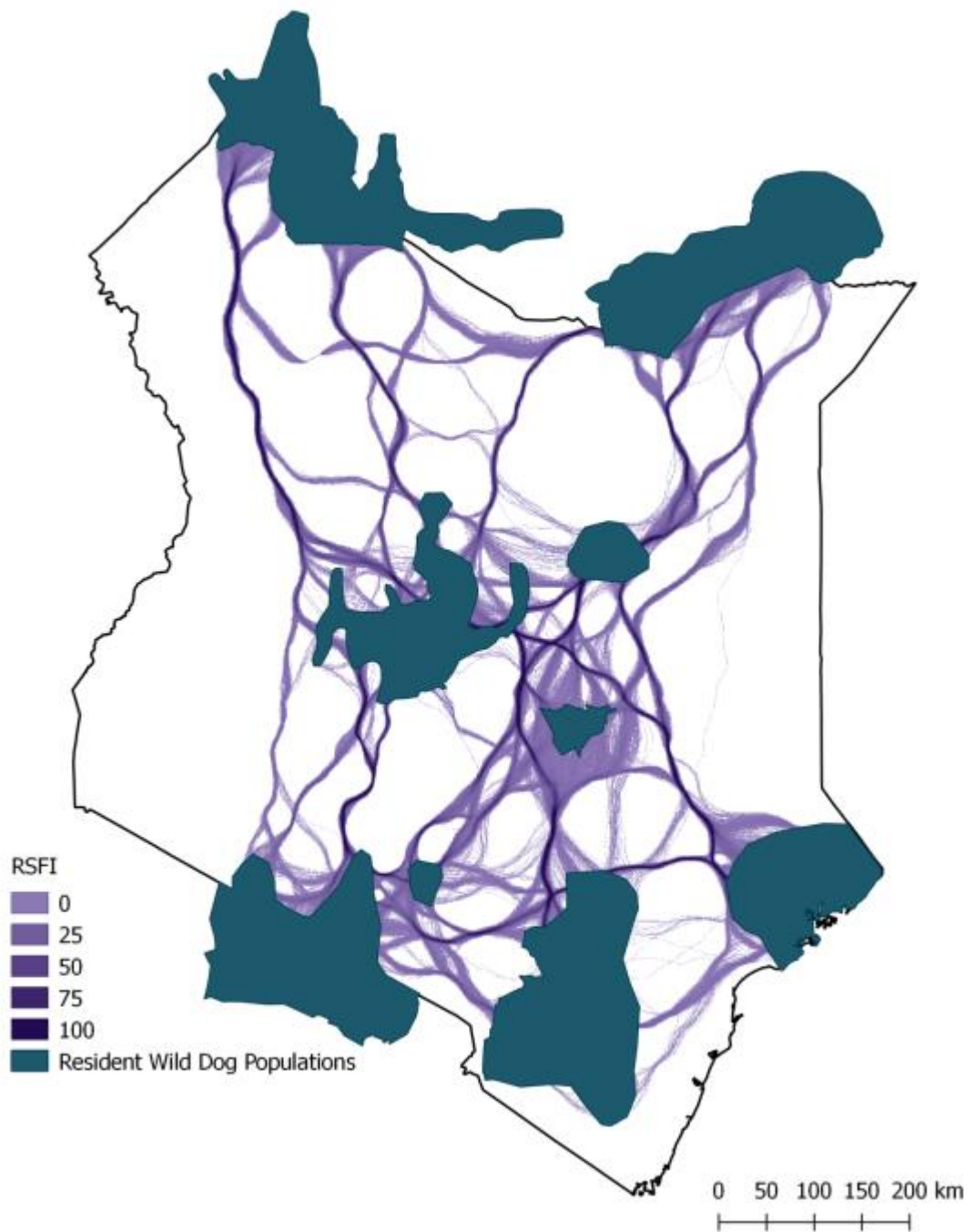
Appendix 2 Figure 11. Connectivity map based on the full RSF model (i) using GPS data from resident packs and a 1500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



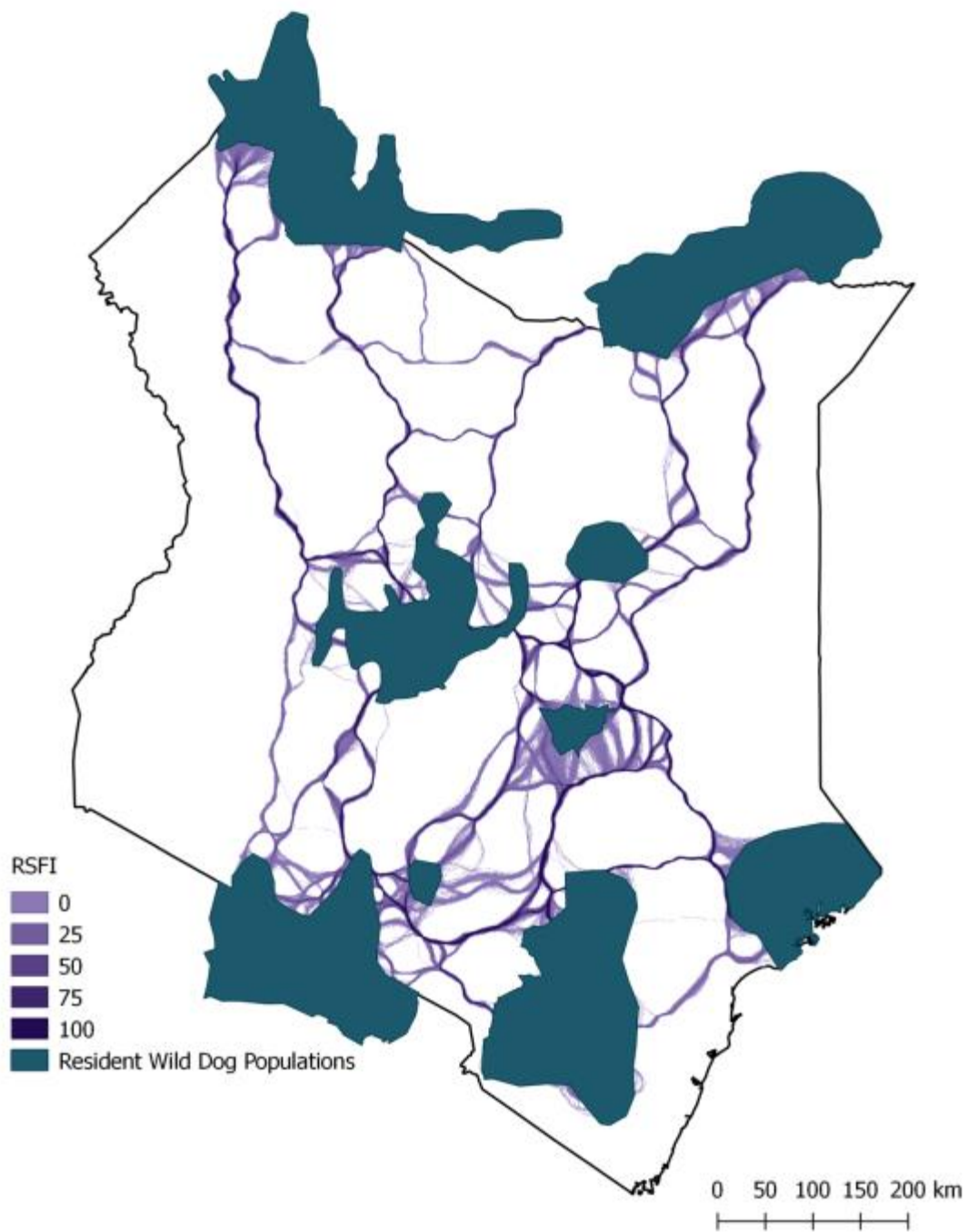
Appendix 2 Figure 12. Connectivity map based on the RSF model not including distance to roads (ii) using GPS data from resident packs and a 1500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



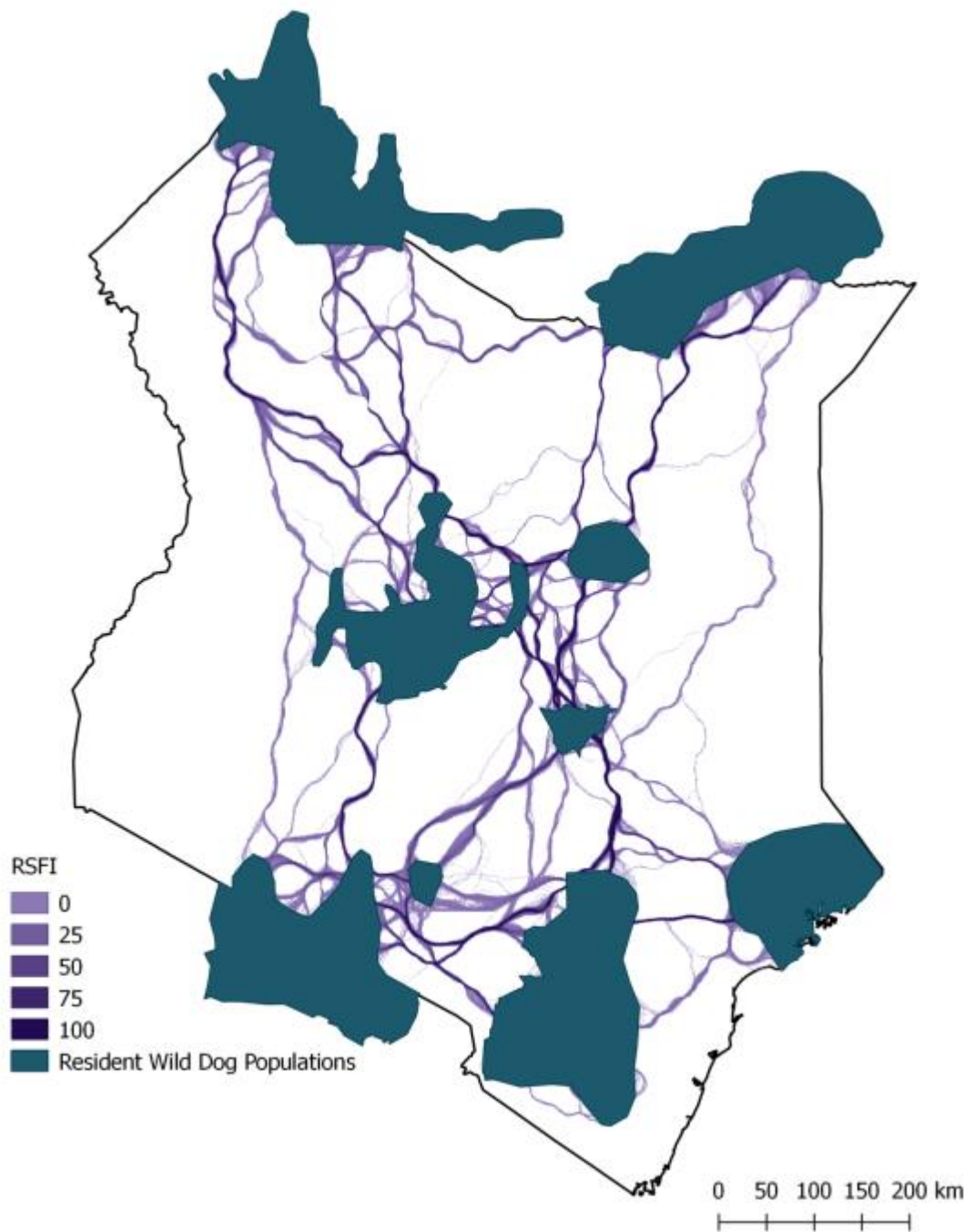
Appendix 2 Figure 13. Connectivity map based on the full RSF model (i) using GPS data from dispersal groups and a 4500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



Appendix 2 Figure 14. Connectivity map based on the RSF model not including distance to roads (ii) using GPS data from dispersal groups and a 4500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



Appendix 2 Figure 15. Connectivity map based on the full RSF model (i) using GPS data from resident packs and a 4500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



Appendix 2 Figure 16. Connectivity map based on the RSF model not including distance to roads (ii) using GPS data from resident packs and a 4500m moving window. Darker purples indicate cells that had higher frequencies of use in the simulations.



Plate 9. A cheetah

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