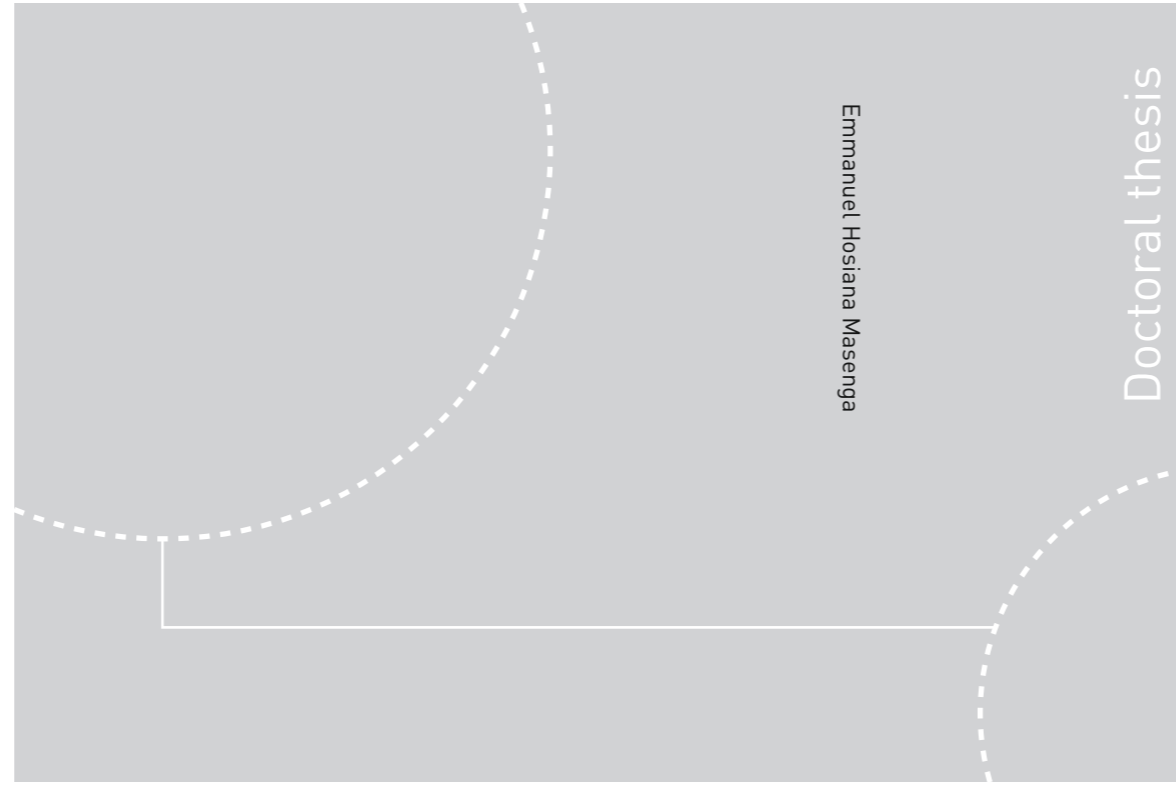


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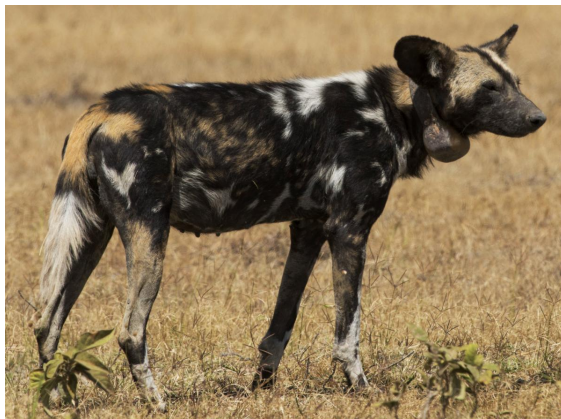
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Thesis for the Degree of Philosophiae Doctor

Trondheim, June 2017

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## Foreword

I remember the year 2005 when I started research on African wild dogs (*Lycaon pictus*) in the Serengeti ecosystem; it was a memorable moment when I fulfilled my dream of working with this endangered carnivore in Africa. During my research, I met several scientists and numerous people of different types. Among those was Prof. Eivin Røskoft of the Department of Biology at the Norwegian University of Science and Technology (NTNU), with whom I discussed conservation ideas, and thereafter, he guided me throughout my PhD study. I am truly thankful for your tireless effort in providing constructive ideas and your dedication in guiding me through my academic career development. I have no more words that I can say to you. *Asante sana!* Special thanks to my second supervisor Dr. Craig Ryan Jackson of the Norwegian Institute for Nature Research (NINA) for his guidance, commitment and constructive ideas during the initial planning of my field work and the writing of my thesis. I thank Dr. Roel May NINA and Dr. Frode Fossøy of NTNU/NINA for providing their expertise and sharing their experiences with me during the data analysis.

I gratefully acknowledge the financial support to SWCP from several donors, including Office of the President of United Republic of Tanzania under the former president, His Excellence Dr. Jakaya Mrisho Kikwete, Tanzania National Parks (TANAPA), Ngorongoro Conservation Area Authority (NCAA), Wildlife Division (WD), BIOTOPE (T) LTD., VODACOM (T) LTD., the Paul Tudor Johns Family Foundation, the Frankfurt Zoological Society, the Legendary Expedition, the Intergovernmental Policy Platform on Biodiversity and Ecosystem Services (IPBES) from the Ministry of Foreign Affairs through the Norwegian Environment Agency to the Norwegian University of Science and Technology (NTNU), and finally the EU-funded AfricanBioServices Project GA 641918 from where I received a scholarship to fulfil this writing.

I additionally wish to express my sincere gratitude to Dr. Simon Mduma the Director General of the Tanzania Wildlife Research Institute (TAWIRI) for his encouragement, advise and logistical support during my research period. I also thank Dr. Robert Fyumagwa, the Director of the Serengeti Wildlife Research Centre (SWRC), for both logistical support and encouraging me to pursue my academic career.

I would like to extend my appreciation to the Serengeti Wild Dog Conservation Project (SWCP), both the Steering and Technical Committee members, for the commitment. The Ngorongoro District Council, NCAA, TANAPA and Wildlife Division (WD) for

permission to allow the reintroduction of wild dogs in Serengeti National Park (SNP). Without their permission, I would not have been able to complete this PhD study.

I would like to express my thanks to Dr. Ernest Mjingo, my project colleague from TAWIRI, for his vigorous efforts in the capture and translocation of the wild dogs. I also thank Drs. Morris Kilewo, Emmanuel Macha and Idrissa Chuma of TANAPA for their routine health monitoring of the dogs in the boma. Dr. Sayalel Kuya of NCAA is also thanked for his support during the fieldwork.

Special thanks go to Mr. Kotikash Ngoya, Mr. Kamomoni Kuluo and Mr. Peter Kuban, the best local field assistants in the Loliondo Game Controlled Area (LGCA), for their dedication in locating the wild dogs; it was a pleasure to work with them! Thanks to the project staff and others for their commitment to monitoring the wild dogs in an area as large as the Serengeti ecosystem; their effort is praiseworthy.

I thank my office mates at the SWRC for carrying out my duties when I was out of the office and my working colleagues in the park, including Mr. Emilian Kihwele, the SNP ecologist, and the SNP management for their good collaboration, Mr. Joel Yesaya of Maswa Game Reserve (MGR) and Mr. Elibariki Bajuta the District Tourism Officer. Within TANAPA, I gratefully thank Mr. Inyasi Lejora (Manager Ecological Monitoring), Mr. Mtango Mtahiko, the retired chief park warden of the SNP, and Mr. William Mwakilema, the current chief park warden, for their logistical and moral support during the wild dog reintroduction programme.

My very special thanks to my lovely wife, Vick Wilfred Msack, and my family. I appreciate your encouragement and the time you have sacrificed to give birth to my last-born Ebenezer Emmanuel Masenga while I was away from home most of the time. Your love, patience, support and prayers are well renowned and appreciated. Thanks to my daughter Angel Emmanuel Masenga and my son Elisha Emmanuel Masenga for your prayers and inspiration to me during my study period while missing my care and guidance.

I extend my special thanks to my parents, Mr. Hosiana Ndesanjusia Masenga, my father, and Ms. Esther Gideon Sambo, my mother, for supporting my early studies and encouraging me to continue with further studies in all steps of life. I will not forget your role in my life; without you, I could not have reached this stage. Lastly but not least, I would like to thank my mother in Norway, Ms. Berit Røskaft, for her care and encouragement during my stay in Norway, in her presence, I felt home away from home, *Takk mamma!*

**THANK YOU ALL!**

Trondheim 2017

Emmanuel Hosiana Masenga

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## List of Papers

This thesis consists of five papers:

- I. Emmanuel Masenga, Craig Jackson, Ernest Mjingo, Roel May, Robert Fyumagwa, Richard Lyamuya and Eivin Røskaft (Submitted). Status of the African wild dog population in Loliondo Game Controlled Area, Tanzania.
- II. Emmanuel H. Masenga, Craig R. Jackson, Ernest E. Mjingo, Andrew Jacobson, Jason Riggio, Richard D. Lyamuya, Robert D. Fyumagwa, Markus Borner and Eivin Røskaft (2016). Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, 54, 95-98.
- III. Emmanuel Masenga, Craig Jackson, Roel May, Ernest Mjingo, Robert Fyumagwa, Mtango Mtahiko, Inyasi Lejora, Richard Lyamuya and Eivin Røskaft (Submitted). Home range utilization and habitat selection by African wild dogs (*Lycaon pictus*) in the Serengeti ecosystem, Tanzania.
- IV. Emmanuel Masenga, Craig Jackson, Roel May, Ernest Mjingo, Robert Fyumagwa, William Mwakilema, Richard Lyamuya and Eivin Røskaft (Submitted). Influence of prey abundance on diet choice by wild dog packs in the Serengeti ecosystem, Tanzania.
- V. Emmanuel Masenga, Ernest Mjingo, Robert Fyumagwa, Julius Keyyu, Craig Jackson, Roel May, Frode Fossøy, Emilian Kihwele, Morris Kilewo, Idrissa Chuma, Kuya Sayalel, Emmanuel Macha, Alex Choya, Elibariki Bajuta, Richard Lyamuya and Eivin Røskaft (Manuscript). Evaluation of the wild dog reintroduction programme into Serengeti National Park, Tanzania.

## Summary

Worldwide, large carnivore conservation has become an increasing challenge in the face of human population growth and anthropogenic development adjacent to protected areas. African wild dogs (*Lycaon pictus*) range widely and have low population densities. Such behaviours may expose the species to more anthropogenic influences than other large carnivores.

The Loliondo Game Controlled Area (LGCA) is characterized by a recently increasing human population with the majority being semi-nomadic Maasai pastoralists. The area has simultaneously accommodated an average of 10 packs of wild dogs, totalling about 120 individuals per year for the past decade. The packs range in different areas, avoiding areas near village centres, and the highest mean numbers of sightings were located in treed shrubland vegetation. Furthermore, retaliatory killings of wild dogs through poisoning of adult wild dogs and burning of pups in dens by local people due to livestock depredation, represents the greatest threats to wild dog conservation in the area.

An analysis of dispersal movement behaviour revealed the longest distances moved by wild dogs recorded to date. The two disperser groups covered straight-line distances of 250.4 and 520 km. We further observed that the dispersers utilized natural vegetation, as opposed to transformed habitats, more than 90% of the time.

In terms of home range utilization and habitat selection by African wild dogs, analysis of GPS satellite collar data revealed that the free-ranging packs had shorter step lengths, higher clustering in June - September and no clear patterns in the net squared displacement (NSD) compared to the reintroduced packs, which had smaller and larger core home range sizes throughout the long and short dry seasons, respectively. The wild dogs also changed foraging behaviours between seasons under different woody covers and selected different landforms during day and night. Hilly areas were preferentially selected during the night, and breaks, hills and low mountains were preferentially selected during daylight hours.

Our results further revealed that ten potential prey species of small to medium size herbivores were found within wild dog home ranges, of which Thomson's gazelle (*Eudorcas thomsonii*), wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and zebra (*Equus quagga*) showed the highest mean densities. Furthermore, a faecal analysis showed that Kirk's dik dik (*Madoqua kirkii*), Grant's gazelle (*Nanger granti*), impala and Thomson's

gazelle had significant spatio-temporal variability. Grant's gazelle and impala were the most preferred species by wild dog packs in the Serengeti ecosystem.

Evaluation of the wild dog reintroduction programme showed mixed levels of success after four packs established home ranges in livestock-free areas in the western part of the Serengeti ecosystem. The NSD model indicated that one reintroduced pack showed high release site fidelity. Survival rates for both the reintroduced and free-ranging male wild dogs to the age of 12 months were relatively high, with 68.29 % (n = 28) and 65.38 % (n = 17) respectively. We found no significant difference in survival rate between free-ranging and released individuals, but females tended to have lower survival than males, and pups had significantly lower survival than adults. Furthermore, two reintroduced packs reproduced successfully with an average of six pups survived after denning.

Based on our findings, effective monitoring of wild dogs in the Serengeti ecosystem should adopt a multi-institutional approach in a joint effort to conserve wild dogs to attain a long-term viable population. A detailed analysis of the movement behaviour of both resident and dispersing wild dog packs between natural vegetation cover and developed human areas is essential for future assessment of available habitat patches and population connectivity for wild dog conservation.

The findings from prey occurrences in the wild dog home ranges suggested that future research should focus on the influence of the landscape features (i.e., topography) on African wild dog prey selection in the Serengeti ecosystem. Lastly, we determined in this study that reintroduction had mixed success based on pack establishment under the two wild dog pack release protocols. Therefore, it is essential to further evaluate the reintroduction programme using longer-term data by incorporating other factors, including the eventual site of establishment, habitat suitability, assessment of community changes in attitudes on livestock depredation incidences by wild dogs in LGCA and wild dog packs utilization during denning into different landscape in the Serengeti ecosystem.

## **Introduction**

Protected areas do not occur in isolation from humans and include more than 12.7% of the world's land surface (Ray et al. 2005; Kemsey et al. 2012). Those protected areas act as biodiversity conservation benchmarks of the world flora and fauna (Chape et al. 2008; Lockwood et al. 2012; Sandilyan & Kathiresan 2012; Geldmann et al. 2013; Joppa et al. 2013; Watson et al. 2014). Although a large network of protected areas is still found in Africa (Newmark 2008), large carnivores have received unequal conservation and management attention by wildlife managers across the region due to their natural behaviour (Mills 1991; Weber & Rabinowitz 1996; Ray et al. 2005; Hayward & Somers 2009). Large carnivores are situated at the apex of the food web, which exposes them to anthropogenic influences from humans as well as challenges related to their ecological role as predators (Hayward & Somers 2009). Thus, large carnivores share common conservation challenges including large area requirements, prey depletion, edge effects of protected areas, low densities, conflict with humans, slow life cycles, diseases, complicated social structures and the effects of climate change (Woodroffe & Ginsberg 1998; Estes et al. 2011; Hermans et al. 2014; Ripple et al. 2014; Jones et al. 2016).

It is well documented that protected areas do not entirely prevent carnivores from moving outside (Woodroffe & Ginsberg 1998; Balme et al. 2010; Dickman et al. 2015). Most protected areas are found in rural areas, where the adjacent communities heavily depend on natural resource utilization, including wildlife harvesting, livestock keeping and the harvesting of forest products (Lockwood et al. 2012; Watson et al. 2014; Sinclair et al. 2015b). Because the human population in Africa has rapidly increased in recent decades, some areas around protected areas have been heavily affected (Ray et al. 2005; Newmark 2008; Sinclair & Dobson 2015). As a consequence, prey depletion, killing of carnivores for cultural motives, retaliatory killing due to depredation of livestock, urbanization and land use changes have recently been recorded in several ecosystems (Ray et al. 2005; Loveridge et al. 2007; Ikanda & Packer 2008; Ellis et al. 2010; Estes et al. 2012; Masenga et al. 2013; Koziarski et al. 2016). For this reason, in some areas, large carnivores have received more protection including fencing and active management actions to protect them, habitat and their prey (Ray et al. 2005; Packer et al. 2013; Woodroffe et al. 2014). This active conservation management approach has been successful in southern part of the African continent (Hayward et al. 2007; Gusset 2009; Hayward & Kerley 2009). In East Africa, the protection

of large carnivores has received unequal emphasis due to the different conservation regulations in different countries. For example, in Tanzania, high commitment has been shown by the government in setting aside 40% of its land as protected (Rija et al. 2013). However, challenges to the conservation of large carnivores remain, as they often move outside their boundaries and attain similar densities to those inside the protected area (Woodroffe & Ginsberg 1998; Maddox 2003).

The African wild dog is one of the world's most endangered large carnivores (Woodroffe & Sillero-Zubiri 2012). They are highly social and cooperative breeders (Girman et al. 1997; Creel & Creel 2015). Alpha pairs are usually responsible for breeding, and to some extent, other members may also breed in the same pack (Malcolm & Marten 1982; De Villiers et al. 2003; Spiering et al. 2010). The large pack size can defend the wild dogs from spotted hyaenas (*Crocuta crocuta*) attacks (Creel & Creel 2002). Pack size varies with and between different ecosystems (Creel & Creel 2002). A crucial pack size consisting of five adult individuals is important in the management and conservation planning of wild dogs (Courchamp et al. 2002).

Carnivore interactions are complex and dynamic (Linnell & Strand 2000; Glen & Dickman 2005). The interactions between African wild dogs, lions and hyaenas, which compete closely for food, may lead to the suppression of species with lower competitive abilities and inhibit population recovery. The interspecific competition between wild dogs with other large carnivores remains a major ecological challenge in conserving the species (Creel & Creel 1996; Creel et al. 2001; Groom et al. 2016). Wild dogs avoid areas with high densities of lions and hyaenas in SNP and Kruger National Park (Mills & Gorman 1997; Swanson et al. 2014; Groom et al. 2016). Presence of lions and hyaenas at high densities have been reported to influence spatio-temporal avoidance by wild dogs (Darnell et al. 2014). Maintaining the wild dog population with large populations of lions has been a major challenge to wild dog conservation, as the later kill wild dog pups (Woodroffe et al. 1997; Creel & Creel 1998; Creel 2001).

African wild dogs that live outside of protected areas are difficult to manage, as they come in contact with human habitats and domestic dogs, which expose them to diseases such as canine distemper virus and rabies (Woodroffe & Ginsberg 1998; Woodroffe 2000; Goller et al. 2010; Lembo et al. 2010). Even in well fenced areas in Southern Africa, reintroduced wild dogs escaped and came into conflict with farmers (Lindsey et al. 2005b; Davies-Mostert

et al. 2009). The species has been reported to cause economic loss due to livestock predation (Lindsey et al. 2005a). Although wild dogs provide economic wealth through tourist game viewing, they are less tolerated by farmers (Lindsey et al. 2005b; Gusset et al. 2008a).

The African wild dog's wide-ranging behaviour has been linked with its occurrence in areas with less large predators where human activities are also concentrated (Woodroffe 2000; Sillero-Zubiri et al. 2004; Woodroffe 2011). However, the level of mortality from humans is largely exemplified by road kills, snaring and poisoning (Woodroffe et al. 1997; Woodroffe et al. 2007a). Wild dogs have extensive home ranges due to their wide-ranging behaviour (Frame et al. 1979; Fuller & Kat 1990; Mills & Gorman 1997; Creel & Creel 2002; Woodroffe 2011). The home range of the wild dogs vary between different seasons (Fuller et al. 1992b). Despite this, territoriality remains a common phenomenon explaining the wild dog home range size variations with respect to resource acquisition (Frame et al. 1979; Mills & Gorman 1997; Creel & Creel 2002; Woodroffe 2011).

The cause of the local extinction of wild dogs in SNP in 1990s was under debate by the scientific community (Burrows 1994; Burrows et al. 1994; Ginsberg et al. 1995; East 1996). The controversy was due to the lack of a clear explanation for the pack disappearance except for the available evidence of interspecific competition with the lion and spotted hyaena and disease outbreaks such as canine distemper virus and rabies (Burrows 1992; Gascoyne et al. 1993; Burrows 1994). Regrettably, the dispersal behaviour has a sexual bias and may result in the long-distance movement of African wild dogs beyond their protected areas, which is well documented in East and South Africa (Frame & Frame 1976; Fuller et al. 1992a; McNutt 1996; Davies-Mostert et al. 2012; Masenga et al. 2016). However, this movement has increased biologists' knowledge to enable them to evaluate their connecting habitats and factors influencing wild dogs' movement in different landscapes (Davies-Mostert et al. 2012; Pomilia et al. 2015; Jackson et al. 2016; Masenga et al. 2016).

Carnivore reintroduction is a complicated management conservation approach (Woodroffe & Ginsberg 1999; Harrington et al. 2013; Batson et al. 2015). Scholars have suggested that, to some extent, the exercise has been unsuccessful because of poor prior planning of the reintroduction and post-release monitoring (Scheepers & Venzke 1995; Hayward et al. 2007; Gusset 2009; Hayward & Somers 2009; Ewen 2012; Harrington et al. 2013). The success of the reintroduction exercise is dependent on the source population as well as a suitable release site and the available resources (Hayward et al. 2007; Jule et al.

2008; Ewen 2012; Harrington et al. 2013). Evidence has shown high survival rates for released individuals and their offspring in successful wild dog re-introductions into small conservation areas in South Africa (Gusset et al. 2008b).

The development of telemetry technology and its application in ecology have improved our ability to link a species' movement behaviour with ecological parameters in different areas (Latombe et al. 2014; Edwards et al. 2015; Jenkins et al. 2015; Bastille-Rousseau et al. 2016). As a consequence, understanding what habitat provides connectivity between populations, including the evaluation of their denning behaviour and habitat selection, has been documented (Darnell et al. 2014; Jackson et al. 2014; Abrahms et al. 2015; Boyce et al. 2016; Jackson et al. 2016). Conserving wild dog habitat contribute not only to the species' conservation but also improves biodiversity conservation in general. It is important to protect wild dogs due to their vulnerability to extinction, and its role in the ecosystem function by using modern technology.

### **Aim of the Thesis**

The aim of this thesis was to examine and assess the behavioural ecology of African wild dogs in the Serengeti ecosystem, Tanzania.

The specific objectives of the study were:

- i. To assess the status of the African wild dog population in Loliondo Game Controlled Area (PAPER I).
- ii. To examine the long-distance dispersal movement of African wild dogs in East Africa (PAPER II).
- iii. To assess the home range utilization and habitat selection by African wild dogs in the Serengeti ecosystem, Tanzania (PAPER III).
- iv. To examine the influence of prey abundance on diet choice by wild dog packs in the Serengeti ecosystem, Tanzania (PAPER IV).
- v. To evaluate the wild dog reintroduction programme into Serengeti National Park, Tanzania (PAPER V).

## Methods

### *Study area*

The Serengeti Ecosystem covers an area of approximately 30,000 km<sup>2</sup> located in northern Tanzania and south-western Kenya, between latitudes 1° and 3° S and longitudes 34° and 36° E (Figure 1). On the Tanzanian side, it is bordered to the east by the Ngorongoro Crater highlands and Rift Valley and to the west by a western corridor that extends to the Speke Gulf of Lake Victoria. On the Kenyan side, it extends from the south-west to the north, bordering the Isuria escarpment and Loita plains (Sinclair et al. 2015a). This area is comprised of protected area network including SNP (14,763 km<sup>2</sup>), Ngorongoro Conservation Area (8,288 km<sup>2</sup>), game reserves (Maswa 2,200 km<sup>2</sup>, Ikorongo 563 km<sup>2</sup> and Grumeti 416 km<sup>2</sup>), Loliondo Game Controlled Area (4,000 km<sup>2</sup>) and the Ikoma open areas 600 km<sup>2</sup> in Tanzania and Maasai Mara National Reserve (1,368 km<sup>2</sup>) in Kenya (Kideghesho et al. 2006). These protected areas network form one of the most important cross-border conservation regions in the world.

The Serengeti ecosystem is surrounded by mostly pastoralist and agro-pastoralist tribes (Sinclair et al. 2015b). The eastern and southern parts are dominated by the Maasai, the south-west is dominated by the Sukuma and the north-west is dominated by the Wakurya (Sinclair et al. 2008). According to human population censuses, over the last decade, in all districts surrounding the Serengeti ecosystem on the Tanzanian side, the population has almost doubled (URT 2012). Consequently, the demand for agricultural land has increased, causing land use conflict between local people and conservationists in the Ngorongoro and Serengeti Districts and Maasai Mara National Reserve (Ogutu et al. 2011; Nelson 2012; Haulle 2015). The current threats to the ecosystem including bushmeat hunting, climate change impacts on wildebeest migration, poverty and a proposed road that will traverse the park (Kideghesho et al. 2006; Setsaas et al. 2007; Holdo et al. 2009; Dobson et al. 2010; Mwakatobe et al. 2012; Fyumagwa et al. 2013; Mwakaje et al. 2013; Hopcraft et al. 2015).

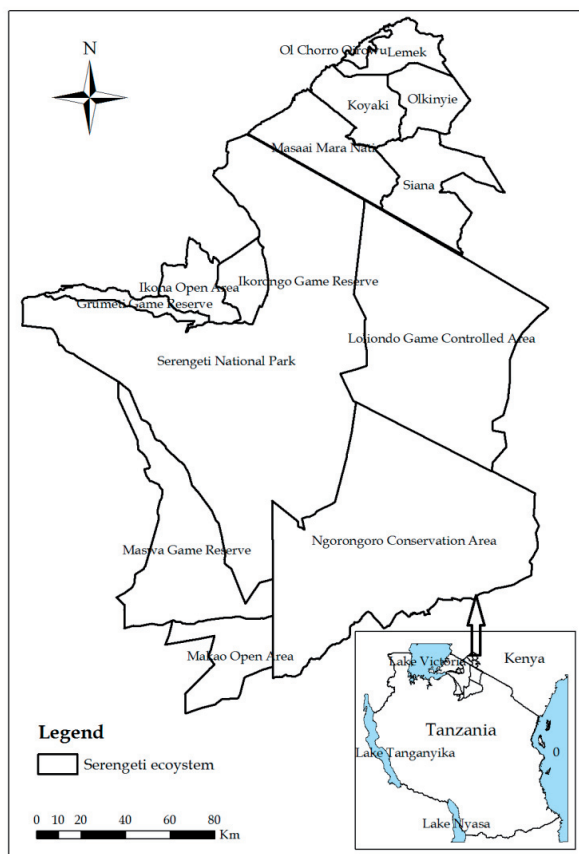
The ecosystem is home to approximately 70 mammal species and some 500 avifauna species (Sinclair & Arcese 1995). It supports one of the largest herds of migrating ungulates and the highest concentrations of large predators in the world (Homewood et al. 2001; Thirgood et al. 2004; Nelson 2012; Craft et al. 2015). Its high diversity in terms of species is a function of its diverse habitats, including riverine forests, swamps, kopjes, grasslands and woodlands. The area is characterised by grassland, mixed woodland, closed canopy riverine



forests, rocky outcrops, rivers and alkaline lakes. The south-eastern part of the area is open grassland, the northern part is largely wooded, and the western region is a mix of open and wooded areas.

The area exhibits a bimodal rainfall pattern, with the annual amount varying from the north-west (mean annual rainfall 1100 mm) to the south-east (500 mm). There is a dry season from July to October and sometimes in January and February, short rains from November to December, and long rains from March to May (Norton-Griffiths et al. 1975). However, in some years, inter-annual variations are inevitable, especially due to the effects of climate change (Wolanski & Gereta 2001). The monthly averages for the maximum temperature in the western Serengeti fluctuate between 25 °C to 32 °C, and the minimum temperatures are between 13 °C and 19 °C in the cold months (Campbell & Hofer 1995).

The region is located on a peneplain tilted up from *c.* 1000 m at Lake Victoria in the west to > 1800 m in the north-east. The soils of the Serengeti plains are of volcanic origin, alkaline, and rich in organic carbon and nutrients (de Wit 1978; McNaughton et al. 1988). In the north, the soils are derived from granite and gneiss and deposited in a complex way across an undulating arrangement of quartzite hills (Anderson et al. 2007).



**Figure 1:** Map of the Serengeti Ecosystem showing different protected areas between Tanzania and Kenya.

### *Study species*

African wild dogs are classified as endangered, with an estimated population of 6,600 individuals (Woodroffe & Sillero-Zubiri 2012). Viable populations are currently found in East and Southern Africa, while they are absent in North and West Africa, and low numbers are found in Central Africa and North-East Africa (Woodroffe & Sillero-Zubiri 2012). In East Africa, few individuals are found in southern Ethiopia, southern Sudan, northern Uganda and southern Somalia, while large populations are present in central and south-eastern Kenya (Figure 1). In Tanzania, wild dogs occur in large numbers within the Selous-Mikumi and

Serengeti-Tarangire-Manyara ecosystems and other protected areas including Mkomazi National Park and Ugalla Game Reserve (TAWIRI 2009).

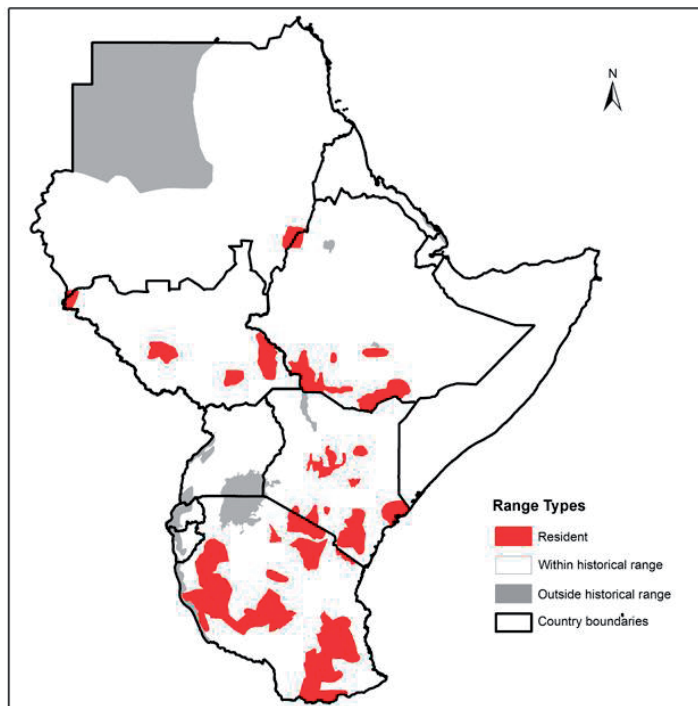
The African wild dog is large wild canid, standing 60-75 cm at the shoulder and weighing 22 to 25 kg on average and up to 30 kg, with long legs, large rounded ears and a very variable coat pattern (Estes 1991; Creel & Creel 2002). They have a short and broad skull, and females are slightly smaller in size than males. The body is identified by a distinctive colour distribution blotched with black, white, yellow and grey and a bushy tail, which frequently has a white end (Sillero-Zubiri et al. 2004).

Wild dogs are highly social and live in packs consisting of 2-27 individuals, although up to 40-100 individuals were occasionally recorded before the recent decline (Estes & Goddard 1967; Frame et al. 1979; Fanshawe & Fitzgibbon 1993; Maddock & Mills 1994; Creel & Creel 2002; Somers et al. 2008). Formerly, alpha pairs were reported to dominate reproduction, with subordinates rarely reproducing (Frame et al. 1979; Malcolm & Marten 1982). Recently, the use of genetic analysis revealed that subordinates may breed more often than was originally thought (Spiering et al. 2010). The breeding period occurs once per year, and the number of pups born averages between 8 and 12 but sometimes exceeds 20 (Frame et al. 1979; Geffen et al. 1996; Woodroffe et al. 1997). In East Africa, there is no fixed breeding season (Creel & Creel 2002), while in Southern Africa, it occurs between April - July (Kingdon 1988).

African wild dogs cooperate in hunting their prey (Creel & Creel 1995). The hunting strategies differs based on the prey size and habitat (Kühme 1965; Kruuk & Turner 1967; Kingdon 1988; Creel & Creel 1995; Hubel et al. 2016). Wild dogs eat 1.2-5.9 kg per dog and feed the pups after hunting (Nowak 2005). The wild dogs prefer to hunt small to medium sized herbivores, particularly hare (*Lepus* spp), oribi (*Ourebia ourebi*), duiker (*Sylvicapra grimmia*), Kirk's dik dik, Thomson's gazelle, impala, zebra, wildebeest, Grant's gazelle, bushbuck, warthog, kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*) and African buffalo (*Syncerus caffer*) calves (Kruuk & Turner 1967; Malcolm & Van Lawick 1975; Kingdon 1988; Creel & Creel 1995; Van Dyk & Slotow 2003; Woodroffe et al. 2007b; Hayward & Kerley 2008; Mbizah et al. 2012).

African wild dogs are found at low population densities and range widely, which exposes them to disease and persecution (Woodroffe & Ginsberg 1998; Woodroffe et al. 2007a; Woodroffe 2011; Masenga et al. 2016). At the landscape scale, wild dogs utilize

habitat types that are associated with lower lion densities (Creel & Creel 1996; Mills & Gorman 1997; Sillero-Zubiri et al. 2004). In some ecosystems, lions kill adult wild dogs and pups, and hyaena kleptoparasitism is another ecological challenge facing wild dogs (Woodroffe et al. 1997; Woodroffe et al. 2007a). Diseases from domestic dogs such as canine distemper and rabies have been reported to kill entire packs of wild dogs in LGCA in Tanzania and around Kruger National Park in South Africa (Woodroffe & Ginsberg 1999; Goller et al. 2010). Snares, road kills and poisoning are contributing factors to wild dog mortality (Woodroffe et al. 2007a; Masenga et al. 2013). Also, habitat loss due to human population increase remains a primary challenge in the conservation of wild dogs.



**Figure 2.** Wild dog resident range showed in red colour in Eastern Africa 2013 (Range Wide Conservation Program for Cheetah and African Wild Dogs).

### ***Data collection***

The wild dog information in this study was collected between 2005 and January 2017 (**Papers I-V**).

### **Population status and distribution**

Packs were searched for by trained village game scouts and researchers to collect information when the dogs were sighted: 1) date; 2) pack size; 3) number of individuals; 4) sex and age (pups and adults); 5) Global Positioning System (GPS) locations; 6) vegetation types; 7) known pack (i.e., those with photo ID available or denning history) and assigned specific names. We defined unknown packs as dispersing groups with 1-8 individuals, as described by McNutt (1996). For the purpose of avoiding pseudo-replication, each sighting was treated independently when observed on different dates (**Paper I**).

### **Movement behaviour**

Wild dogs were immobilised by veterinarians using a 100-mg total dose of Zoletil, projected from a gas-powered dart gun (Dan-Inject MOD JM, Denmark). Two individuals in each pack, preferably adults, were equipped with GPS satellite collars (African Wildlife Tracking, Pretoria, South Africa). The collars were set to deliver positions at least two to six times (05:00, 08:00, 12:00, 17:00, 19:00 and 0:00) per day. The distance moved by each pack was determined based on the closest locational fixes to 00:00 and 12:00 hrs from the planned schedule to facilitate the movement, diet choice, home range and habitat selection analyses (**Papers II, III, IV & V**).

### **Wild dog prey data**

Four reintroduced packs and two free-ranging packs fitted with GPS satellite collars were located in the early morning and evening as per the monitoring schedule (**Paper III**). Random transects were placed heading either towards the north, south, east or west away from the location of the pack. In the case of inaccessible areas, the closest road was selected. Our transects varied in length from 2 to 12 km due to terrain variations where the packs were

sighted. A Land Rover 4x4 pickup was driven at a speed of 20 km/hr, with two observers standing on the back. The prey species were recorded within a distance of 100 m on both the right and left sides along the transect. The counting started between 7:00 am to 10:00 am and resumed between 4:00 pm to 6:00 pm. In each transect, start and end times were recorded. The vehicle was stopped when an individual animal or a group of animals was sighted. For each sighting, the following information was recorded; date, pack GPS location, rain, potential prey species observed, total number of individuals in a group, and age class. The total distance covered at the end of each transect was also recorded using a vehicle odometer (**Paper IV**).

#### **African wild dog faecal samples**

The wild dog packs were located as described in **Paper IV**. A sample collected immediately after defecation was referred to as a fresh sample, while a sample that was collected in the absence of dogs was referred to as an old sample (see Breuer 2005). Thereafter, the collected faecal samples were stored inside a plastic container with ice packs and then labelled and stored in a -20 °C freezer, until the end of each month, for analysis (**Paper IV**).

#### **Survival of wild dogs**

Both the free-ranging and reintroduced wild dog packs were monitored by visual sightings and radio-telemetry (**Papers II-V**). The age classes were defined as pups when <12 months of age, yearlings 12-24 months and adult dogs >24 months of age, as described by Gusset and Macdonald (2010). The individuals in each pack were identified by age and sex, and the cause of mortality for each individual was established (**Paper V**).

## **Major Results**

### ***Status of wild dog population - Paper I***

Overall, the LGCA had a resident wild dog population with an average of 10 packs sighted per year. The pack consists of an average of 12 individuals per pack. The average number of adult dogs per pack was 9.5, although it varied between years. The total population was approximately 120 individuals. The estimated home range size varied between different packs (i.e., 53 to 2347 km<sup>2</sup> for the 95% minimum convex polygon), with a median of 335 km<sup>2</sup>. Most of the packs were found outside the village centre locations, with the highest mean sightings recorded in the treed shrubland vegetation type. The greatest threats practised by local people to kill the wild dogs were poisoning and burning of their den sites.

### ***Long-distance dispersal - Paper II***

The study findings revealed the furthest wild dog dispersal distance ever recorded. The two dispersal incidents occurred from different places: group I dispersed from SNP and group II from LGCA, both towards the neighbouring country Kenya. The straight-line distances covered by the two groups were 202.4 km and 520.4 km, respectively. Group I comprised only single female, while group II had both sexes. Group II traversed different protected areas including Mount Suswa Conservancy, Loitokitok Forest Reserve, Longonot, Hell's Gate, Tsavo West and Chyulu Hills National Parks in Kenya and Mkomazi and Kilimanjaro National Parks in Tanzania before the collar battery expired.

### ***Home range utilization and habitat selection - Paper III***

The results from this study suggest that the free-ranging packs had shorter step lengths and high clustering during July to September and utilized smaller areas compared to the reintroduced packs. The NSD model revealed distinguished movement patterns for the free-ranging and reintroduced packs. For the free-ranging packs, shorter step lengths coincided with the peak denning period of wild dogs occurring between June and September in the Serengeti ecosystem. The model best explaining the variation in home range size at 95% and 50% kernel density isopleths was based on season. Small and large home range sizes for free-ranging packs were recorded during the long dry and short rain periods, respectively. Both the free-ranging and reintroduced packs exhibited larger home range sizes during the short rain and short dry periods. In this study, the habitat selection model including interactions between woody cover, season and landform performed better in explaining the resource

selection by African wild dogs. The wild dogs selected against denser woody cover during the short dry and long rain seasons and the opposite for the other two seasons. The wild dogs had a significantly higher preference for irregular plains and breaks during the night compared to the time of day where they preferred breaks, hills and low mountains.

#### ***Prey abundance and diet choice by wild dogs - Paper IV***

Conserving the prey species available within the wild dogs' home range is essential for species management planning (Krüger et al. 1999; Hayward et al. 2006; Woodroffe et al. 2007b; Mbizah et al. 2012; Ford et al. 2015). The results showed that the spatial and temporal mean densities for the impala, zebra, Thomson's gazelle and wildebeest were higher in the wild dog home ranges among the ten species recorded. Within the packs, the wildebeest densities were higher for the Kikwete and Osinoni packs' home ranges, while zebra and Thomson's gazelle densities were higher for the Nyasirori and Osinoni packs' home range. Topi (*Damaliscus lunatus*) density was higher in the Nyasirori pack home range. During the long rain, short dry, and long dry seasons, the zebra, Thomson's gazelle and wildebeest densities were higher compared to those in the short rain season. The modelling approach revealed that apart from reedbuck, all other prey species showed spatio-temporal variation in their densities. Impala and Grant's gazelle were the most preferred prey species. The wild dog prey preferences were in agreement with the increase in prey densities in the wild dog home range.

#### ***Evaluation of wild dog reintroduction programme - Paper V***

In recent decades, the improvement of wildlife monitoring through the application of GPS satellite collars has been particularly useful for the close monitoring of individuals released as part of species reintroduction programs (Vandel et al. 2006; Devineau et al. 2010; Hebblewhite & Haydon 2010; Lewis et al. 2012). To evaluate the initial project success of a reintroduction exercise, 12 months of post-release monitoring data from six wild dog packs released into SNP were used. Our results showed that of the six released packs, four packs established home ranges in livestock-free areas (SNP, MGR and Ikorongo Grumeti Game Reserves). Differences in wild dog pack release protocols; those packs in which some members were released and others left inside the boma established home range close to the boma than those packs that were released with all members established home range away from the release site. Our survival modelling approach showed there was no statistically significant difference in survival rate between reintroduced and free-ranging wild dog packs.



Two reintroduced packs were found denning, and an average of six pups survived after the denning period.

## **Discussion**

It is known that large carnivore populations are declining globally (Chape et al. 2008; Ripple et al. 2014). Thus, conservationists have suggested different approaches to enhance human-carnivore co-existence and carnivore population management (Hayward et al. 2007; Davies-Mostert et al. 2009; Hayward & Somers 2009; Ewen 2012; Msuha et al. 2012; Packer et al. 2013; Riggio et al. 2013; Durant et al. 2015; Sarkar et al. 2016). Large carnivores have been reported to move outside protected areas, which has made their protection by managers or conservationists more difficult (Woodroffe & Ginsberg 1998; Woodroffe 2000; Balme et al. 2010; Woodroffe 2011). In Tanzania, large carnivores have already experienced consequences within the Ruaha, Tarangire-Manyara and Serengeti ecosystems (Dickman 2010; Craft et al. 2015; Dickman et al. 2015; Koziarski et al. 2016). African wild dogs are found in different habitats and are able to thrive well in a diverse of habitats including human-dominated areas (Creel & Creel 2002; Woodroffe 2011). However, interspecific competition with lions and hyaenas and diseases from domestic dogs have been suggested to cause the local extinction of wild dogs on the short-grassland plain in the SNP in the 1990s (Gascoyne et al. 1993; Ginsberg et al. 1995). Fortunately, part of the same population persisted outside SNP (Burrows et al. 1994; Masenga & Mentzel 2005; Lyamuya et al. 2016), and this population formed the basis of our current effort to protect the wild dogs in the Serengeti ecosystem. Therefore, in this part, I examine how the results from this study contribute to wild dog conservation in Tanzania as well as the whole of East Africa. The information obtained forms a platform for current species behavioural ecology knowledge such as wild dog co-existence with humans, movement behaviour, home range utilization, habitat selection, prey preferences, dispersal abilities, threats from humans and the short-term evaluation of reintroduced wild dog packs. These findings should be well considered by management authorities in the planning and management of the wild dog population in order to prevent the future extinction of this species in the Serengeti ecosystem.

### ***Status of wild dog population***

In this paper, the major finding was the presence of an established resident population of wild dogs in the LGCA. The mean of 12 individuals per pack, totalling 120 animals, approaches the values of other well-established populations (Maddock & Mills 1994; Courchamp & Macdonald 2001; Creel & Creel 2002; Creel et al. 2004; Lindsey et al. 2004; Sillero-Zubiri et al. 2004; Woodroffe et al. 2005; McNutt & Silk 2008). Nonetheless, no free movement of wild dog packs has occurred to recolonize the SNP during this study period. The interspecific competition with lion and hyena populations (Schaller 2009; Swanson et al. 2014) may exclude the wild dog population from the SNP and limit the protected areas' feasibility to conserve a large population of wild dogs. The majority of the wild dog sightings were in treed shrubland vegetation, which has diverse habitats that support a reasonable number of herbivore species, which attract the wild dogs (Sinclair et al. 2002).

Anthropogenic influences, including poisoning and the burning of wild dogs' den sites, have serious consequences for the wild dog population's growth. Similarly, the retaliatory killing of wild dogs by local people is difficult to prevent, and human-wild dog conflict is well-known in the area (Masenga et al. 2013; Lyamuya et al. 2014). Human development, including the construction of a major road that will pass through both LGCA and SNP (Fyumagwa et al. 2013), may also limit the future growth of the wild dog population due to the road mortality caused by the increased traffic volumes and speeds, as reported elsewhere (Creel & Creel 2002; Woodroffe et al. 2007a).

### ***Long-distance dispersal***

Previous studies from southern Africa documented that long-distance dispersal is male-biased (McNutt 1996; Davies-Mostert et al. 2012), although the two longest dispersals recorded in East Africa (77 and 195 km) were groups of females (Fuller et al. 1992a; Creel & Creel 2002). In this study, single-sex and mixed-sex dispersal groups were recorded and closely monitored by GPS satellite collars. Ground-truthing showed that group I found mates and settled in Kenya, while group II wandered through different protected areas within Kenya and Tanzania. The low wild dog population densities are likely the explanation of why the dogs of group II were unable to find mates. GPS satellite collars also provide important information on how wild dogs strategically avoid different human-dominated landscapes. During their movements, their GPS relocations were mostly detected in natural vegetation types.

### ***Home range utilization and habitat selection***

The results support our hypothesis (Paper\_III). The free-ranging packs' short step lengths coincided with the peak denning period occurring between June and September in the Serengeti ecosystem. During denning, packs stay close to one central location (the den) for three months to care for the pups, resulting in greatly reduced movement. The differences in NSD is attributed to this behavioural change. The explanation of why the free-ranging packs had small NSDs is most due to established territories in human-dominated areas (Paper\_I), while reintroduced packs may wander more within an area unfamiliar to them.

The results from this study showed variations in the home range sizes between seasons. The long dry period coincided with the denning season, when the packs confined themselves to small areas to raise the pups, leading to reduced movement (Frame et al. 1979; Creel & Creel 2002). Both the free-ranging and reintroduced packs exhibited larger home range sizes during the short rain and short dry periods. The shift of the home range was attributed to the seasonal movement of large migratory herbivores, as reported in earlier studies (Frame et al. 1979; Fuller et al. 1992b).

The wild dogs also used denser woody cover during the short rain and long dry seasons. Wildebeests favoured similar habitats when migrating toward the northern or southern parts of the Serengeti ecosystem (McNaughton 1979; Thirgood et al. 2004; Hopcraft et al. 2014). The wildebeests use more open habitats for calving and nursing their young (Estes 1976). The behavioural shift of the wildebeest suggests that wild dogs may select habitats that maximize the best forage areas. The wild dogs selected hilly areas during the night and breaks, hills and low mountains during the daytime hours.

### ***Prey abundance and diet choice by wild dogs***

The seasonal variation in the home range size (Paper\_III) corresponds to the spatio-temporal variation in the mean densities of prey species occurring in the wild dog home range (Paper\_IV). This wild dog behaviour improves resource acquisition while increasing their close contact with a diversity of prey species in different seasons. For example, the highest topi density was observed in the Nyasirori pack's home range, explaining why this pack lived in one place for most of their time was strongly influenced by the remaining packs members' presence in the holding facility (Paper\_V), and also impalas were frequently sighted in wooded habitats. Evidence from another study conducted in the SNP showed that impalas

occurred at the highest density inside the park and of recently adjacent reserves (Setsaas et al. 2007; Goodman 2014).

Among other factors (i.e., rainfall, nutrients and vegetation types) described in earlier studies (Holdo et al. 2009; Hopcraft 2010), the spatial variation in prey species densities is affected by a combination of predation pressure from large carnivores (Sinclair 1985; Hofer & East 1995; Sinclair et al. 2003; Grange et al. 2004; Hopcraft et al. 2014), as well as high poaching pressure and an increase in the human population surrounding SNP (Makacha et al. 1982; Campbell & Borner 1995; Loibooki et al. 2002; Rentsch & Damon 2013).

As also observed in earlier studies in East and South Africa (Kruuk & Turner 1967; Fanshawe & Fitzgibbon 1993; Creel & Creel 1996; Carbone et al. 2005; Woodroffe et al. 2007b; Ramnanan et al. 2013; Arts et al. 2014), our findings suggest that wild dogs' potential prey species are Kirk's dik dik, impala, Grant gazelle and Thomson's gazelle. Our results are consistent with previous findings (Estes & Goddard 1967; Hayward et al. 2006; Mbizah et al. 2012). Similarly, observations of wild dog hunts showed that Thomson's gazelles were frequently hunted in the Serengeti ecosystem (Frame 1986; Fuller & Kat 1990; Carbone et al. 2005).

Many other studies in southern Africa suggested that wild dogs prefer impala (Mills & Gorman 1997; Hayward et al. 2006; Van der Meer et al. 2011; Mbizah et al. 2012). The wild dog packs were mostly found in wooded habitats; therefore, most of our surveys were conducted in such habitats (Paper\_III). Impala and Grant's gazelle showed a positive functional response in the wild dogs' diet, which supports our hypothesis that African wild dogs kill prey species relative to their availability.

#### ***Evaluation of wild dog reintroduction***

Our results showed that, based on reintroduction evaluation criteria from earlier studies (Gusset et al. 2008b; Gusset 2009), the project experienced a mixed success. The majority of the reintroduced packs showed no homing behaviour with respect to their movement towards the capture site. In this study, we found that the differences in pack movement and settlement near the release site revealed by the NSD model were mostly based on the altered social bonds. The differences in the acclimatization period for the released packs are because some members were retained in the enclosure due to whelping shortly before the release. However,

the first released wild dog pack, wandered in large areas within the park and adjacent areas, suggesting that there were no other wild dog packs in SNP (Paper\_II ; Paper\_V).

We found effect of sex and age on wild dog survival corroborating with previous studies, which showed sex difference in wild dogs' survival (Burrows et al. 1994; Maddock & Mills 1994; McNutt 1996; Creel & Creel 2002). Our field observations showed that females are responsible in first-line chasing prey which predispose them to injuries/death from attack by both prey and large predators, similar to what was described previously (Estes & Goddard 1967; Schaller 1972), thus resulting in low survival of females. Such behaviour probably increased mortality risk in areas where large intra-guild competitors are found. In this study, pup mortality was associated with release age (i.e., less than 12 months indicated high mortality) for reintroduced packs and persecution from humans for free-ranging packs. Indeed, persecution remained a possible contributing factor to the pups' low annual survival rate in the area (Paper\_I).

We found that there was no significant difference in the pack annual survival between the reintroduced and free-ranging packs in the Serengeti ecosystem. This is clearly explained by the ability of the wild dog packs to select a suitable home range and foraging habitat in different seasons (Paper\_III ; Paper\_IV). Likewise, the suitability of habitat similarities within the current range showed that the wild dogs selected more rugged terrain (Jackson 2014), which is unsuitable for lions (Jackson et al. 2014). Our current wild dog packs' denning sites were located on hilly areas that are less favoured by both lions and hyaenas, which have probably increased the survival of the pups that were born by the reintroduced packs. The average survival of six pups after denning is promising for the conservation of the wild dogs in the SNP, as the number approaches the value reported in their study by Frame et al. (1979).

### **Conclusions and recommendations**

The results of this thesis provide current knowledge for the conservation of wild dogs in the Serengeti ecosystem. The study findings broaden our knowledge on the species ecological habitat requirements and home range utilization, prey preferences and adaptation behaviour for the reintroduced wild dog packs in the SNP. The results from this study were thoroughly discussed and future perspectives suggested in each paper.

## ***Conclusions***

Our findings suggest that the LGCA supports a sizeable wild dog population and remains an important area for the conservation, not only of the endangered African wild dogs, but also the different wildlife species within the Serengeti ecosystem. The current population is facing threats from human population growth and livestock population increase. Whilst the SNP is a well-protected area, we have noted that wild dogs are unable to move freely from LGCA and establish populations due to interspecific competition from both lions and hyaenas.

The knowledge acquired from GPS satellite collars improved our understanding of wild dog dispersal movements. The wild dogs showed distinguished movement decisions between natural habitats and disturbed habitats. The current information provides evidence on potential areas for wild dog conservation planning, despite the small sample size due to the endangered status of the species. The lack of pack formation for group II may be an evidence of the lack of neighbouring packs in the areas the pack traversed, combined with their mixed-sex pack composition during dispersal.

The results from this study reveal that the variability in the wild dog movement patterns in the Serengeti ecosystem can be primarily attributed to the status of the two study groups. The free-ranging packs showed shorter movement, while the reintroduced packs moved longer distances in exploring the safe habitats in livestock-free areas (i.e., SNP, MGR and IGGRs). Survival strategies for wild dogs were also recognised in different woody covers and landforms between seasons and time of day. The use of hills during the night provided a safe habitat for wild dogs for resting, and the use of breaks, hills and low mountains during the time of day increased the wild dogs' foraging behaviour in areas where the lions and hyaenas are fewer.

The findings from this study showed the spatio-temporal variation of the prey densities in the wild dog home ranges in the Serengeti ecosystem. The Thomson's gazelle, wildebeest, impala and zebra were found at high mean densities for all seasons and pack locations. The Kirk's dik dik, impala, Grant's and Thomson's gazelles were significantly represented in faeces, and they made up the wild dogs' diet in the Serengeti ecosystem. The impala and Grant's gazelle were the most preferred species by the African wild dog in the Serengeti ecosystem.

The results from this study suggest that the conservation of African wild dog populations through reintroduction is challenging in areas in which the species suffers both interspecific competition and persecution from humans. We observed that some of the reintroduced wild dog packs settled with only two packs having reproduced successfully after being released into SNP during the first year of post-monitoring.

### ***Recommendations***

Conservation efforts for the wild dog population in the LGCA need to involve local people to enhance their future co-existence in the area. Controlling both human and livestock population increases should be the first step in ensuring the long-term conservation of a viable population of wild dogs in protected areas occupied by humans (i.e., LGCA and NCA). Furthermore, long-term follow-up of the current known wild dog packs using GPS satellite collars is necessary. This will strengthen future collaboration with local people in controlling depredation incidences through following the wild dogs' daily movements and relocations. Additionally, mobile telephone technology will be applied by the village game scouts (VGS) to notify the local community of the areas where the wild dogs are denning and protect them by not sending their livestock near those dens. This will help to investigate community attitudes towards wildlife conservation in the future through research. To manage this, the studies recommend that the free-ranging packs in the LGCA and Ngorongoro Conservation Area should be equipped with GPS satellite collars to understand their movement behaviour, pack overlap, dispersal abilities and threats imposed on them, including diseases as well as persecution.

Although limited by the GPS collar battery lifespan providing data for less than a year, the study recommends that multinational and transboundary conservation approaches to wild dogs are essential, as the dispersing groups use different areas in Kenya and Tanzania. This will facilitate the exchange of collars when batteries expire in the neighbouring country. We further suggest that the two countries' conservation authorities should initiate and implement the proper sharing of wild dog sighting information across borders. Such collaborative monitoring will advance the ground-truthing of wild dogs in order to improve our knowledge of the depredation incidences caused by wild dogs, finding of mates and threats such as snaring and persecution from humans in Kenya and Tanzania. A further analysis of the dispersal movement behaviour will be performed using available large data sets to evaluate the connecting habitat of wild dogs during their movement between Tanzania

and Kenya. This information will further our knowledge of the management of wild dogs in the Eastern Africa region.

Based on the findings on the differences in movement behaviours of wild dogs between seasons and the habitat selection in different woody covers and landscapes, the current emphasis should be the protection and setting-aside of patches containing such landforms in multiple-use land use areas. Future studies should thereby focus on understanding how fine-scale foraging behaviour of wild dogs in different landforms are affected by human activities such as livestock herding. This information will help the responsible authorities in planning future conservation of wild dogs in the Serengeti ecosystem as well as other areas with similar conservation challenges.

The study further recommends that because most of the wild dog packs occurred in multiple-use areas, the protection of the prey species in these areas is important to support the persistence of the wild dog population. Also, work should be done on reducing bushmeat hunting, as well as limiting livestock populations to avoid overgrazing in multiple-use areas as well as adjacent national parks and game reserves whereby livestock grazing is prohibited. We further recommend that future research should focus on the influence of landscape features (i.e., topography) on the African wild dog prey selection in the Serengeti ecosystem. Within this setting, more insight should be obtained on how wild dogs are able to dynamically respond to spatio-temporal fluctuations in the prey availability.

Lastly, we recommend that the replacement of the GPS satellite collars after the battery expires should be performed in a timely manner to ensure our long-term reintroduction evaluation. Continued ground-truthing through close follow-up of the wild dog population in the Serengeti ecosystem is essential to understand the pack recruitment, dispersal abilities, survival, and influence of rugged terrain on the wild dog survival and denning patterns in the long term.



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# Paper I







































