Identifying potential corridors and conservation strategies for large terrestrial mammals in north-central and north-eastern Namibia

Identifizierung potenzieller Korridore und Artenschutzstrategien für große Landsäugetiere in Nordzentral- und Nordostnamibia

Master's Thesis for the Attainment of the Degree Master of Science at the
TUM School of Life Sciences of the Technical University of Munich

Supervisor: Prof. Dr. Ralph Kühn
Chair of Zoology

Co-supervisors: Piet Beytell
Namibian Ministry of Environment, Forestry and Tourism

Kenneth Uiseb
Namibian Ministry of Environment, Forestry and Tourism

William Versfeld
Ongava Research Centre

Course of study: Sustainable Resource Management

Submitted by: Corsa Lok Ching Liu
Matriculation number: 03708708

Submitted on: 13.06.2022

Acknowledgements

First of all, I would like to express my sincere gratitude to my supervisor Prof. Dr. Ralph Kühn, from the Chair of Zoology at the Technical University of Munich, for giving me the opportunity to work on this project and providing me valuable guidance and feedback.

Furthermore, I would like to thank William Versfeld from the Ongava Research Centre, supported by SAVE Wildlife Conservation Fund, for providing me with an insight into the country, the culture and the conservation of wildlife in Namibia, as well as the data used in this project.

I would also extend my thanks to Dr. John Mendelsohn from the Ongava Research Centre and Katharina Diedericks from NACSO for the data support.

A special thanks also goes to Piet Beytell from the Ministry of Environment, Forestry and Tourism of Namibia for sharing his professional knowledge, expertise and data of lions and elephants in the north-east of Namibia.

Besides, I want to thank Elisabeth Kirchner for her kind assistance in the GIS modelling.

Finally, I would express my deepest gratitude to my family for providing me with unfailing support and continuous encouragement through the process of writing my thesis.

Abstract

Many African large terrestrial mammals move through landscapes in search of food and water. In north-central and north-eastern Namibia, high numbers of large mammals are present with important economic and cultural values. However, these mammals are threatened by increasing anthropogenic pressures, habitat loss and loss of migratory routes. Connectivity conservation can help reverse the effects of habitat loss and fragmentation on large mammals and strengthen the resilience of ecological reserve networks to climate change. The study examined the changes in distribution and movement patterns of African lions (*Panthera leo*) and African savanna elephants (*Loxodonta africana*) over three time periods and identified potential corridors for these two mammalian species. To reconstruct the species' past occurrences, historical maps were digitalised, and shapefiles for their distributions were created. With the help of ArcGIS software, potential corridors for lions and elephants were detected through the development of habitat suitability and least-cost connectivity models. The selection and weighting of species' habitat factors were based on literature findings and expert knowledge. The model outputs were validated by expert opinions making use of the species' home ranges and core ranges derived from telemetry data. The results of the investigation showed that Namibian lions and elephants, and likely other large terrestrial mammals, have experienced substantial range contractions and reduced movements due to human activities dominated by land use changes, associated habitat loss and fragmentation. Suitable habitats for lions and elephants were found to be mainly in protected areas, including Etosha, Mangetti and Khaudum National Parks and along the Omatako River. Potential least-cost paths connecting these major habitats were detected for lions and elephants, but the implementation would be challenging due to high human occupancies in the area. Alternative strategies may have the potential to recover large mammal movements and maintain the viability of their populations within the study area, e.g. promotion of the development of wildlife-based land uses in communal conservancies and freehold farms, careful planning of fences, educational programme and species translocation. Further research is required to confirm the preliminary results of the lion and elephant corridors and to evaluate the effectiveness of alternative conservation strategies.

Zusammenfassung

Viele große Landsäugetiere Afrikas legen auf der Suche nach Nahrung und Wasser weite Strecken zurück. In Nordzentral- und Nordostnamibia gibt es eine große Anzahl großer Säugetiere von hohem, ökonomischen und kulturellen Wert. Diese Tiere sind jedoch zunehmend durch anthropogenen Druck und den Verlust von Lebensraum und Migrationsrouten bedroht. Die Erhaltung von landschaftlicher Konnektivität kann helfen, die Effekte des Lebensraumverlusts und der Fragmentierung großer Säugetierbestände umzukehren und die Widerstandsfähigkeit ökologischer Reservenetzwerke gegenüber dem Klimawandel zu stärken. Diese Arbeit hat die Entwicklung der Verbreitung und der Bewegungsmuster Afrikanischer Löwen (*Panthera leo*) und Afrikanischer Elefanten (*Loxodonta africana*) über drei Zeiträume untersucht und potenzielle Korridore für diese Arten identifiziert. Um frühere Vorkommen der Arten zu rekonstruieren, wurden Shapefiles ihrer Verbreitung erstellt und historische Karten digitalisiert. Mithilfe der ArcGIS Software und der Entwicklung von Modellen für Lebensraumeignung und kostengünstige Konnektivität, wurden potenzielle Korridore für Löwen und Elefanten ermittelt. Die Auswahl und Gewichtung der Faktoren der Lebensraumeignung erfolgte auf Grundlage von Literaturrecherchen und Expertenwissen. Unter Verwendung der Heimatreviere und aus Telemetriedaten abgeleiteten Bewegungsprofilen, wurden die Modellergebnisse durch Expertenmeinungen validiert. Die Ergebnisse der Untersuchung zeigten, dass namibische Löwen und Elefanten eine substanzielle Verkleinerung ihres Lebensraums und Einschränkung ihrer Bewegungsprofile erlebt haben, die durch menschliche Aktivitäten, wie eine veränderte Landnutzung und damit einhergehende Fragmentierung ausgelöst wurden. Geeignete Lebensräume für Löwen und Elefanten wurden hauptsächlich in geschützten Gebieten wie den Etosha-, Mangetti- und Khaudum National Parks entlang des Omatako gefunden. Potenzielle, kostengünstige Pfade, die diese Haupt-Lebensräume miteinander verbinden, wurden ermittelt, allerdings stellt die Implementierung aufgrund der hohen Anzahl von Menschen auf dem Gebiet eine große Herausforderung dar. Alternative Strategien könnten das Potenzial haben, die Bewegungen großer Säugetiere wiederherzustellen und die Lebensfähigkeit ihrer Population im untersuchten Gebiet zu erhalten, z.B. die Förderung der Entwicklung von Wildtier-basierter Landnutzung in kommunalen Naturschutzgebieten und auf privatem Grundbesitz, sorgfältige Planung von Zäunen, Bildungsprogramme und die Umsiedlung bestimmter Arten. Weitere Untersuchungen sind erforderlich, um die vorläufigen Ergebnisse der Korridore für Löwen und Elefanten zu bestätigen und die Wirksamkeit alternativer Schutzstrategien zu bewerten.

Table of Contents

List of Figures

List of Tables

Abbreviations

CBNRM	Community-based natural resources management
DEM	Digital elevation model
EHRA	Elephant Human Relations Aid
HSM	Habitat suitability model
KAZA	Kavango-Zambezi Transfrontier Conservation Area
KCR	Kavango Cattle Ranch
MEFT	Ministry of Environment, Forestry and Tourism
NDC	Namibia Development Corporation
NGO	Non-governmental organisation

1 Introduction

Many African savanna species move across landscapes to take advantage of more favourable conditions with respect to various intrinsic and environmental factors, including the availability of food and water, mating opportunities and safety from predation (Ojwang et al., 2017). Their movements can be categorised into two systems: migration and dispersal. Migration usually refers to regular seasonal movements of animals from one spatial unit to another with a return journey (Ojwang et al., 2017). It is an adaptive response to living in seasonal environments and to the spatiotemporal distribution of resources. Purdon et al. (2018) further noted that the migrations of large herbivorous mammals between dry and wet season ranges are attributed to high forage quality and availability. Additionally, dispersal is the movement of animals leaving their maternal home range to establish new territories and find mates that maintain healthy genetic and demographic diversity (Ament et al., 2014).

However, in the wake of increasing anthropogenic pressures and land use transformations, movements of these savanna species are impeded or extinguished, resulting in isolated populations (Brennan et al., 2020; Dolrenry et al., 2020; Naidoo et al., 2016; Thomson et al., 2013). The expansions of human activities have also resulted in the loss, fragmentation or degradation of wildlife habitats, particularly outside protected areas. Mammalian species are most vulnerable to habitat loss and fragmentation due to intrinsic biological traits, including large body sizes, extensive home range requirements, low densities and slow population growth rates, together with external threats (Crooks et al., 2011). Moreover, climate change aggravates the problem of isolation as fragmented landscapes are less resilient to ecological disturbances, to resist the loss of native species and to minimise emerging risks, such as diseases (Ament et al., 2014).

Connectivity conservation has been widely recognised as a key strategy to the adverse effects of habitat loss and fragmentation on biodiversity (Pulsford et al., 2015). It also strengthens the resilience of ecological reserve networks to climate change (Rudnick et al., 2012). While there are multiple benefits of connecting wildlife habitats, some potential negative social impacts should also be considered, for instance, negative public perception of large carnivores repopulating to areas close to human dwellings (Ament et al., 2014). It is essential to improve the connectivity of ecologically important areas and at the same time minimise human-wildlife conflicts between conserved areas and surrounding communities with inclusive planning and collaboration.

1.1 State of knowledge

Namibia is the most arid country in sub-Saharan Africa, known for its diverse and unique landscapes, as well as its richness in species (Schalkwyk et al., 2010). The Namibian economy is highly dependent on its natural resources and major economic sectors, namely agriculture, mining and tourism (Reid et al., 2007). With the continuing growth of human population, there is an increasing demand for food, energy and other resources, driving conversions of land originally protected for wildlife to settlements, agriculture or mining uses (Cushman et al., 2018; Ojwang et al., 2017; Stoldt et al., 2020). Consequently, it leads to the shrinking of wildlife habitats and ecosystem degradation, loss of wildlife dispersal areas, migratory routes and corridors, changes in wildlife populations and increasing human-wildlife conflicts (Ojwang et al., 2017). Populations of large terrestrial mammalian carnivores and herbivores such as African lions (*Panthera leo*) and African savanna elephants (*Loxodonta africana*) are increasingly fragmented (Stoldt et al., 2020; Trinkel, 2013).

Fences and roads are environmental concerns to large terrestrial mammals. The intensity and scale of fencing have increased since the 1970s, particularly on Namibia's communal land (Van Der Wulp & Hebinck, 2021). On the one hand, fences (e.g. veterinary control fences, stock fences and game-proof fences) have been used to delineate boundaries, limit the spread of diseases between wildlife and livestock, control invasive species and mitigate human-wildlife conflicts. On the other hand, they can hinder the movements of free-ranging wildlife and fragment landscapes (Ferguson & Hanks, 2012; Pekor et al., 2019; Stoldt et al., 2020; Van Der Wulp & Hebinck, 2021). For example, the erecting of fences around the Etosha National Park interfered the migration of wildebeest (*Connochaetes taurinus*) with substantial declines (Berry, 1982, 1997; Bolger et al., 2008). Previous studies have also found that fencing prevents elephants from accessing water sources and forces them to break through fences into neighbouring lands and villages (Adams et al., 2017; Stoldt et al., 2020). Similarly, roads, highways and their associated traffic volume can negatively impact wildlife through alteration of movement patterns and behaviours, traffic collisions and population fragmentation, although road development can bring economic and social benefits (Newmark et al., 1996; Shepard et al., 2008).

In addition, the high reliance on natural resources and the existing fragility of the environment have contributed to making Namibia one of the most vulnerable countries to climate change (Ministry of Environment and Tourism, 2011a). Changes in rainfall, evaporation and temperature patterns directly influence the range, geographical distribution, abundance and life cycles of wildlife species and ecosystems (Ministry of Environment and Tourism, 2011a; Thuiller et al., 2006). The combination of rising temperatures and inconsistent rainfall leads to higher risks of drought and fire, placing further pressure on natural resources.

Human-wildlife conflicts in Namibia are complex issues and remain challenging in wildlife conservation. Such conflicts are influenced by economic, political and social factors, including attitude and perception that may further erode local support for conservation (Rust et al., 2016). The land area and wildlife populations on freehold (private) and communal lands have increased dramatically since the creation of new property rights systems. Majority of wildlife (82%) occurs on freehold land, whilst 12% occurs on communal land and only 6% occurs in national parks (Brown, 2019). This could potentially give rise to conflicts due to competition of space and resources between humans and wildlife. Numerous studies have indicated that large iconic species such as lions and elephants exhibit population declines in areas where livestock production is the main source of income (Dolrenry et al., 2020; Rust & Marker, 2014). These declines are driven by removal of the problem animals in response to livestock depredation, crop damage, damage of water facilities and attacks on humans. To minimise the conflicts between livestock farmers and large carnivores, a variety of measures have been developed and applied, including translocation of problem animals, the use of livestock guardian animals and herders, exclusion of predators from farms and killing of recurrent problem animals (Rust et al., 2016). Besides, measures such as constructing elephant drinking dams adjacent to main dams for settlements in communal areas, protecting the main water supply with a sturdy stone wall, placing pointy rocks on the ground, and using traditional or innovative deterrents (chilli peppers, beehives) have been applied for mitigating human-elephant conflicts. In some cases, these techniques have successfully limited livestock depredation, crop-raiding and damage of water supplies, but there are still many reports of problems with large carnivores or herbivores within the country.

Rust et al. (2016) and Stoldt et al. (2020) further suggested that the increase of wildlife populations resulting from effective conservation efforts will contribute to rising human-wildlife conflicts. The reason for this is that the growing wildlife populations cannot be confined to human defined ranges. If current conservation initiatives neglect the wildlife populations living outside protected areas, only small, isolated populations confined to national parks and other protected areas remain. Hence, there is a need to maintain and enhance connectivity, such as through wildlife corridors, which help expand wildlife space and facilitate species movements throughout the country with changing seasons and climates (Ament et al., 2014; Ojwang et al., 2017). They also help increase biodiversity and resilience in degraded ecosystems and safeguard genetic flow between populations. Apart from sufficient habitats, the tolerance of human communities is another fundamental element for wildlife population connectivity and long-term viability, especially for large carnivores (Dolrenry et al., 2020).

1.2 Research gap

Studies about the dispersal of large terrestrial mammals, their survival outside protected areas and the population connectivity between protected and non-protected areas are limited in Namibia. Furthermore, most of the projects are based in north-western Namibia or the Zambezi Strip. Increasing impacts on wildlife movements and rising human-wildlife conflicts involving elephants and other species have also been seen in north-central and north-eastern Namibia (R. Kühn, personal communication; Movirongo, 2021). Therefore, this research could support current conservation efforts in these two sections of the country by understanding the possible connectivity that might be suitable for animals between the wildlife important areas (e.g. Etosha, Mangetti and Khaudum National Parks).

1.3 Objectives and research questions

The thesis aims to examine the changes in distribution and movement patterns of large terrestrial mammals over time and their interactions with humans in north-central and north-eastern Namibia. It also provides insights on potential migration and dispersal recovery strategies for the mammalian species. In order to increase animal movements and enhance their population viability, potential wildlife corridors are identified between Etosha National Park and Khaudum National Park, which could further be used to connect other ecologically important areas inside or outside the country.

The following questions form the basis of this research:

- How did the distributions and movements of large terrestrial mammals, namely lions and elephants, change over time?
- What are the factors influencing the distribution and movement patterns of large mammalian carnivores and herbivores?
- What are the preconditions for planning and implementing wildlife corridors between Etosha National Park and Khaudum National Park?
- How feasible is the implementation of the proposed wildlife corridors in the study area?
- What are the other potential migration and dispersal recovery strategies that could be applied by governmental organisations, non-governmental organisations (NGO), environmental education institutions in Namibia, as well as local communities?

2 Socio-economic development and conservation in Namibia

2.1 Human population and its distribution

Covering an area of about 824,000 km^2, Namibia has a population estimated at 2.5 million with an annual growth rate of 1.8%. It is also one of the most sparsely populated countries, with an average of three people per km^2 (Figure 1). Namibians are of diverse ethnic origins; the largest ethnic group is the Ovambo, making up half of the population. Other ethnic groups include Kavango, Herero, Damara, Nama, Caprivians, San, Tswana, Whites, Coloureds and Basters. As shown in Table 1, the population is unevenly distributed. Many more people live in northern Namibia than in the central and southern regions due to a more favourable agricultural climate, along with the past colonial and apartheid interference. It is estimated that 50% of Namibia's population lives in the rural parts of northern communal areas, whereas the other half resides in cities and urban areas (Namibia Statistics Agency, 2019).

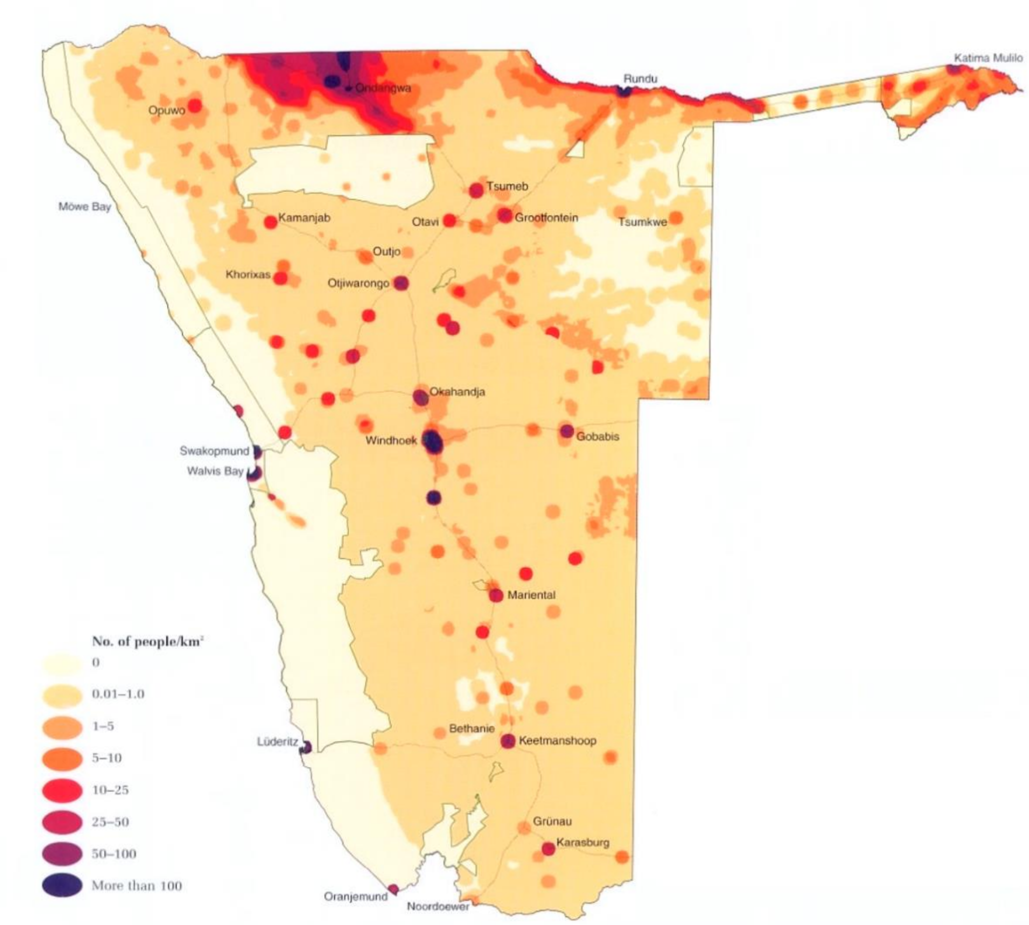


Figure 1. Human population density in Namibia.

Table 1. Population distribution by regions in Namibia (adapted from Namibia Statistics Agency, 2019)**.**

Regions	Number of people	Percentage
North central (Omusati, Oshana, Ohangwena, Oshikoto)	908,384	37.7
North-east (Kavango East, Kavango West, Zambezi)	346,033	14.3
North-west (Kunene)	102,485	4.2
East (Otjozondjupa, Omaheke)	233,971	9.7
South (Karas, Hardap)	179,482	7.4
Central (Khomas, Erongo)	643,288	26.7
Total	2,413,643	100

2.2 Land use and tenure

Namibia, formerly South West Africa, was colonised by Germany from 1884 to 1914, followed by the South African administration until its Independence in 1990. The country inherited the two contrasting land ownership systems from the colonial rule: private land ownership and communal land ownership. According to Mendelsohn et al. (2012), commercial farmland, mainly in the south and central Namibia, were reserved for private ownership by Whites throughout the colonialism period, while homelands and tribal lands for non-whites were re-designated as communal lands at Independence. To this day, 58% of Namibia’s land is owned by the central government, while 42% belongs to private individuals and companies. Of the total government-owned land, 35% is allocated as communal land and managed under various customary governance systems. Another 23% of the state land consists of national parks, restricted areas, townland boundaries, research farms and resettlement farms (Namibia Statistics Agency, 2018).

Agriculture remains the prime economic activity on most of the communal and freehold land (Figure 2). It provides food, income and employment, together with supporting rural subsistence farmers. Due to differences in soil fertility, vegetation types and aridity, the uses of communal land across the country vary greatly. In the higher rainfall areas of north-central and north-eastern Namibia, both crop cultivation (mainly pearl millet, maize and sorghum) and livestock rearing (goats and cattle) are practised (Mendelsohn et al., 2012). Besides, there are large sectors of remaining commonage for grazing, hunting, firewood collection and plant harvesting. Several private commercial farms have also emerged in northern communal areas, such as Kavango, Oshikoto and Otjozondjupa. By contrast, pastoral livestock farming predominates in freehold farms in the more arid areas of central, southern and western Namibia, while tourism and wildlife have also become increasingly popular (Mendelsohn et al., 2012).

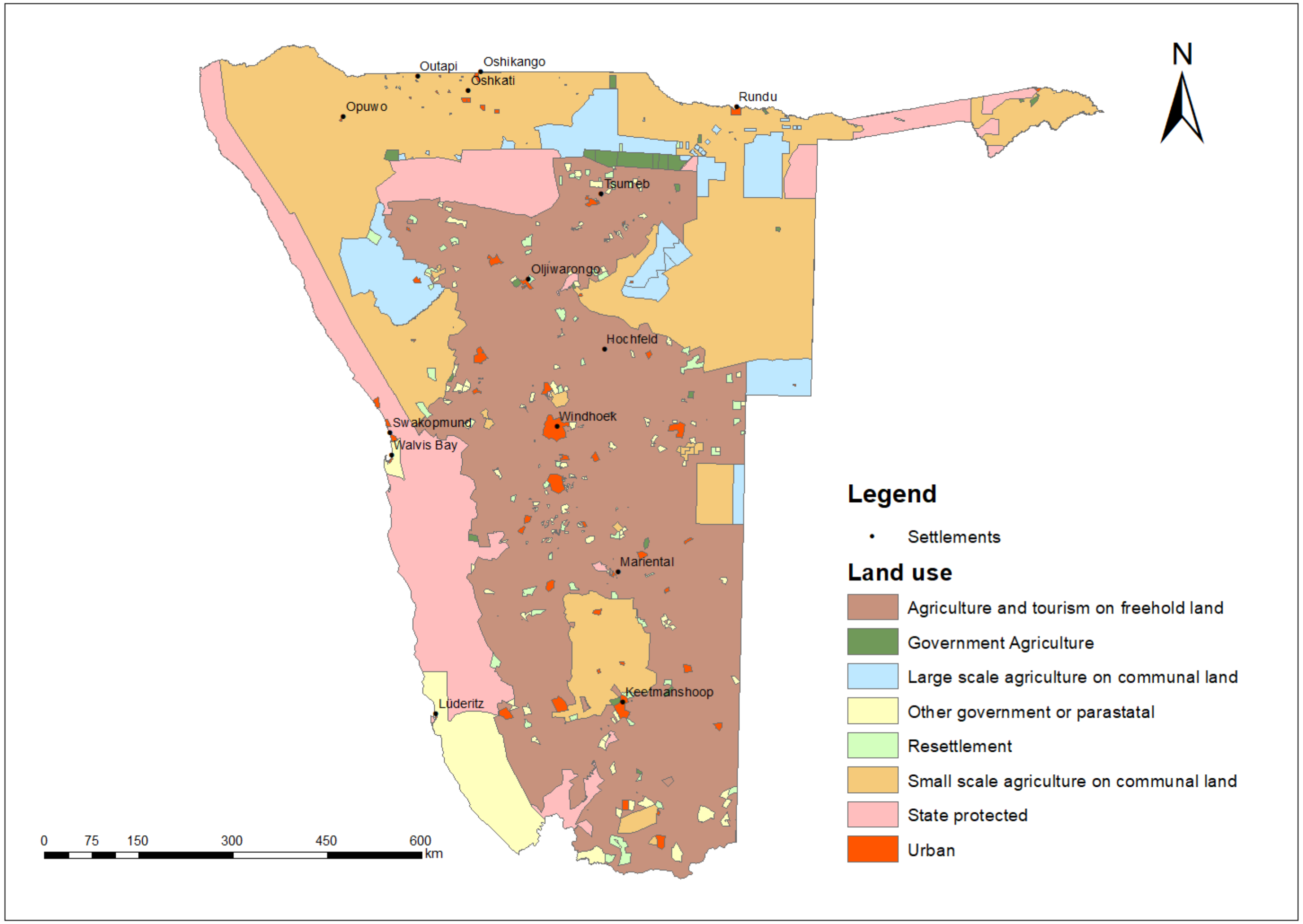


Figure 2. Major land uses and distribution in Namibia.

2.3 Wildlife ownership and conservation

Wildlife is an important national asset. Before the era of colonisation, it was part of rural livelihood strategies, and wildlife numbers were around 8-10 million in 1770 (Brown, 2017). However, wildlife populations experienced a rapid decline under the colonial administration, as depicted in Figure 3. During the 19^{th} and 20^{th} centuries, wildlife populations decreased drastically as a consequence of disease outbreaks and overexploitation by European explorer-hunters and settlers (Lindsey, 2011). To protect wildlife and keep out commercial hunters, the Governor of German South West Africa proclaimed Etosha Pan (Game Reserve No. 2) as one of three game reserves in 1907 under Ordinance 88 (Dieckmann, 2007; Ministry of Environment and Tourism, 2010). The other two were Omuramba Omatako (Game Reserve No. 1) and Namib-Naukluft (Game Reserve No. 3). At the time, Game Reserve No. 2 encompassed the Etosha Pan and the Kaokoveld from the Kunene River in the north to the Hoarusib River in the south (about 90,000 km^2), making it the world's largest nature reserve (Barnard et al., 1998). Certain species like elephants, lions, black rhinos (*Diceros bicornis*) and white rhinos (*Ceratotherium simum*) were absent from the game reserve. Although lions were not documented until 1912, there were still no elephants or rhinos recorded in the earliest wildlife census (1926) on account of large inaccessible areas in Etosha (Berry, 1997). Following the rinderpest epidemic in 1896, the early Etosha National Park also served as a buffer zone to protect the livestock of the settlers (Ministry of Environment and Tourism, 2010).

Over the years, there have been numerous changes in the boundaries of Game Reserve No. 2, mainly in response to political decisions rather than conservation reasons (Berry, 1997; Dieckmann, 2007). Major boundary alterations took place between 1958 and 1970 (Figure 4). For example, in 1958, the valuable cultivated land to the east of Etosha (Game Reserve No. 1) was exchanged for a large game-rich corridor to the south-west of Etosha (Barnard et al., 1998). Boreholes were drilled in western Etosha in 1961 for attracting elephants from farms in the Outjo and Kamanjab districts into the park (Martin, 2005; Ministry of Environment and Tourism, 2010). Within the same year, the construction of a high game-proof fence began along the eastern and southern border of the park (Berry, 1997). The recommendations of the Odendaal Commission (1963) further demarcated Etosha's present boundary in 1970, reducing the park size to 22,270 km^2. Most of the excised land became communal homelands for Ovambo, Herero and Damara peoples (Barnard et al., 1998). The park was also completely enclosed with fencing in 1973.

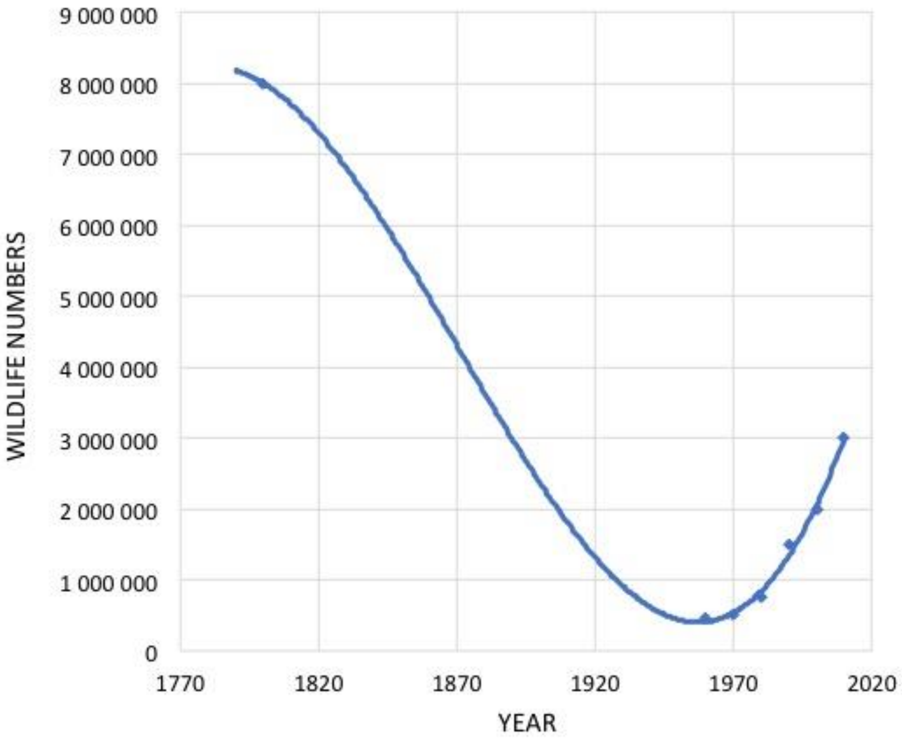


Figure 3. Wildlife trends in Namibia from 1770 to 2015 (Brown, 2017)**.**

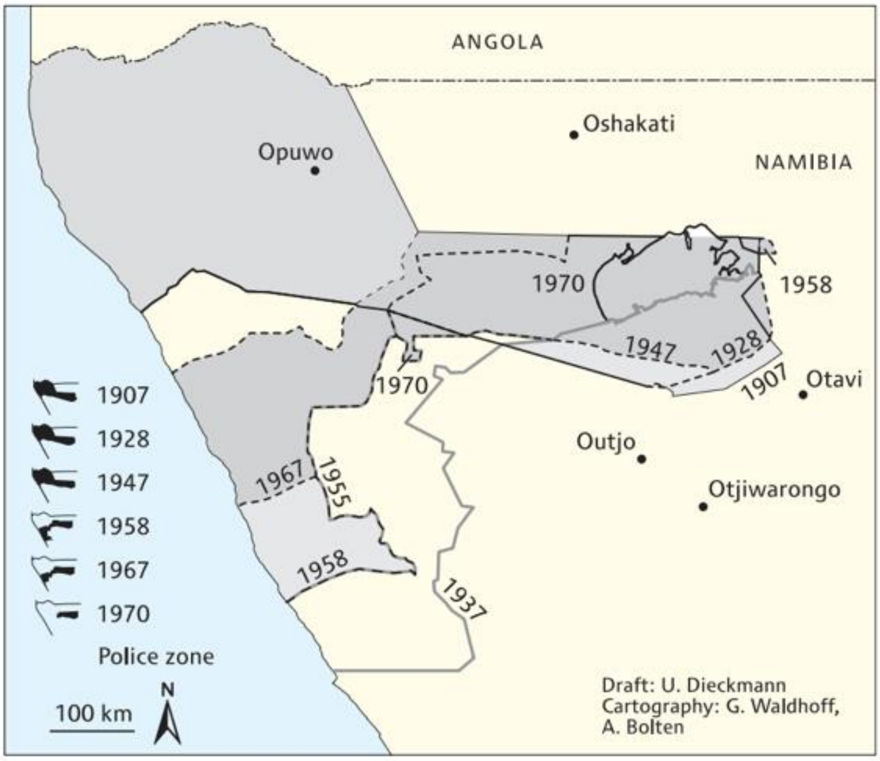


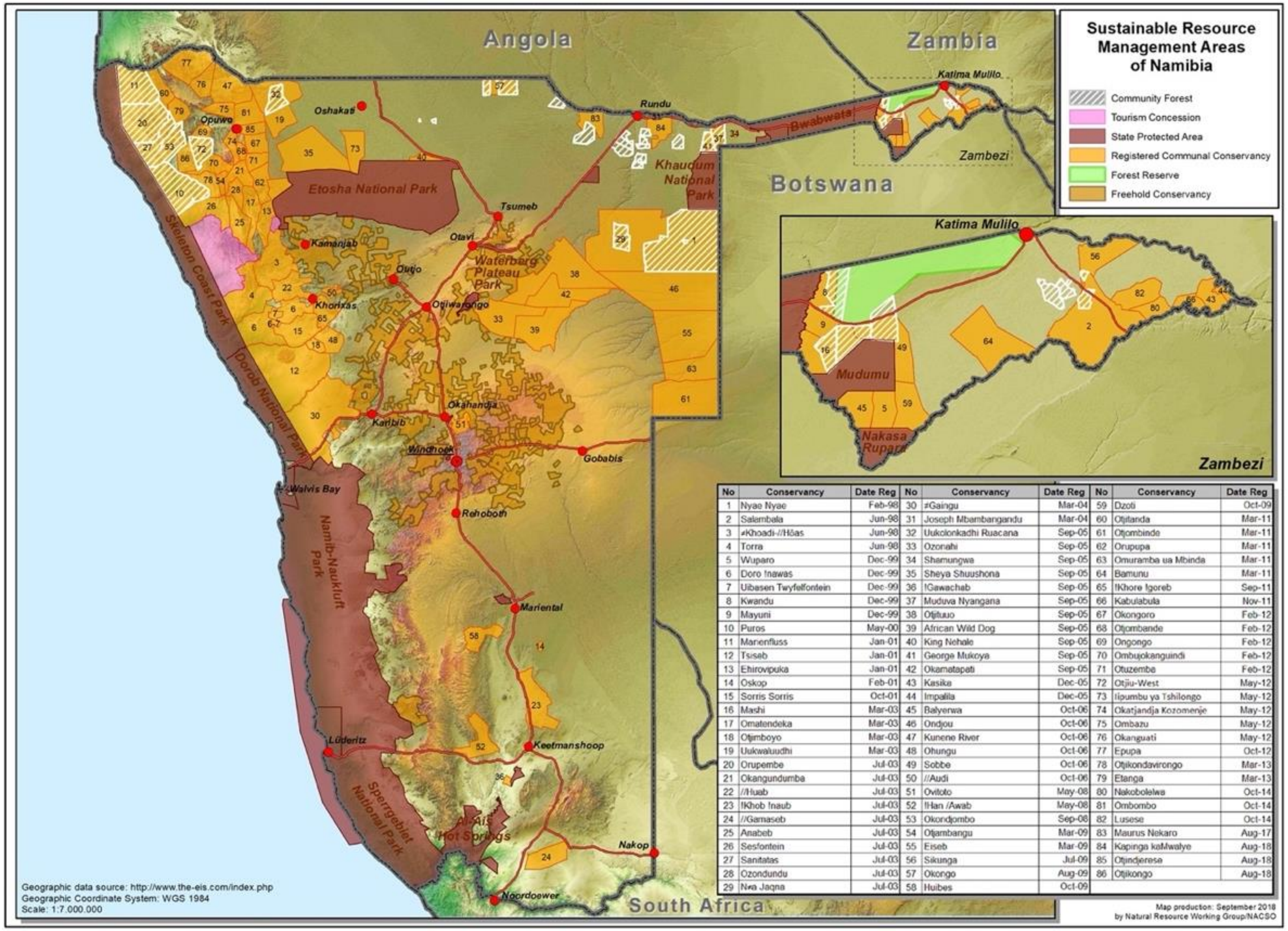
Figure 4. Etosha boundary alterations between 1907 and 1970 (Dieckmann, 2007)**.**

By the 1960s, wildlife populations in Namibia reached their lowest point due to a mixture of unregulated hunting, competition with livestock, fences and veterinary controls (Brown, 2017; Lindsey et al., 2009). Negative wildlife trends improved considerably when individual landowners were given conditional rights to utilise wildlife in 1967 (Schalkwyk et al., 2010). The Nature Conservation Ordinance No. 4 of 1975 further provided a framework for consumptive utilisation, thereby increasing wildlife populations on Namibia's freehold farmland by 80% (Lindsey et al., 2013; Schalkwyk et al., 2010). Besides, portions of communal land were allocated to individual farmers by the previous government between the 1960s and 1980s, with farms being used for commercial cattle farming, such as those at the Mangetti Kavango Cattle Ranch (KCR). The trend of commercial farms in communal areas continued to increase, and the Ranch has also become a favoured area for elephants. From the early 1990s, an expansion in wildlife-based land uses on private land has promoted the establishment of freehold conservancies, in which commercial farmers collaborate to improve wildlife management across large landscapes (Ministry of Environment and Tourism, 2010). These conservancies have largely focused on ecotourism or consumptive activities.

Apart from freehold conservancies, Namibia's protected area network was strengthened by the addition of more game parks under the South African administration (Mendelsohn et al., 2002; Ministry of Environment and Tourism, 2010). An example is the Khaudum National Park, which is also one of the focal areas of this study. Khaudum is a true wilderness and supports many iconic species, with an area of 3,842 km^2. It was initially proclaimed as a game reserve in 1989 and was given a national park status in 2007. The protected area network has continued to extend during the post-independence period. To date, the country has around 20 state-run protected areas.

Conversely, wildlife on communal land still declined in the 1980s because of drought, diseases and poaching for meat and other products by South African officials and local people (Ministry of Environment and Tourism, 2014). After independence, the new Namibian government implemented the Nature Conservation Amendment Act of 1996 (an amendment to the 1975 Ordinance) that enabled rural communities to obtain ownership and use rights over wildlife and tourism through the formation of conservancies (Jones, 2007; Lindsey et al., 2013). In 1998, the first four communal conservancies were gazetted: Nyae Nyae, Salambala, ≠Khoadi-//Hôas and Torra (NACSO, 2013). These changes have encouraged communities to manage wildlife sustainably, and thus catalyse a remarkable wildlife recovery on communal land.

Figure 5 shows an overview of the areas under wildlife management in Namibia. There are currently 86 registered communal conservancies, 1 community conservation association and 43 registered community forests under the community-based natural resources management (CBNRM) programme, covering 21.9% of Namibia (MEFT/NACSO, 2021). Combined with freehold conservancies (6.1%) and state protected areas including tourism concessions (17.6%), the total land available to wildlife is about 45.6%. The continued expansion of conservancies and community forests may help combat habitat fragmentation and climate change, as well as increasing connectivity of ecological corridors at large landscape scales. Nevertheless, growing wildlife populations and range expansions have created further opportunities for conflicts between people and animals, particularly elephants and predators. If effective mitigation strategies are not introduced and applied, these conflicts could undermine the conservancy movement.



No	Conservancy	Date Reg	No	Conservancy	Date Reg	No	Conservancy	Date Reg
1	Nyae Nyae	Feb-98	30	≠Gaingu	Mar-04	59	Dzoti	Oct-09
2	Salambala	Jun-98	31	Joseph Mbambangandu	Mar-04	60	Otjitanda	Mar-11
3	≠Khoadi-//Hôas	Jun-98	32	Uukolonkadhi Ruacana	Sep-05	61	Otjombinde	Mar-11
4	Torra	Jun-98	33	Ozonahi	Sep-05	62	Orupupa	Mar-11
5	Wuparo	Dec-99	34	Shamungwa	Sep-05	63	Omuramba ua Mbinda	Mar-11
6	Doro !nawas	Dec-99	35	Sheya Shuushona	Sep-05	64	Bamunu	Mar-11
7	Uibasen Twyfelfontein	Dec-99	36	!Gawachab	Sep-05	65	!Khore !goreb	Sep-11
8	Kwandu	Dec-99	37	Muduva Nyangana	Sep-05	66	Kabulabula	Nov-11
9	Mayuni	Dec-99	38	Otjituuo	Sep-05	67	Okongoro	Feb-12
10	Puros	May-00	39	African Wild Dog	Sep-05	68	Otjombande	Feb-12
11	Marienfluss	Jan-01	40	King Nehale	Sep-05	69	Ongongo	Feb-12
12	Tsiseb	Jan-01	41	George Mukoya	Sep-05	70	Ombujokanguindi	Feb-12
13	Ehirovipuka	Jan-01	42	Okamatapati	Sep-05	71	Otuzemba	Feb-12
14	Oskop	Feb-01	43	Kasika	Dec-05	72	Otjiu-West	May-12
15	Sorris Sorris	Oct-01	44	Impalila	Dec-05	73	Iipumbu ya Tshilongo	May-12
16	Mashi	Mar-03	45	Balyerwa	Oct-06	74	Okatjandja Kozomenje	May-12
17	Omatendeka	Mar-03	46	Ondjou	Oct-06	75	Ombazu	May-12
18	Otjimboyo	Mar-03	47	Kunene River	Oct-06	76	Okanguati	May-12
19	Uukwaluudhi	Mar-03	48	Ohungu	Oct-06	77	Epupa	Oct-12
20	Orupembe	Jul-03	49	Sobbe	Oct-06	78	Otjikondavirongo	Mar-13
21	Okangundumba	Jul-03	50	//Audi	Oct-06	79	Etanga	Mar-13
22	//Huab	Jul-03	51	Ovitoto	May-08	80	Nakobolelwa	Oct-14
23	!Khob !naub	Jul-03	52	!Han /Awab	May-08	81	Ombombo	Oct-14
24	//Gamaseb	Jul-03	53	Okondjombo	Sep-08	82	Lusese	Oct-14
25	Anabeb	Jul-03	54	Otjambangu	Mar-09	83	Maurus Nekaro	Aug-17
26	Sesfontein	Jul-03	55	Eiseb	Mar-09	84	Kapinga kaMwalye	Aug-18
27	Sanitatas	Jul-03	56	Sikunga	Jul-09	85	Otjindjerese	Aug-18
28	Ozondundu	Jul-03	57	Okongo	Aug-09	86	Otjikongo	Aug-18
29	N≠a Jaqna	Jul-03	58	Huibes	Oct-09			

Figure 5. Areas in Namibia under wildlife management (NACSO, 2018)**.**

3 Materials and methods

This study is based on a mixed methods research design integrating both quantitative and qualitative data collection and analysis methods.

3.1 Literature review

Literature review was conducted to acquire background information about the socio-economic development and ecological conservation in Namibia (Chapter 2); to collect historical and recent information of species distribution and wildlife corridors; to collect environmental and anthropogenic parameters (geodata) for habitat suitability analysis; and to identify the factors influencing the distributions and movements of large terrestrial mammals. It was also used to research the preconditions of creating effective wildlife corridors, as well as examples of other possible conservation strategies. The review included academic journal articles (e.g. articles from Biological Conservation and Journal of Applied Ecology), theses, government reports, publications by local (Namibia) and/ or international agencies and institutions working in the field of wildlife conservation. The TUM Library Access of E-Journals, electronic databases such as Scopus, Web of Science, ScienceDirect, as well as the eLibrary of Namibia Environmental Information Service were used for literature search with the keywords including wildlife corridor, wildlife distribution, animal movement, dispersal, migration, landscape connectivity, human-wildlife conflicts, conservation, population recovery, large terrestrial mammals, large carnivores, large herbivores, African lion *Panthera leo*, African elephant *Loxodonta africana*, Namibia and southern Africa.

Moreover, the selection of literature was based on:

- relevance to the key themes (wildlife movement, wildlife corridor, wildlife population recovery)
- date of publication (preference for more recent studies while still taking account of important older publications)
- language of study (preference for studies conducted in English)
- number of citations (preference for high number of citations)
- types of journal articles (preference for fully published peer-reviewed journal articles)

3.2 Study area

The study area is situated in north-central and north-eastern Namibia, totalling 179,280 km^2 (Figure 6). It borders with Angola and Botswana in the north and east, respectively. In the west, it is limited by the city of Otjiwarongo and covers the eastern side of the Etosha National Park. The Omatako River serves as the furthest point of the study area in the south. The study site consists of communal land including conservancies, freehold farms, state protected areas, major road sections (e.g. B8 Grootfontein-Rundu and B1 Tsumeb-Ondangwa) and part of Namibia's veterinary cordon fence (the Red line fence) within the administrative regions of Ohangwena, Oshikoto, Kavango East, Kavango West, Otjozondjupa and Omaheke.

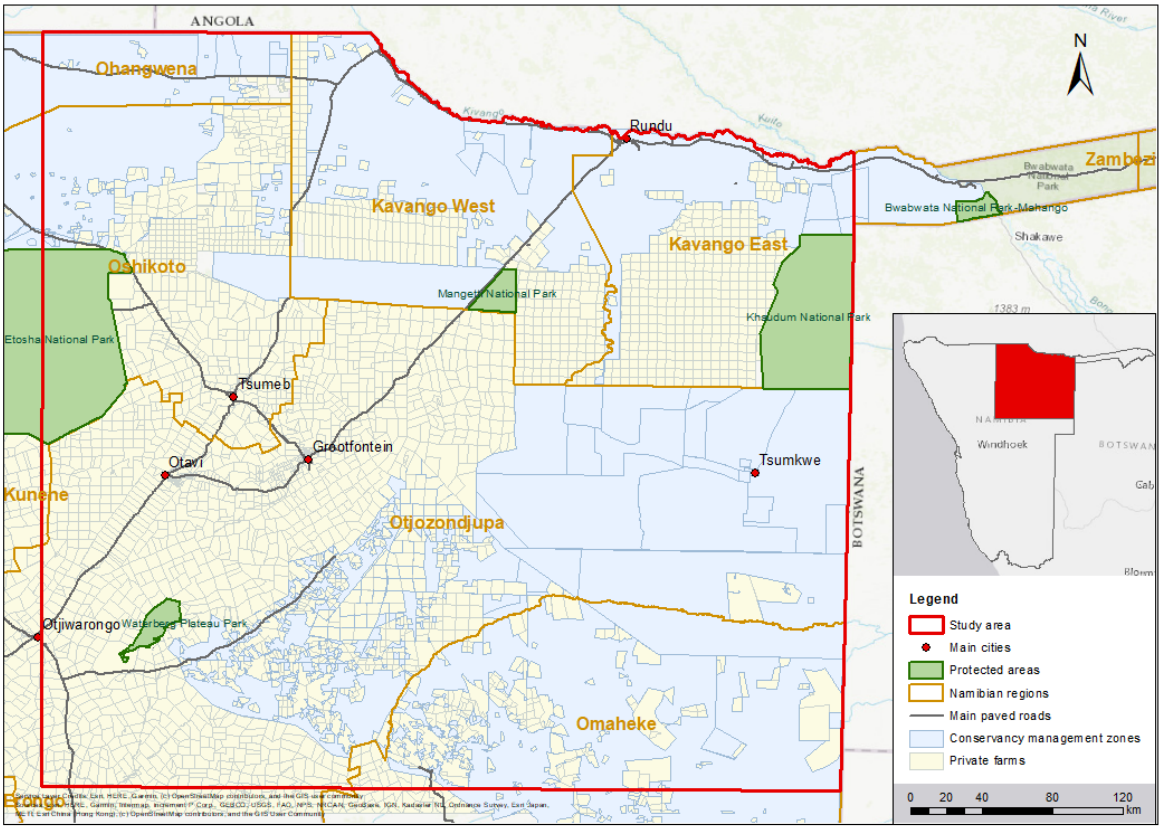


Figure 6. Map of the study area located in the north-central and north-eastern Namibia.

3.2.1 Climate

Namibia has a subtropical desert climate with unpredictable rainfall patterns, high temperature variability and persistent droughts. The country generally follows a decreasing rainfall gradient from just above 600 mm in the north-east to less than 50 mm in the south-west (Figure 7a). The inland temperatures are also higher than the coastal zones, with warmer days and cooler nights (Mendelsohn et al., 2002). In the study area, precipitation ranges between 350 mm and 600 mm, and most rain occurs in summer between November and April (Mendelsohn et al., 2002). Additionally, the maize triangle of Tsumeb, Grootfontein and Otavi receives more rainfall (500-600 mm) as a result of moist air being forced upwards by hills and mountains (Mendelsohn et al., 2002). Average annual temperatures are around 20°C to 22°C and can reach above 22°C in the regions along the Angolan border (Figure 7b). Based on climate models, Namibia is predicted to become hotter and drier with increased rainfall variability (Ministry of Environment and Tourism, 2011a).

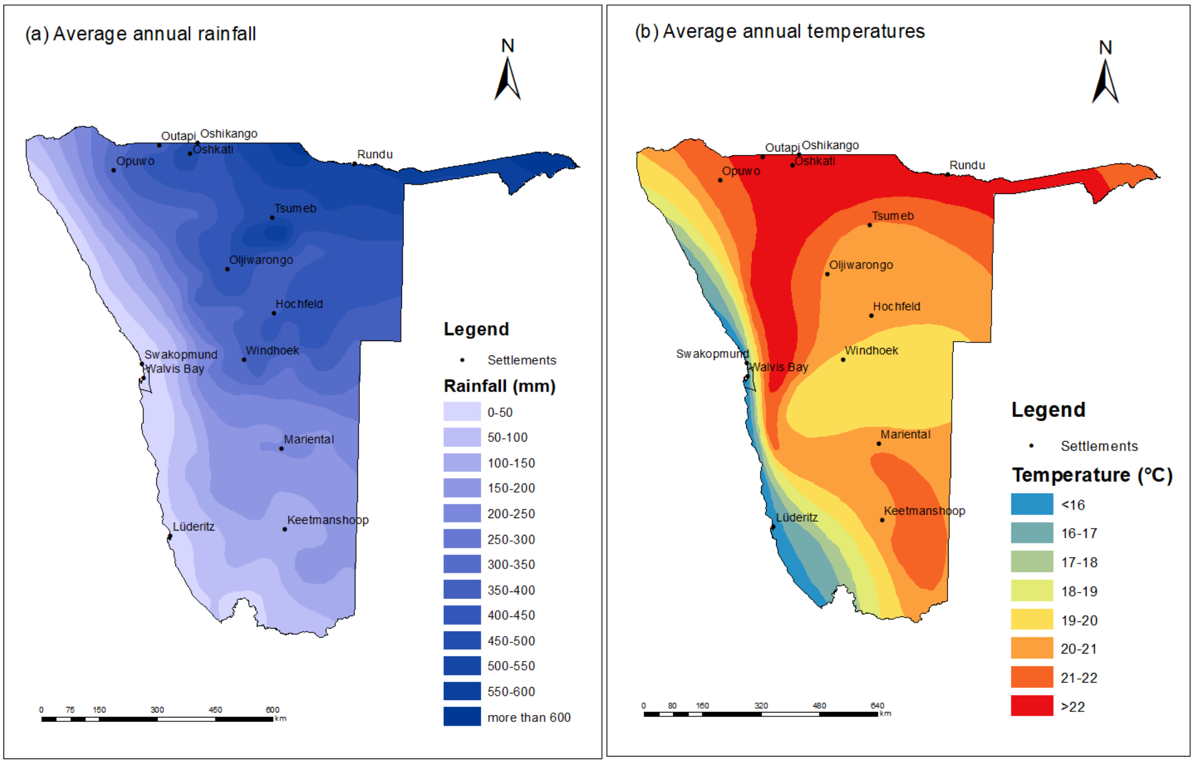


Figure 7. Average annual (a) rainfall and (b) temperature in Namibia.

3.2.2 Hydrology

Figure 8 shows the distribution of main rivers and waterholes in the study area. The major water source is the perennial Okavango River, which supports the rural communities concentrated along the river for domestic and agricultural purposes. The Omuramba Omatako is also a Namibian ephemeral tributary of the Okavango River (Pinheiro et al., 2003). Furthermore, groundwater reserves in Namibia are closely linked to the geological formations that make up the Earth's crust. Kalahari aquifers hold water in intergranular pore spaces and are common in the Kavango and north-western Otjozondjupa regions, whereas fractured aquifers can be found near the Tsumeb-Grootfontein area (Christelis & Struckmeier, 2011; Mendelsohn et al., 2002). Besides, the distribution of boreholes and dug wells in Kavango is associated with the settlements, mostly along the Okavango River, the Omatako valley and the main roads from Grootfontein to Rundu (Christelis & Struckmeier, 2011). Water points are more dispersed in the north-eastern Otjozondjupa and northern Omaheke regions because of poor groundwater availability in north-eastern areas. A few water schemes are used for veterinary border posts as well.

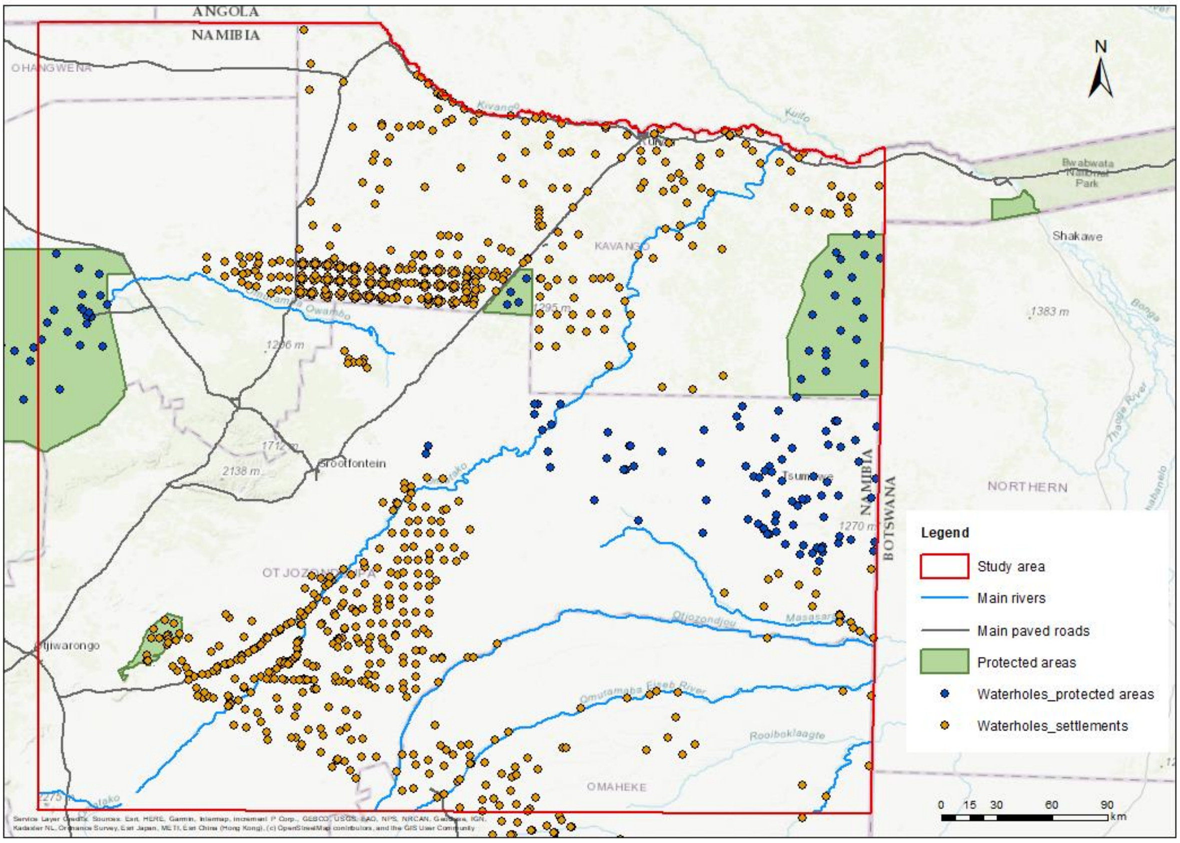


Figure 8. Distribution of main rivers and waterholes in the study area.

3.2.3 Topography and soils

The study area extends from the Central Plateau towards the eastern Kalahari Basin. The elevation in north-central Namibia varies between 1,000 m and 1,800 m, with landscapes ranging from mountains near the Otavi region to flat plains (Figure 9). In the Kavango regions, the landscape is uniform, having a plain topography with an average elevation of 1,100 m above sea level. Various soil types can also be found within the subject area, with ferralic arenosols predominantly in the north-eastern regions (Mendelsohn et al., 2002). Other soil types include calcisols, cambisols, fluvisols, leptosols and regosols. Additionally, the north-central regions with highly fertile eutric cambisols have the highest potential for crop cultivation (Mendelsohn et al., 2002).

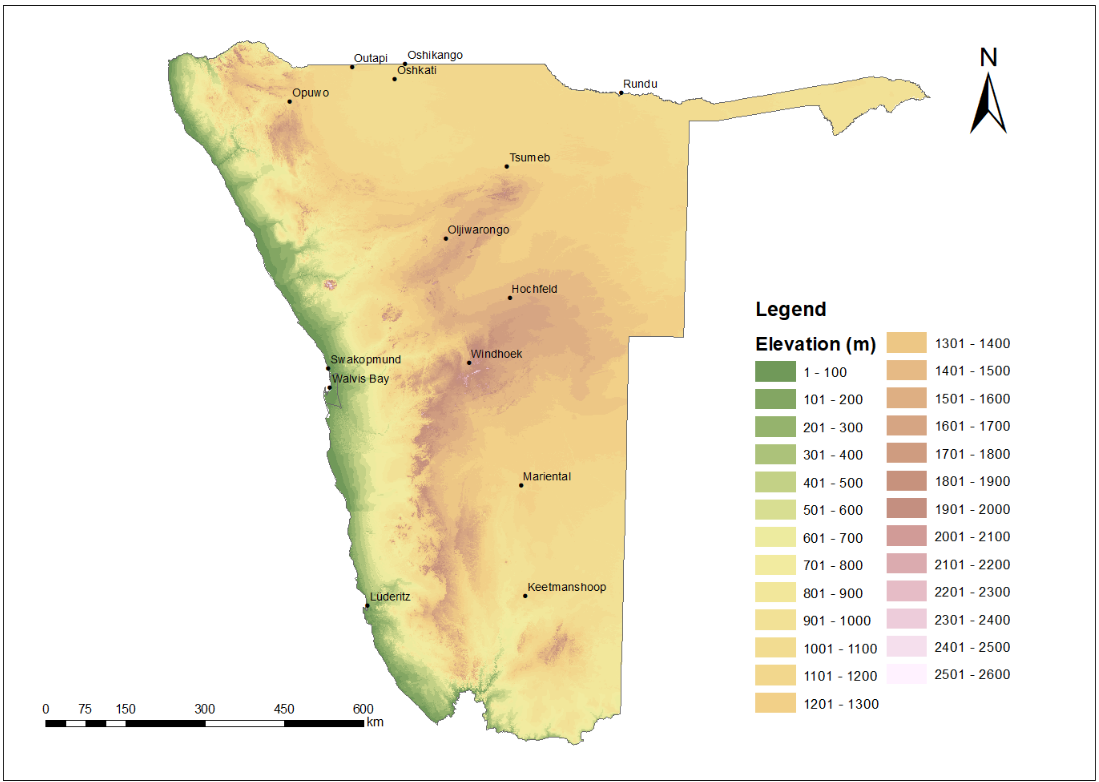


Figure 9. Elevation and relief in Namibia.

3.2.4 Flora

Vegetation in Namibia is determined by climate variables, soil types and landscapes (Mendelsohn et al., 2002). Trees in the northern, wetter parts are taller and denser than the rest of the country. There are five main vegetation type units within the study area (Figure 10). The north-eastern sector is covered by North-eastern Kalahari Woodland, Eastern Drainage and Northern Kalahari, which comprises broad-leaved, deciduous woodlands with varying bush and grass undergrowth. Common tree species include *Burkea africana*, *Baikiaea plurijuga*, *Pterocarpus angolensis*, *Guibourtia coleosperma*, *Schinziophyton rautanenii*, *Terminalia sericea* and *Strychnos cocculoides* (Mendelsohn & El Obeid, 2005). The vegetation in Oshikoto and north-western Otjozondjupa is classified as Karstveld and made up of mixed woodlands. Dense woodlands are located on the dolomite hills around the Grootfontein area, while the surrounding lowlands are dominated by *Acacia* species, *Terminalia prunioides*, *Combretum apiculatum* and *Dichrostachys cinerea* (Mendelsohn & El Obeid, 2005; Starik et al., 2020). Further south of the study area (near Otjiwarongo) belongs to Thornbush Shrubland, consisting of *Acacia* trees surrounded by grassland and patches of shrubland (Mendelsohn et al., 2002). Tree species such as *Terminalia sericea* and *Ziziphus mucronate* are abundant in this region.

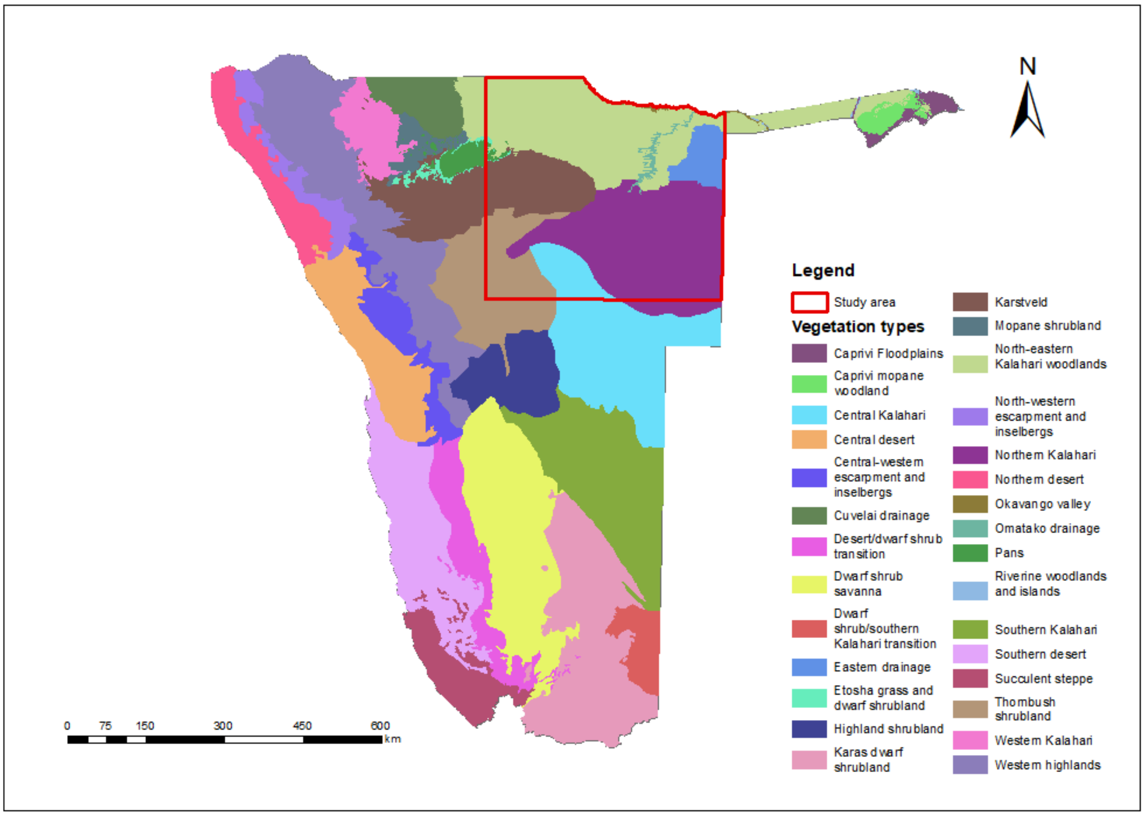


Figure 10. Vegetation types in Namibia.

3.2.5 Fauna

Namibia is currently home to 229 mammal species, with rodents (53 species) as the largest group, followed by bats (43 species) and carnivores (35 species) (Mendelsohn et al., 2002; Ministry of Environment and Tourism, 2014). The study area covers 4 national parks and 15 registered communal conservancies, which support a high abundance and diversity of large herbivorous and carnivorous mammals (Figure 11). In Etosha National Park, a total of 114 species of mammals are found, including four of the African Big Five and many more rare and endangered species (Ministry of Environment and Tourism, 2010). Giraffe (*Giraffa giraffa*), zebra (*Equus quagga*) and wildebeest are also common and easily spotted in the park. Furthermore, the Khaudum National Park in Kavango East forms part of the Kavango-Zambezi Transfrontier Conservation Area (KAZA), enabling important migratory routes, particularly for elephants (Stoldt et al., 2020). Khaudum has been viewed as a stronghold of Namibia's lion and wild dog (*Lycaon pictus*) populations as well. Between Etosha and Khaudum is the Mangetti National Park. It is one of the country's latest national parks, proclaimed in 2008, and promotes economic growth through tourism development and joint management with local communities, while hosting a thriving collection of wildlife (Ministry of Environment and Tourism, 2010).

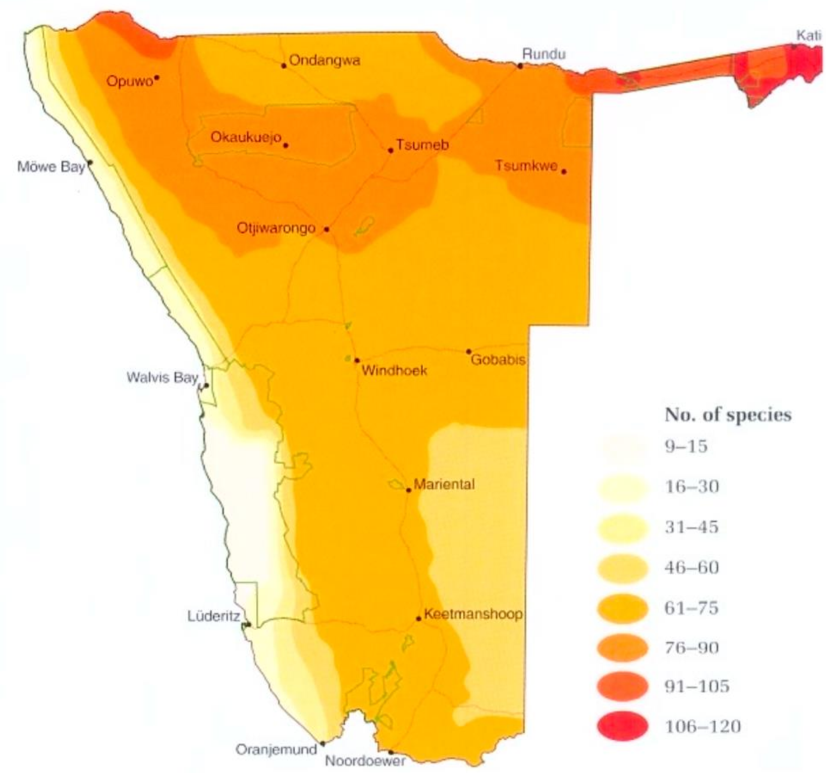


Figure 11. Diversity of mammals in Namibia (Mendelsohn et al., 2002)**.**

3.3 Focal species

Large carnivores, particularly apex predators, are valuable candidates for connectivity analysis due to their important ecological roles, significant spatial requirements and vulnerability to altered landscapes. For instance, African lions are classified as vulnerable on the IUCN Red List, as they have suffered extensive range contractions with population declines and currently occupy only 8% of their historic range (Bauer et al., 2016; Sargent et al., 2021). Inbreeding and diseases have also been underlined as a major threat to some subpopulations if limited connectivity is present (Cushman et al., 2018; Trinkel et al., 2010).

Lions are highly mobile animals whose spatio-behavioural strategies depend not only on targeting resource-rich areas but also on complex social interactions (Everatt et al., 2019). They are the most gregarious felids, with related females residing together in prides and related or unrelated males forming coalitions that compete over pride tenure (Bauer et al., 2016). Feeding upon large herbivores such as zebras and wildebeests, they also help control numbers of these species' populations. The size of lion home ranges can vary widely from 20-45 km^2 in places like Manyara National Park and Ngorongoro Crater to more than 2,000 km^2 in the semi-arid ecosystems such as Etosha National Park (Lehmann et al., 2008; Lesilau et al., 2021; Loveridge et al., 2009; Stander, 1991).

Apart from lions, large herbivores such as savanna elephants are considered endangered and threatened by habitat loss and fragmentation, along with poaching (Gobush et al., 2021). Elephants are known to range over vast areas, with individual range sizes from 10 km^2 to over 10,000 km^2 (Douglas-Hamilton et al., 2005; Lindsay et al., 2017; Lohay et al., 2020; Ngene et al., 2017). They can travel long distances in response to seasonal changes and droughts. Depending on productivity and water availability, they exhibit range residency, migratory or nomadic movement patterns (Gobush et al., 2021; Purdon et al., 2018). As the largest of all land mammals, elephants play a crucial role in maintaining ecological balance. They transform woody vegetation into grasslands through feeding activities or trampling, aid in seed dispersal and often co-occur with other large mammal species (Adams et al., 2017; Purdon et al., 2018; Young et al., 2009).

In addition to the above-mentioned characteristics, lions and elephants in Namibia are of tremendous tourism and cultural value and predominantly reside in national parks. Some populations roam beyond conservation areas into human communities and are exposed to higher human-caused mortalities. Moreover, fencing and heavily used roads in north-central and north-eastern Namibia might act as barriers to the movements of both species. Therefore, this study selected lions and elephants as focal species to understand the dynamics of their movement patterns and detect suitable habitat patches and potential corridors.

3.4 Habitat use and selection by species

3.4.1 Lion

Lions are most active at night and have a broad habitat tolerance. The drivers of lion habitat selection and their relative importance vary across studies. Macdonald (1983) only considered the distribution and availability of prey as the main factor determining home range size and group size of carnivores. In contrast, several authors identified that lion distribution and movement is largely influenced by land cover type, water availability, prey abundance and proximity to human settlements (Abade et al., 2014; Sargent et al., 2021; Spong, 2002). Jackson et al. (2016) included the density of main roads as the influencing factor, together with land cover and human population density. In Namibia, the Large Carnivore Atlas (Hanssen & Stander, 2004) also documented different habitat types used by lions. Most of them were observed in waterholes (28%), followed by woodlands (23%), mountains (16%), dry river beds (11%), plains (9%), coastal areas (1%), and the rest in other habitats.

Land cover

Lions generally prefer habitats with high prey abundance; this includes grassland, savanna, plains, dense shrubs and open woodland (Sargent et al., 2021; Spong, 2002). Elliot et al. (2014) also investigated the differences in habitat selection according to age and sex groups and found that adults of both sexes mainly select grassland and shrubland for habitats. However, dispersing males show the opposite trend and occur mostly in woodland and land use types with high human interference (agricultural land, highways and humans).

Elevation

To facilitate movement, lions tend to select low elevations and flat slopes (Sargent et al., 2021; Yiu et al., 2019). Lions living on plains might also use view-sheds from rocky outcrops to increase their view range during hunting (Hopcraft et al., 2005). To our knowledge, elevation has not been recorded as a major factor influencing lion space use.

Rivers

Although lions in Etosha National Park can survive 10 days without drinking water, they like to live near rivers because of the constant water supply and higher prey availability (Abade et al., 2014; Department of Agriculture and Nature Conservation, 1989; Spong, 2002). Furthermore, river beds can provide dense cover for both hunting and shade. In Namibia, the Omuramba Omatako has been of great importance to several large game species, such as wild dogs and elephants (Hines, 1993). Lions were also spotted roaming along this dry river bed historically (Shortridge, 1934) and could still possibly use it in present times.

Waterholes

Waterholes are a significant determinant of lion distribution in arid and semi-arid savannas. According to Valeix et al. (2010), lions spend more time in the vicinity of waterholes, where prey are relatively more abundant and accessible. The study also found that lions move slower, cover shorter distances and follow a more tortuous path within 2 km of a waterhole than further from a waterhole. Besides, a positive correlation was evident between the high lion density in west Etosha and the density of artificial water points and prey (Stander, 1991).

Roads

Mammals with low reproductive rates and high mobility are more vulnerable to negative road effects (Rytwinski & Fahrig, 2012). The degree of impacts on species movements also depends on the type of road surface and amount of traffic. In Namibia, the road sections between Grootfontein and Rundu (B8) and between Ondangwa and Tsumeb (B1) are significant paved roads with high traffic volume, which might limit lion movements between Khaudum and Etosha National Parks (P. Beytell, personal communication; Kioko et al., 2015).

Fences

Fences have been an effective management strategy for conserving lions, especially in severe conflict areas (Di Minin et al., 2021). However, extensive fencing can fragment populations and eliminate existing connectivity and dispersal between subpopulations, leading to genetic isolation (Cushman et al., 2016). The ability of lions to cross fences is determined by the type (i.e. height and material), maintenance and quality of the fence. While electrified, elephant- and predator-proof fencing has the lowest crossing probability for lions, a 1.5-metre-high stock fence has almost no effect on large mammal movements (P. Beytell & W. Versfeld, personal communication). Owing to the lower quality of the existing boundary, approximately 118 km of the Etosha northern boundary fence has been upgraded recently. Moreover, veterinary fences in the north-east were suggested to have considerable influence on the range of lions and other large mammals (Stoldt et al., 2020).

Settlements

Lions avoid areas with increased human disturbance, but their avoidance varies individually depending on the season, time of day and lion behaviour (Sargent et al., 2021; Snyman et al., 2018; Valeix et al., 2012). In addition, female adult lions were found to have the highest aversion to settlements, followed by dispersing males and adult males (Elliot et al., 2014).

Area status

The types of land use (area status) govern the distribution of lions (W. Versfeld, personal communication). Lions display a strong preference for protected areas, including state national parks, concessions and wildlife protected areas in the communal conservancies, and avoid agro-pastoral lands (Elliot et al., 2014; Sargent et al., 2021). National parks assuredly provide safe refuge for lions, elephants and other wildlife while conserving high-quality habitats. However, many conservancies have zoned their areas for settlement or multiple-use purposes (e.g. hunting and livestock priority) apart from wildlife protection, which might be less suitable for lions due to higher occurrences of conflicts and anthropogenic mortality.

3.4.2 Elephant

Savanna elephants have been extensively studied (Chibeya et al., 2021; Purdon et al., 2018; Sach et al., 2019). They occur in 23 African countries and live across a variety of habitats, from open and wooded savannas to deserts and forests. The largest populations are in southern and eastern Africa (Botswana, Zimbabwe, Tanzania, Kenya, Namibia, Zambia and South Africa), and KAZA is home to more than 50% of the savanna species (Naidoo et al., 2022). As generalist herbivores, elephants consume a range of grasses, leaves, twigs, fruits, barks, herbaceous material and soil. They require enormous amounts of feed and water to survive and drink regularly. Their diet composition may also vary regionally and seasonally (Sach et al., 2019). Key variables contributing to elephant spatial use and distributions include elevation, vegetation cover, water sources, land use, human presence and associated activities (settlements, roads and fences) (Adams et al., 2017; Chibeya et al., 2021; Harris et al., 2008; Ngene et al., 2017; Roever et al., 2013; Sach et al., 2019).

Land cover

The structure and greenness of vegetation can serve as an important indicator of elephant habitat use, because it provides food and shade. Savanna elephants are found most often in grasslands, savannas and woodlands. However, previous studies have indicated different conclusions regarding elephants' preference of woody versus grass habitats. Several authors noted that elephants feed on nutritious green grass during the early wet season, thereby selecting seasonally variable landscapes such as grasslands, shrublands and open woodlands (Chibeya et al., 2021; Loarie et al., 2009a; Newmark et al., 1996). In the dry season, they switch to browsing and prefer less variable and more consistently green landscapes that include well-wooded areas and closed woodlands (Loarie et al., 2009a). Tsalyuk et al. (2019) also reported that elephants in Kenya had a preference for high tree density, whereas Etosha elephants selected areas with high grass biomass due to greater reliance on grazing rather than browsing. Additionally, elephants displayed sexual habitat segregation in relation to vegetation characteristics (De Knegt et al., 2011). For instance, male elephants in Kruger National Park selected high tree cover and low herbaceous biomass, but female elephants preferred high herbaceous biomass and low tree cover. Moreover, wetlands, croplands and bare soils are considered somewhat suitable habitats for elephants (P. Beytell, personal communication). With the easy accessibility of food, elephants are even more attracted to croplands than lions.

Elevation

Elephants tend to avoid high elevation sites and steep slopes owing to their large body size and energetic constraints (Chibeya et al., 2021; Roever et al., 2013; Sach et al., 2019). Based on energy landscape computations, minor hills can even be significant energy barriers for an elephant (Wall et al., 2006). In addition to slope, there may be other relevant motives for the elephants' general evasion of climbing mountainous terrain, such as overheating, risk of injury, water scarcity or unavailability of forage (Wall et al., 2006).

Rivers

Water availability has been shown to strongly influence elephant movement patterns (Sach et al., 2019; Wato et al., 2018). Being a water-dependent species, they regularly go to the rivers for drinking and bathing and use dry river beds as walkways (W. Versfeld, personal communication). Furthermore, elephants tend to congregate around permanent water sources in the dry season and disperse during the wet season (Purdon et al., 2018). Another reason for the higher preference of river course habitats is the availability of abundant and high-quality forage. Viljoen (1989) also highlighted that riverine habitat is the desirable habitat for elephants and the only one upon which the species can depend for long-term survival.

Waterholes

When surface water is scarce in semi-arid environments, elephants concentrate around waterholes, leading to higher local elephant densities. According to Loarie et al. (2009b), artificial waterholes can increase the dry season range of elephants and allow them to use formerly inaccessible areas. Khaudum Game Reserve is an example where enough permanent water was previously lacking to support elephants during the dry season. Similarly, boreholes in Etosha provide additional water for wildlife (Young et al., 2009). Another study by De Beer et al. (2006) suggested that Etosha elephants prefer to use areas within 4 km of water throughout the year. Besides, elephants increased their speeds during the dry season to minimise the travelling time between water and food sources (Chamaillé-Jammes et al., 2013).

Roads

Research increasingly shows that main roads can be considerable barriers to elephant movements (Brennan et al., 2020; Naidoo et al., 2012; Naidoo et al., 2018). A certain number of elephants will avoid roads entirely (Okita-Ouma et al., 2021; Roever et al., 2013). P. Beytell (personal communication) further mentioned that the barrier effect of high traffic-volume paved roads on elephants is stronger than on lions, especially the Grootfontein-Rundu road in Namibia.

Fences

The influence of veterinary fences on migratory ungulates and elephants is profound (Mbaiwa & Mbaiwa, 2006; Stoldt et al., 2020; van Aarde et al., 2021). Due to maintenance shortfalls, elephants will create breakages on veterinary fences. Electric fencing is increasingly used as a tool to separate elephants and humans. In Namibia, part of the Etosha northern boundary fence is electrified and is effective for elephants. There are also some game-proof fences around commercial farmland (e.g. areas with tourism, hunting, and conservation priority) that can strongly restrict the movements of elephants (P. Beytell, personal communication). Nevertheless, as lions, elephants have the highest crossing probabilities of stock fences.

Settlements

Elephants avoid areas of high human population density and settlements, with cows more so than bulls (Chibeya et al., 2021; Harris et al., 2008; Roever et al., 2013). Cushman et al. (2010) also found that elephants showed significant avoidance of towns at distances of up to 5 km and avoidance of villages and huts at a finer spatial scale of up to 1 km.

Area status

Elephants may choose habitat utilisation in protected areas to minimise human influence and allow the occurrence of natural ecological processes (Robson et al., 2017). Yet, many of them have large ranges that exceed protected area boundaries (Wall et al., 2021). Some national parks (e.g. Kruger and Etosha National Park) also constrain elephant distributions by fences, and some (e.g. Waterberg Plateau National Park) do not accommodate elephants and lions (P. Beytell, personal communication). In addition, the effect of conservancies on elephants is dependent on their zonation use. When humans and elephants interact, conflicts may arise from crop-raiding and damage of water installations (Green et al., 2018). In this regard, zonings with high human activities such as cropping, pastoralism and settlements are considered non-suitable habitats for elephants. Moreover, there is an exception of small elephant populations residing in farmland outside protected areas, notably Kavango Cattle Ranch.

3.5 Analysis of historical and recent distribution patterns of focal species

This study selected three time spans for analysing the distribution and movement patterns of Namibian lions and elephants: 1925-1935, 1965-1975 and 2005-2015. The choice of periods depended upon the availability of data. To reconstruct past species occurrences, historical maps were used and digitalised and shapefiles for their distributions were created. The distribution ranges for both species within 1925-1935 were derived from Magistral Papers (1925/26) and Shortridge (1934), while the 1965-1975 ranges were originated from Joubert and Mostert (1975). The Magistral Papers (1925/26) is also known as the wildlife census, as mentioned in Chapter 2.3. It documented various mammal species that were present around Etosha Pan and the neighbouring regions. The recent 2005-2015 ranges of lions and elephants were based on the Namibia Large Carnivore Atlas (Stein et al., 2012) and the African Elephant Status Report (Thouless et al., 2016), respectively. The total area of each species distribution range was furthermore calculated using the *Calculate Geometry* function in ArcMap (Esri, 2019).

3.6 Habitat suitability and corridor analyses

Habitat models have been commonly used as conservation tools for spatial prioritisation and corridor planning (Osipova et al., 2019). As the primary focus of the thesis was on detecting possible connectivity for large terrestrial mammals rather than in-depth movement patterns, two simple habitat suitability models (HSM) were created for lions and elephants to allow assessment of habitat suitability on a year-round basis. Corridor analyses were then performed based on the habitat suitability maps generated from these models. All the habitat suitability and connectivity models were computed using various ArcGIS tools (Esri, 2019). Furthermore, both environmental and anthropogenic parameters were chosen to develop the HSMs, including land cover, digital elevation model (DEM), rivers, waterholes, roads, fences, settlements and area status. The selection and weighting of these parameters were in reference to the ecological knowledge of the species through literature review and expert interviews (Chapter 3.4). In addition, all the spatial (base) data of the parameters used in the habitat and corridor analyses were made available free of charge on request from the partner research institution in Namibia, Ongava Research Centre. The datasets were preprocessed in ArcGIS for further use and set to the Namibian Universal Transverse Mercator coordinate system. As recommended in a habitat suitability study for Namibian lions and zebras (Kirchner, 2020), all the geodata were converted to raster layers with a cell size of 250 m and clipped to the extension of the study area.

3.6.1 Habitat suitability model for lions

The habitat suitability model for lions was computed in the ArcGIS ModelBuilder with the selected parameters. Most of the analysis tools applied for this model were included in the ArcGIS Spatial Analyst toolbox (Esri, 2019). The input base data or derived data were transformed to a scale between 0 (no suitability) to 100 (high suitability) regarding their influence on habitat quality, except for NoData cells replaced by -9. After reclassification, all the parameters were combined using the weighted sum approach to produce the final suitability surface. An overview of the evaluation categories of parameters and model tools was presented in Table 2.

Table 2. Overview of the parameters used in the development of the habitat suitability model for each species with details on ArcGIS tools and evaluation categories.

Parameters	**Description**	**ArcGIS tools**	**Categories of reclassification – Lion**	**Categories of reclassification – Elephant**
Land cover	Preferred land cover types by species	Resample, Reclassify, Extract by Mask	Forestland: 60 Woodland: 60 Grassland:100 Shrubland: 80 Savanna grassland: 100 Cropland: 20 Wetland: 0 Waterbody: 0 Settlement:0 Rock outcrop: 40 Bare soil: 40 Desert Dune: 0 Desert Sand: 0 NoData: -9	Forestland: 80 Woodland: 80 Grassland: 100 Shrubland: 80 Savanna grassland: 100 Cropland: 60 Wetland: 60 Waterbody: 60 Settlement: 0 Rock outcrop: 0 Bare soil: 60 Desert Dune: 0 Desert Sand: 0 NoData: -9
DEM	Slope inclination	Resample, Slope, Reclassify, Extract by Mask	0-20.847683°: 100 20-41.695366°: 60 41-62.543049°: 10 NoData: -9	0-20.847683°: 100 20-41.695366°: 60 41-62.543049°: 10 NoData: -9
Rivers	Distance at which species remain to rivers	Multiple Ring Buffer, Polygon to Raster, Reclassify, Extract by Mask	*Buffer distances (m)*: 500, 2000	*Buffer distances (m)*: 500, 2000
			Reclassify: 500 m: 100 500-2000 m: 20 NoData: -9	*Reclassify*: 500 m: 100 500-2000 m: 20 NoData: -9
Waterholes (protected area and settlement area)	Distance at which species remain to waterholes	Multiple Ring Buffer, Polygon to Raster, Reclassify, Extract by Mask	*Buffer distances (m)*: 500, 1500, 3500, 6000	*Buffer distances (m)*: 500, 1500, 3500, 6000
			Reclassify: 500-1500 m: 90 1500-3500 m: 60 3500-6000 m: 30 NoData: -9	*Reclassify*: 500-1500 m: 90 1500-3500 m: 60 3500-6000 m: 30 NoData: -9
Roads	Accessibility of species through heavily used roads	Polyline to Raster, Reclassify, Extract by Mask	Unpaved road: 80 Main paved road: 20 NoData: -9	Unpaved road: 80 Main paved road: 10 NoData: -9

Fences	Accessibility of species through the fence sections	Merge, Polyline to Raster, Reclassify, Extract by Mask	*Accessibility values*: NE Etosha fence: 10 Red Line fence: 40 Mangetti farm fence: 90 Private farm fences: - Hunting priority: 40 - Livestock priority: 90 - Mining priority: 90 - Protected area: 40 - Settlement/ Resettlement: 90 - Settlement & cropping: 90 - Tourism priority: 40 - Trophy hunting: 40 - Waterberg National Park: 40 - Unknown: 0	*Accessibility values*: NE Etosha fence: 10 Red Line fence: 40 Mangetti farm fence: 90 Private farm fences: - Hunting priority: 40 - Livestock priority: 90 - Mining priority: 90 - Protected area: 40 - Settlement/ Resettlement: 90 - Settlement & cropping: 90 - Tourism priority: 40 - Trophy hunting: 40 - Waterberg National Park: 40 - Unknown: 0
			Reclassify: 0: -9 0-10: 10 10-40: 40 40-90: 90 NoData: -9	*Reclassify*: 0: -9 0-10: 10 10-40: 40 40-90: 90 NoData: -9
Settlements	Distance at which species avoid human settlements	Euclidean Distance, Reclassify, Extract by Mask	*Maximum distance (m)*: 6000	*Maximum distance (m)*: 6000
			Reclassify: 0-500 m: 0 500-1500 m: 30 1500-3500 m: 60 3500-6000 m: 90 NoData: -9	*Reclassify*: 0-500 m: 0 500-1500 m: 30 1500-3500 m: 60 3500-6000 m: 90 NoData: -9
Area status	Effect of area protection status on species	Merge, Polygon to Raster, Reclassify, Extract by Mask	*Priority values (1-5 scale)*: Protected areas: - Etosha National Park: 5 - Khaudum National Park: 5 - Mangetti National Park: 5 Management zones: - Exclusive wildlife (all wildlife utilisation): 4 - Exclusive wildlife (no disturbance): 4 - Exclusive wildlife (tourism only): 4 - Exclusive wildlife (trophy hunting only): 4 - Forests: 4	*Priority values (1-5 scale)*: Protected areas: - Etosha National Park: 5 - Khaudum National Park: 5 - Mangetti National Park: 5 Management zones: - Exclusive wildlife (all wildlife utilisation): 4 - Exclusive wildlife (no disturbance): 4 - Exclusive wildlife (tourism only): 4 - Exclusive wildlife (trophy hunting only): 4 - Forests: 4

			- Multiple use (hunting priority): 3 - Multiple use (livestock priority): 1 - Multiple use (tourism priority): 4 - Human occupation/ unzoned area: 1 - Settlement & cropping: 1 - Unknown: 1 Private farms: - Hunting priority: 3 - Livestock priority: 1 (*except farms west of Khaudum: 3*) - Mining priority: 3 - Protected area: 4 - Settlement/ Resettlement: 1 - Settlement & cropping: 1 - Tourism priority: 4 - Trophy hunting: 3 - Waterberg National Park: 1 - Unknown: 1	- Multiple use (hunting priority): 3 - Multiple use (livestock priority): 1 - Multiple use (tourism priority): 4 - Human occupation/ unzoned area: 1 - Settlement & cropping: 1 *(except Mangetti cattle farms: 3)* - Unknown: 1 Private farms: - Hunting priority: 3 - Livestock priority: 1 (*except farms west of Khaudum: 3*) - Mining priority: 3 - Protected area: 4 - Settlement/ Resettlement: 1 - Settlement & cropping: 1 - Tourism priority: 4 - Trophy hunting: 3 - Waterberg National Park: 1 - Unknown: 1
			Reclassify: 1-2: 30 2-3: 50 3-4: 70 4-5: 90 NoData: -9	*Reclassify*: 1-2: 30 2-3: 50 3-4: 70 4-5: 90 NoData: -9

Land cover

Land cover data was provided in the form of a raster file that can be used directly in the model. The default categories of land cover types were reclassified and evaluated using the *Reclassify* tool in accordance with the land cover preference of lions. Due to a higher preference for grassland by lions, this land cover type was given to a value of 100, followed by shrubland (80), woodland (60), rock outcrop (40), bare soil (40) and cropland (20). The remaining types were assigned to 0 (Table 2).

DEM

DEM was used as the elevation parameter and to generate a slope raster in ArcGIS using the *Slope* tool. The slope values were then reclassified into three categories and rated with values from 0 to 100. The class with lower slope values (flatter terrain) was given a higher ranking (Table 2).

Rivers

As mentioned in Chapter 3.4.1, lions prefer habitats in close proximity to water sources. The main rivers in the polyline shapefile were first buffered with distances of 500 m and 2000 m using the *Multiple Ring Buffer* tool, followed by the vector to raster conversion and reclassification. Rivers within 500 m were rated with a higher habitat suitability value of 100, while rivers further than 500 m were given a value of 20 (Table 2).

Waterholes

The number and location of waterholes can affect the space use and movement patterns of lions, as well as the viability of their populations. The original shapefile of waterholes was therefore separated into two shapefiles, with one containing water points inside protected areas and the other outside protected areas. These two files were buffered with distances of 500 m, 1500 m, 3500 m and 6000 m, then rasterised and divided into three classes. The evaluation was also similar to the river parameter. Habitat suitability values decreased with increasing distance to waterholes (Table 2).

Roads

Traffic can be considered a factor influencing the habitat quality of lions adversely due to disruption of movement patterns. In the study area, unpaved roads have little or no effect on lion movements. However, major paved road sections such as Grootfontein-Rundu and Tsumeb-Ondangwa appear to have certain barrier effects. The *Polyline to Raster* tool was used to convert the polyline shapefile into a raster file. Unpaved roads were further rated with a higher suitability value than paved roads due to the higher chances of crossing for lions (Table 2).

Fences

The fences in the study area consist of the Red Line (veterinary fence), the northern Etosha fence, as well as fences in the Mangetti farming area and other private farms. These fences vary in height, material and condition. Besides, the spatial data of these fences were first merged into a single polyline shapefile, then rasterised and subsequently evaluated according to the accessibility of lions crossing through the fence sections. The Etosha fence is an electric fence, and it has the highest blockage effect on lions compared to the Red Line and stock fences. It was therefore also given the lowest habitat suitability value of 10 (Table 2).

Settlements

Lions tend to avoid human settlements due to high disturbance rates. The settlement parameter was derived from the density map of villages in Namibia (raster format). In order to determine the possible distance from settlements, the straight-line (Euclidean) distance was calculated within 6000 m using the *Euclidean Distance* tool. The distance values were reclassified into four classes, and the habitat suitability values decreased towards settlements (Table 2).

Area status

The area status parameter contains the polygon shapefiles of protected areas, conservancy management zones and privately owned farms in Namibia. These areas were assessed with a scale of 1-5 regarding their effects on wildlife protection and the resulting priority values were added to the attribute tables. A value of 5 is the highest priority conservation area, while a value of 1 is the lowest. Most national parks in the study area have the largest positive effect on protecting wildlife, except for Waterberg National Park, where lions and elephants are barely tolerated. In addition, the effectiveness of conservancy management zones and private farms on wildlife conservation are dependent on their subcategories. Within each subcategory, various human activities are allowed or discouraged. Areas dedicated to wildlife and tourism were also considered suitable habitats for lions and were thus assigned a higher conservation value than residential, livestock and cropping areas. These shapefiles were further merged into one shapefile and converted into a raster file. Afterwards, these priority field values were transformed to a 0-100 scale and high priority conservation areas were given the highest suitability values (Table 2).

Weighting of parameters for lion model

In order to generate a lion habitat suitability map, all reclassified parameter layers were combined using the *Raster Calculator* tool in ArcGIS with the weighted sum calculation. The final suitability raster was computed by multiplying the cell values (rasters) of the parameters with their corresponding weights, followed by a summation of the results (Meyer et al., 2020; Ntukey et al., 2022). The weights assigned to each parameter were based on their relative importance to the species' ecological needs. Water sources can influence prey distribution, with lions having higher hunting success in areas around waterholes. In addition, lions were observed using the dry Omatako River as a movement corridor. Therefore, waterholes inside protected areas were given the highest percentage weight (25%), followed by rivers (20%). Area status (20%) and land cover (10%) were also considered essential habitat factors due to a mixture of land uses within the study area and the provision of optimal shelter for lions. Lions tend to avoid risky areas such as agricultural land with a high incidence of retaliatory killings. Other parameters such as settlements, roads and fences received relatively low percentage weightings due to their influences as barriers (Table 3).

Table 3. Percentage contribution of each parameter to the habitat suitability model for each species.

Parameters	Percentage contribution to overall model – Lion	Percentage contribution to overall model – Elephant
Land cover	10	12
DEM	5	5
Rivers	20	19
Waterholes – protected area	25	26
Waterholes – settlement area	5	8
Roads	4	8
Fences	5	6
Settlements	6	6
Area status	20	10
Total	**100**	**100**

3.6.2 Habitat suitability model for elephants

The same overall procedures of the lion habitat suitability model were applied to the creation of the elephant habitat suitability model. Parameters included in this model were land cover, DEM, rivers, waterholes, roads, fences, settlements and area status. A habitat suitability surface for elephants was also produced by combining raster layers using the weighted sum. However, due to different habitat preferences between elephants and lions, the evaluation values within individual parameters and the percentage contributions of the parameters used in this elephant model differed slightly from the lion model.

Land cover

Elephants inhabit a variety of habitats and mostly prefer grasslands, shrublands and woody vegetation. As a result, grasslands were assigned with the highest value of 100, and the latter two land cover types were rated as 80. Cropland and bare soil were also given a value of 60 because elephants are attracted to food crops. Unlike lions, rock outcrops were considered unsuitable for elephants and thus receiving the lowest suitability value (Table 2).

DEM

Elephants tend to avoid steep slope. In this model a maximum slope of about 62° was generated from the DEM. These slope values were divided into 3 classes and evaluated. Slope below 20° were assigned a value of 100, slope between 20° to 41° was assigned a value of 60 and slope above 41° was assigned a value of 10 (Table 2).

Rivers

Elephant distribution is significantly influenced by the distribution of surface water. In order to classify the habitat suitability with consideration of the possible distance from rivers, a multiple ring buffer analysis was performed for the river shapefile. The buffer distances were set to 500 m and 2000 m. The shapefile was then converted to a raster file and classified. The shorter the distance from the river, the higher the suitability value (Table 2).

Waterholes

In addition to rivers, elephants were observed to prefer staying near waterholes inside wildlife protected areas and sometimes in agricultural areas. The shapefiles of waterholes for both protected areas and settlement areas were buffered with a maximum distance of 6000 m before they were rasterised and reclassified. Due to the positive impact of areas close to waterholes on elephants, the distance range of 500 m to 1500 m was given the highest value of 90. The distance ranges between 1500 m and 3500 m and between 3500 m and 6000 m were given 60 and 30, respectively (Table 2).

Roads

Paved roads with high traffic volume negatively affect elephants like other large terrestrial mammals. The major tar roads within the study area are expected to have a higher barrier effect on elephants than lions. Therefore, the polyline road shapefile was first rasterised and later classified with a low suitability value of 10 for paved roads. A value of 80 was given to unpaved roads or low traffic paved roads due to their relatively low influence as a barrier (Table 2).

Fences

The electric fence in northern Etosha, the Red Line and electric fencing in private farms restrict elephant movement. As the electric fence was considered to have the lowest crossing probability for elephants, it was assessed with a value of 10. Some private farms may contain game-proof fences and have a similar blockage effect as the Red Line fence. Hence, they were given a lower suitability value of 40. With the increased probability of crossings for elephants, most farm fences (stock fences) were rated as 90 (Table 2).

Settlements

Human settlements can create a barrier to elephant movement and contribute to increased human-wildlife conflicts, posing a threat to the long-term viability of elephant populations. Proximity to settlement raster was first created using the Euclidean Distance analysis with a maximum distance of 6000 m. The distance values were then divided into four classes and the classes with increasing distance to settlements were given a higher suitability value (Table 2).

Area status

The area status parameter was generated with the datasets of protected areas, conservancy management zones and Namibia’s private farms. These area type files were also evaluated according to their conservation effectiveness on elephants and merged into a single shapefile. Afterwards, the shapefile was converted into a raster dataset, and the priority values were reclassified with a scale of 0-100. State protected areas and wildlife exclusive management zones were assigned with a higher habitat suitability value due to their high levels of positive effects on animal conservation. In contrast, agricultural and residential areas were given the lowest ranking values for conservation priority and habitat suitability. Nevertheless, two farming regions were considered moderately suitable habitats for elephants: the Mangetti Cattle Ranch and private farmland west of Khaudum National Park (Table 2).

Weighting of parameters for elephant model

All parameters selected for this elephant model were combined in the same way as the lion model in order to produce a final elephant habitat suitability surface. To further increase the accuracy of the elephant's suitability surface, the weights of the parameters were slightly adjusted according to the ecological requirements of elephants. Since water is a critical resource for elephants, waterholes within protected areas and rivers were the two factors with the highest weightings of 26% and 19%, respectively. Furthermore, land cover received a slightly higher value of 12% than area status (10%) because of its role in providing high-quality forage and shelter for elephants. Despite the importance of water to elephants, water points in residential areas were given a lower value of 8% as they could be a potential source of human-elephant conflicts. Similar to the lion model, the parameters of roads, settlements and fences were assigned with a lower weighting. Besides, the slope parameter derived from the DEM was given the lowest percentage weight due to the relatively flat landscape of the study area, which has little influence on elephant habitat quality (Table 3).

3.6.3 Resistance surface construction for lions and elephants

The construction of resistance surfaces (also known as cost surfaces) is recognised as an important component in connectivity analyses (Carroll et al., 2020; Cushman et al., 2010; Cushman et al., 2014; Wade et al., 2015; Zeller et al., 2018; Ziółkowska et al., 2016). Furthermore, the least-cost path modelling coupled with resistance surface analysis has been frequently used for the connectivity assessments of large mammals (Smith et al., 2019). A resistance surface is a raster layer that reflects the relative difficulty or resistance for the focal species to move through a given pixel (cell) of the landscape. Pixels with low resistance values indicate greater ease of movement, while high values represent greater frictions to movement. As suggested by Beier et al. (2007) and Kirchner (2020), this study used the inverse of habitat suitability (resistance = 100 – pixel habitat suitability) to compute the resistance surfaces for lions and elephants with the help of the *Raster Calculator*. The habitat suitability values were also rescaled to a range of 0-100 before translating into relative resistances. After defining the resistance surfaces for each species, potential corridors were mapped by the least-cost path modelling. This modelling approach identifies the most optimal travel paths by selecting combinations of cells that represent the least resistance with the shortest distance between two points (LaRue & Nielsen, 2008).

3.6.4 Habitat patches and least-cost connectivity analyses for lions and elephants

For the development of corridor models, it is essential to first identify regions (i.e. habitat patches) that fulfil specified habitat requirements for the target species (Beier et al., 2007; Esri, 2019; Wade et al., 2015). These patches will further serve as the start and end points for corridors. Beier et al. (2007) additionally stated that the minimum patch size should be large enough to allow a breeding event to take place, which is usually equal to the home range size. To identify suitable habitat patches and least-cost connectivity for lions and elephants in the north-central and north-eastern Namibia, this study adopted the settings of the corridor model developed by Kirchner (2020) for the north-western Namibian lions. Habitat patches for both species were computed from the habitat suitability maps for three trials using the ArcGIS *Locate Regions* tool, with the maximum number of patches set as 5, 10 and 16. The minimum size of a habitat patch was defined as 250 km^2, while the maximum size was set at 5870 km^2. These areas were chosen based on the recorded minimum and maximum home ranges of lions in Etosha National Park (Kirchner, 2020). With the resistance surface and the suitable patches as the input data, a network of least-cost paths, also referred to as corridors, was generated as a line shapefile using the *Cost Connectivity* tool in the ArcGIS Spatial Analyst toolbox (Esri, 2019).

4 Results

4.1 Changes in distribution and movement patterns of lions and elephants

Figure 12 and Table 4 show the distribution patterns and total range areas of lions and elephants in 1925-1935, 1965-1975 and 2005-2015.

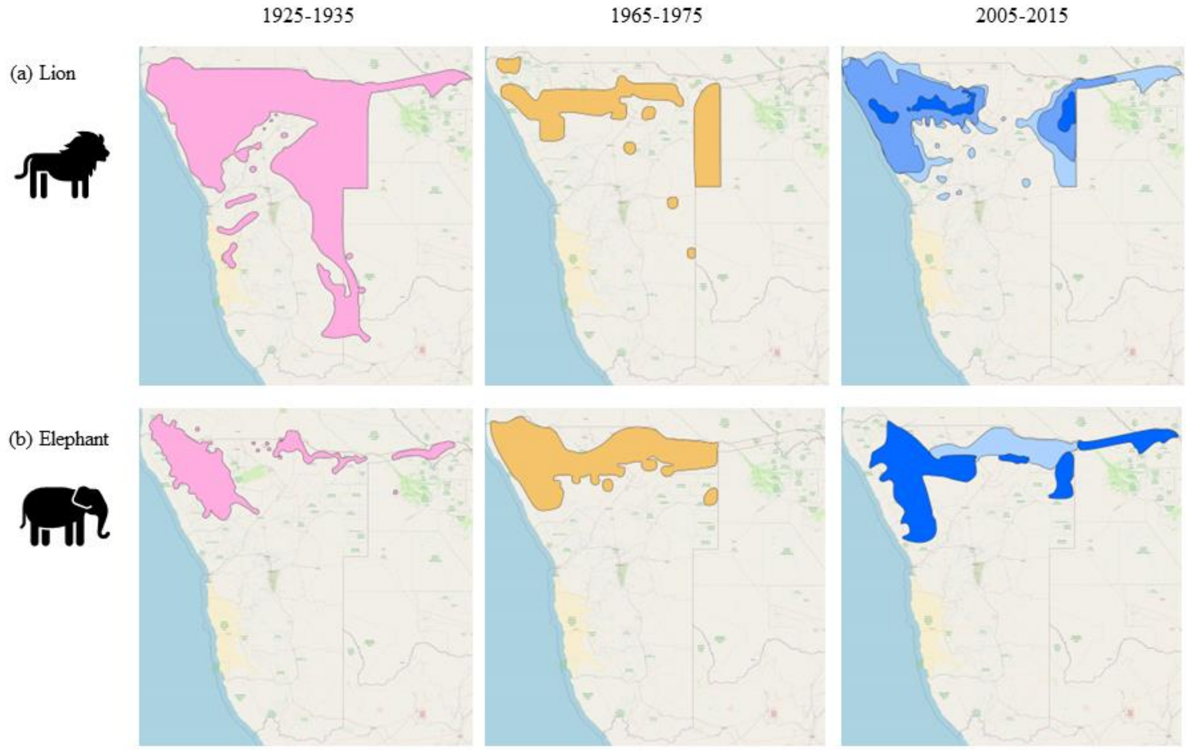


Figure 12. Distribution patterns of selected species in 1925-1935, 1965-1975 and 2005-2015.

The maps show the distribution ranges of (a) lion and (b) elephant in 1925-1935 (pink), 1965-1975 (orange) and 2005-2015 (blue). In addition, the 2005-2015 lion distribution map indicates the density of lion populations: high density (dark blue), medium density (blue) and low density (light blue). For the elephant, the 2005-2015 range is further categorised into known range (blue) and possible range (light blue).

Table 4. Approximate distribution areas of lions and elephants.

Year	Approximate total distribution area of lions (km^2)	Approximate total distribution area of elephants (km^2)
1925-1935	453,403	110,430
1965-1975	136,135	173,586
2005-2015	240,681	175,927

Lion

Comparing the occurrences of Namibia's lions among the three periods, the range has declined substantially since 1935. According to Magistral Papers (1925/26), lion distributions were officially recorded in Ovamboland, Namutoni, Outjo, Otjiwarongo, Omaruru, Gobabis, Aroab and Gibeon, with some periodic visits made from the Outjo district to the south-west portion of Grootfontein. Several lions were also observed at the waterholes north of the Waterberg-East Native Reserve and a few migrated from the west of Waterberg in the Otjiwarongo area to the east and returned during the months of August and September. Following the Magistral Papers (1925/26), Shortridge (1934) reported their occurrence over a larger area, mainly in the north-west, north-east and east of South West Africa. Shortridge added that lions had nearly disappeared below 25ºS latitude, but a certain number still existed in the Namib mountainous valleys as far south as the Kuiseb River. Several lions followed prey along the Auob River to the south-east around Upington. In former Damaraland, they sometimes occurred among the coastal ranges from the Swakop and lower Kuiseb Rivers in the south, around the Spitzkop Mountain, to the north of the Ugab River. Lion populations were widely distributed across the Kaokoveld, with the highest densities around the Kunene Valley and some northern local villages. Within the Otjiwarongo and Grootfontein districts, Shortridge (1934) recalled the lion visits to waterholes north of Waterberg mentioned in the Magistral Papers (1925/26) and further reported the constant observation of lion spoor along the river bed of Omatako. In the late dry season, lions followed the antelope and zebra from Grootfontein area into the Okavango Valley. Moreover, lions were common in the Okavango, former Caprivi and Ovamboland except in the south of Etosha Pan, where much trapping and poisoning occurred (Shortridge, 1934).

By 1975, the overall range of lions decreased from 453,403 km^2 (1925-1935) to 136,135 km^2. Joubert and Mostert (1975) highlighted the absence of lions from all farmland, Ovamboland and the Kaokoland plateau due to systematic eradication. A fair number persisted in the north-western corner of Damaraland and Kaokoland. Other lion regions included the Etosha National Park, southern Kavango along the Botswana border, as well as further south in Bushman- and Hereroland (Joubert & Mostert, 1975). The Human-Lion Conflict Management Plan further suggested that autocratic political structures, land reform (such as the Odendaal Plan) and the growth of agriculture post-1970 were the contributing factors of the dramatic lion population decline in the Kunene region (Ministry of Environment and Tourism, 2017).

Today, the range is noticeably smaller despite a slight expansion in some established territories (Stein et al., 2012). Lions have disappeared from the Kavango West region in northern Namibia and most of the southern and central portions of the country. The total population is estimated to be 800. As shown in Figure 12a, high lion densities only occur in Etosha National Park, Khaudum National Park/ Nyae Nyae Conservancy and parts of the Kunene region, with a combined area of 25,771 km^2 (Stein et al., 2012). It is undoubtedly that the source populations for lions are north-west Botswana and Etosha National Park; however, the Kunene populations have established healthy prides that may provide dispersal adults to surrounding areas through conflict mitigation (Stein et al., 2012). In the Zambezi region, the high frequency of conflicts with humans and associated retaliatory killing has resulted in low lion numbers, even though it is part of the KAZA connectivity zone. Lions additionally occur in the Otjiwarongo area but at a low density due to constant persecution by commercial farmers.

Elephant

The Namibian elephant distribution pattern has also changed considerably between 1925 and 2015 (Figure 12b). Magistral Papers (1925/26) first reported that about 40-50 elephants occurred in eastern Ovamboland, with a small number visiting the western part from the Kaokoveld in the wet season. Additionally, there were 200 individuals present in Outjo but none in the Namutoni Reserve. Records indicated that the last herd of elephants in Namutoni was exterminated in 1881 (Magistral Papers, 1925/26; Martin, 2005; Ministry of Environment, Forestry and Tourism, 2020b). With the demand for ivory, elephants continued to decrease in the northern areas. By 1934, the range expanded slightly but was limited to the Kaokoveld and the Caprivi regions, with occasional migrants in Outjo, Ovamboland and Okavango (Shortridge, 1934). During the rainy season, some elephant residents in the northern and central Kaokoveld migrated southward as far as the Ugab River. Shortridge (1934) also noted a few elephants crossed the Okavango River from south-east Angola before the rains. Another key elephant regions were the Omatako and the Khaudum/Shadum, where the omurambas flow into the Okavango and Tshodilo Hills (Shortridge, 1934).

The range of elephants extended across northern Namibia, and the size increased from 110,430 km^2 in 1935 to 173,586 km^2 in 1975. Several reports indicated that elephants recolonised the Halali and Namutoni areas in the 1950s (Martin, 2005; Ministry of Environment, Forestry and Tourism, 2020b). By 1975, Etosha National Park had the highest concentrations of elephants with various migratory movements around the Park (Joubert & Mostert, 1975). For instance, elephants migrated eastward along drainage lines merging into the Okavango River. Besides, small numbers of herds moved into Ovamboland from central Etosha, while some herds moved down the Hoanib drainage system into the western Etosha. There were limited elephant movements from the Otjovansandu and Onaiso regions to north-west Ovamboland and into the Kaokoland (Joubert & Mostert, 1975). However, elephant subpopulations in north-western Namibia and the Caprivi disappeared due to war-related poaching in the 1960s-1980s (Martin, 2005). An annual migration route from the Kunene River to the Hoarusib River was then destroyed by 1980 (Martin, 2005; Viljoen, 1987). Consequently, these pressures on elephants may have contributed to the rapid increase of the resident population in Etosha.

Covering 175,927 km^2, the present range of elephants (2005-2015) is very similar to the 1965-1975 range. There are currently over 22,000 elephants in Namibia. Their distribution can be considered into two parts – the north-eastern (Khaudum/ Nyae Nyae Conservancy and the Zambezi) and the north-western (Etosha National Park and neighbouring Kunene region) (Thouless et al., 2016). The elephant populations in Khaudum/ Nyae Nyae have been established since the 1980s and form the largest group in the country with the development of artificial water and cross-border movements from Botswana (Martin, 2005; Thouless et al., 2016). For the north-western populations, they have recovered from historical over-hunting and expanded south to the Omaruru River and the edge of the Erongo mountains. Between Khaudum and Etosha, a small population occurs in the Mangetti area. While some elephants occupy the Mangetti National Park, some concentrate around the Kavango Cattle Ranch to the west and extend into the Ukwangali communal area to the north (Thouless et al., 2016). In addition, the 2014-2015 KCR collar data demonstrated southward movements of elephants onto the commercial farms in Grootfontein during the wet season (Ministry of Environment, Forestry and Tourism, 2020b). The African Elephant Status Report has further identified the rest of the Kavango region and a small area right above the Etosha as *possible* range (48,054 km^2), in which occasional sightings have been made (e.g. elephant movements between Angola/Kavango to the north-west of Khaudum). Despite the successful population recovery, there have been additional movement challenges to Namibian elephants. Firstly, Etosha elephants have become increasingly isolated since the upgrade of perimeter fencing in recent years (Thouless et al., 2016). Secondly, a potential (historical) corridor used by elephants between the north-east Etosha and the Mangetti area (via the Omuramba Ovambo) has been interrupted by fencing and the expansion of settlements and farms (Ministry of Environment, Forestry and Tourism, 2020b). In Khaudum, elephant populations have also lost their important wet dispersal area due to the agricultural development west of the Park (Ministry of Environment, Forestry and Tourism, 2020b). Moreover, fences along the Namibia-Botswana border have hampered large-scale elephant movements between the permanent waters of Okavango Delta and wet season habitats of the Nyae Nyae pans and Khaudum omurambas (Loarie et al., 2009b; Naidoo et al., 2022).

4.2 Habitat suitability surface for lions

Habitat suitability serves as the basis for the resistance surfaces and core areas employed in the corridor analyses. The lion habitat suitability model generated a map of predicted suitable habitats for lions within the study area based on nine environmental and anthropogenic parameters (Figure 13). These included the preferred land cover types, slope derived from DEM, proximity to rivers and waterholes (inside and outside protected areas), distance to human settlements, area status and the accessibility of crossing fences and main paved roads. In the lion habitat suitability surface, the predicted habitat suitability values were represented as a constant colour ramp, with dark blue indicating the highly suitable species habitats and red representing uninhabitable areas.

The most suitable habitats for lions were mainly found near the waterholes in Etosha National Park, Mangetti National Park, as well as Khaudum National Park/ Nyae Nyae Conservancy. A number of river beds, such as the Omatako River, were also considered suitable to highly suitable habitats. With the presence of rivers and water points inside protected areas, a small, connected area of suitable habitats was formed in the north-eastern part of the study area, stretching from Khaudum/ Nyae Nyae to the N≠a Jaqna Conservancy and the Omatako River. In contrast, the rest of the study area was considered moderately suitable to poorly suitable habitats due to high levels of human occupation. These areas are dominated by freehold farms or communal conservancies with priorities for settlement, cropping and livestock. The habitat suitability surface further indicated that the northern part of the study area (i.e. areas above Etosha and along the Angola-Namibia border) and the south-eastern corner (below Nyae Nyae Conservancy) had the lowest suitability values.

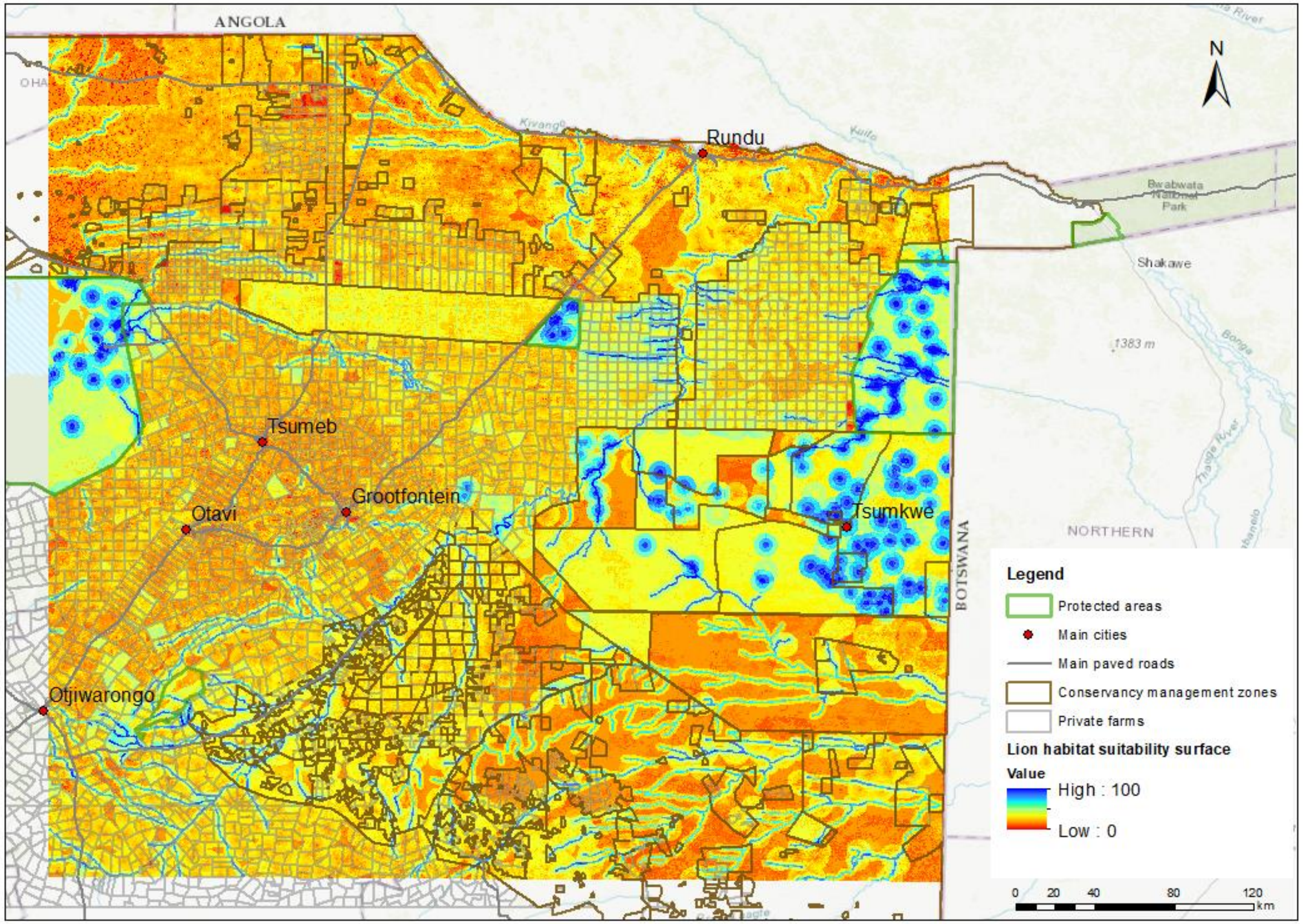


Figure 13. Final habitat suitability surface for lions based on the habitat suitability model using the nine selected parameters.

The predicted habitat suitability for lions, with values ranging from 0 to 100, is depicted using a blue-green-red colour ramp. Dark blue colour indicates high habitat suitability while red colour indicates low habitat suitability.

4.3 Core habitats and least-cost paths for lions

The best available lion habitat patches were computed in three trials based on the lion habitat suitability surface, with a maximum number of 5, 10 and 16 patches. Each habitat patch was uniquely numbered with values. Potential least-cost paths connecting these major habitat patches were identified with the input of lion resistance surface under the connectivity analysis. Overall, the three sets of core habitats showed a similar pattern with suitable habitat patches around protected areas and along the Omatako River (Figure 14). Habitat patches were also found within Khaudum and Etosha National Parks in all three trials.

The core habitat analysis determined the five most suitable habitat patches in the Khaudum/ Nyae Nyae area, Etosha National Park, east of Mangetti National Park, and east of Waterberg Plateau National Park (Figure 14 upper left). A least resistant corridor connected the Khaudum/ Nyae Nyae and Mangetti areas through habitat patches numbered 1, 3 and 4. Furthermore, habitat patches 3 and 5 formed a pathway following along the Omatako River from the Mangetti to the regions east of Waterberg Plateau Park. This corridor further extended to the Etosha National Park by connecting habitat patches 2 and 5.

In the trials with 10 core areas (Figure 14 upper right) and 16 core areas (Figure 14 lower left), the first three most suitable habitats for lions were found in the Khaudum National Park, Nyae Nyae Conservancy and Etosha National Park. The relatively less suitable habitats were in farming areas such as east of Waterberg, west of N≠a Jaqna Conservancy, and the small-scale commercial farms in western Khaudum. By comparing these two trials, the 16-core area trial contained one additional habitat patch each in Etosha and Nyae Nyae and on the Omatako River. In the same trial, habitat patches 5, 6, 9 and 11 were directly on the Omatako and connected as a corridor. This Omatako corridor extended eastwards to the Eiseb River via habitat patches numbered 9, 12, 14 and 16. Besides, habitat patches in Khaudum and Nyae Nyae connected through the patches in N≠a Jaqna Conservancy and parts of the farming area next to Khaudum. Contrastingly, the habitat patches between Khaudum and Nyae Nyae were linked directly in the 10-core area analysis. Habitat patches around the Omatako River and their associated least-cost paths were also slightly shifted away from the river in this trial.

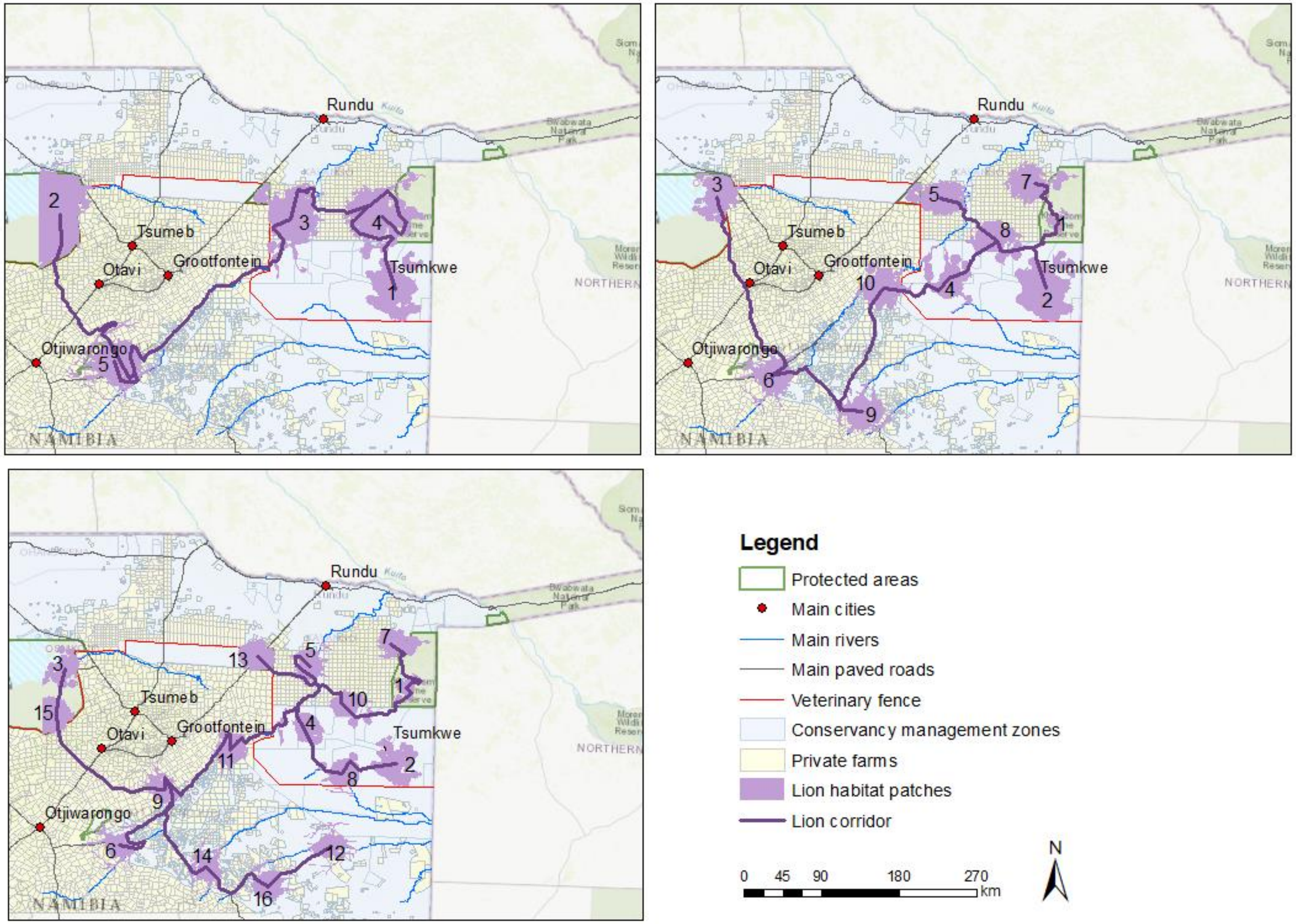


Figure 14. Habitat patches and least-cost paths for lions with a maximum number of 5 patches (upper left), 10 patches (upper right) and 16 patches (lower left).

4.4 Habitat suitability surface for elephants

The habitat suitability surface for elephants was produced the same way as for lions, but with slightly different weights within each parameter and between the parameters used in this elephant habitat suitability model (Chapter 3.6.2). The representation of the elephant suitability map also followed the same logic of values and colours as the lion suitability surface. As depicted in Figure 15, there were very limited suitable habitats for elephants in the study area, similar to the results of the lion habitat suitability model (Figure 13). Much of the study site was classified as marginally suitable and unsuitable habitats for elephants due to high intensity of human activities. On the contrary, areas with higher habitat suitability values were restricted to protected areas, especially around waterholes. These areas included Etosha, Mangetti and Khaudum National Parks, along with the two conservancies adjoining south of Khaudum. The perennial Okavango River, Omuramba Omatako and some other rivers were also considered suitable to highly suitable habitats for elephants. However, the habitat suitability of areas adjacent to the Okavango and Omatako rivers was low because of the negative impact of the large number of settlements. Moreover, this elephant model predicted the Kavango Cattle Ranch as a slightly more suitable habitat patch.

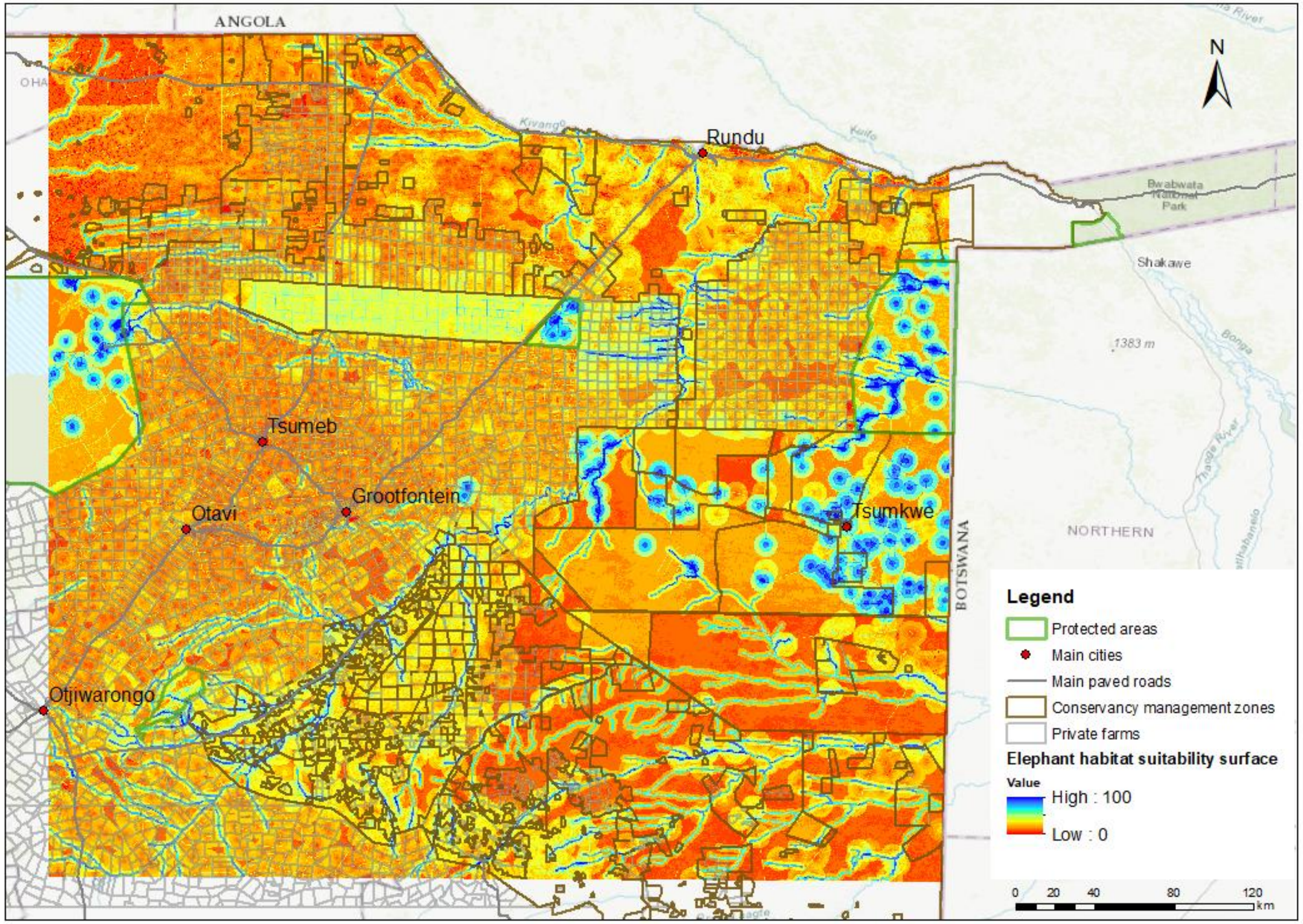


Figure 15. Final habitat suitability surface for elephants based on the habitat suitability model using the nine selected parameters.

The predicted habitat suitability for elephants, with values ranging from 0 to 100, is depicted using a blue-green-red colour ramp. Dark blue colour indicates high habitat suitability while red colour indicates low habitat suitability.

4.5 Core habitats and least-cost paths for elephants

To maintain consistency between models of focal species, the elephant connectivity model generated three sets of core habitats and potential corridor networks for elephants, with the maximum numbers of patches set as 5, 10 and 16. In all three trials, highly suitable habitats were found in protected areas and along the Omatako River (Figure 16). However, the potential linkages estimated in the 5-core habitat trial differed slightly from the other two trials.

The optimal habitats for elephants predicted from the core habitat analysis with five patches were located in Nyae Nyae Conservancy, Etosha National Park, the farms east of Waterberg Plateau National Park and the farm blocks between Mangetti and Khaudum National Parks (Figure 16 upper left). Habitat patches numbered 1, 3 and 5 connected Nyae Nyae to the Mangetti area through Khaudum. Furthermore, the ephemeral Omatako River functioned as a movement corridor by connecting habitat patches 2 and 3. The linkage of habitat patches 2 and 4 formed another pathway between Waterberg and Etosha. However, habitat patches of Etosha and east of Waterberg were not connected in both trials with 10 core habitats (Figure 16 upper right) and 16 core habitats (Figure 16 lower left). Instead, a passage linked Khaudum/ Nyae Nyae area to the Etosha National Park through the habitat patches in the Mangetti National Park and the Kavango Cattle Ranch.

In addition, the trials with 10 and 16 core habitats demonstrated a similar pattern in terms of habitat patches and corridor networks. The highly suitable habitats were mainly in Khaudum, Nyae Nyae and Etosha, whereas the less suitable habitats were in the agricultural areas (e.g. Kavango Cattle Ranch, Khaudum west and the eastern areas of Waterberg). Apart from the corridor between Khaudum/ Nyae Nyae, Mangetti and Etosha, the Omatako River also formed part of the linkages from the Etosha to the Waterberg east. In the trial with 16 core habitats, the Omatako pathway extended to the east until the Eiseb River by linking the habitat patches of 5, 9, 10 and 12.

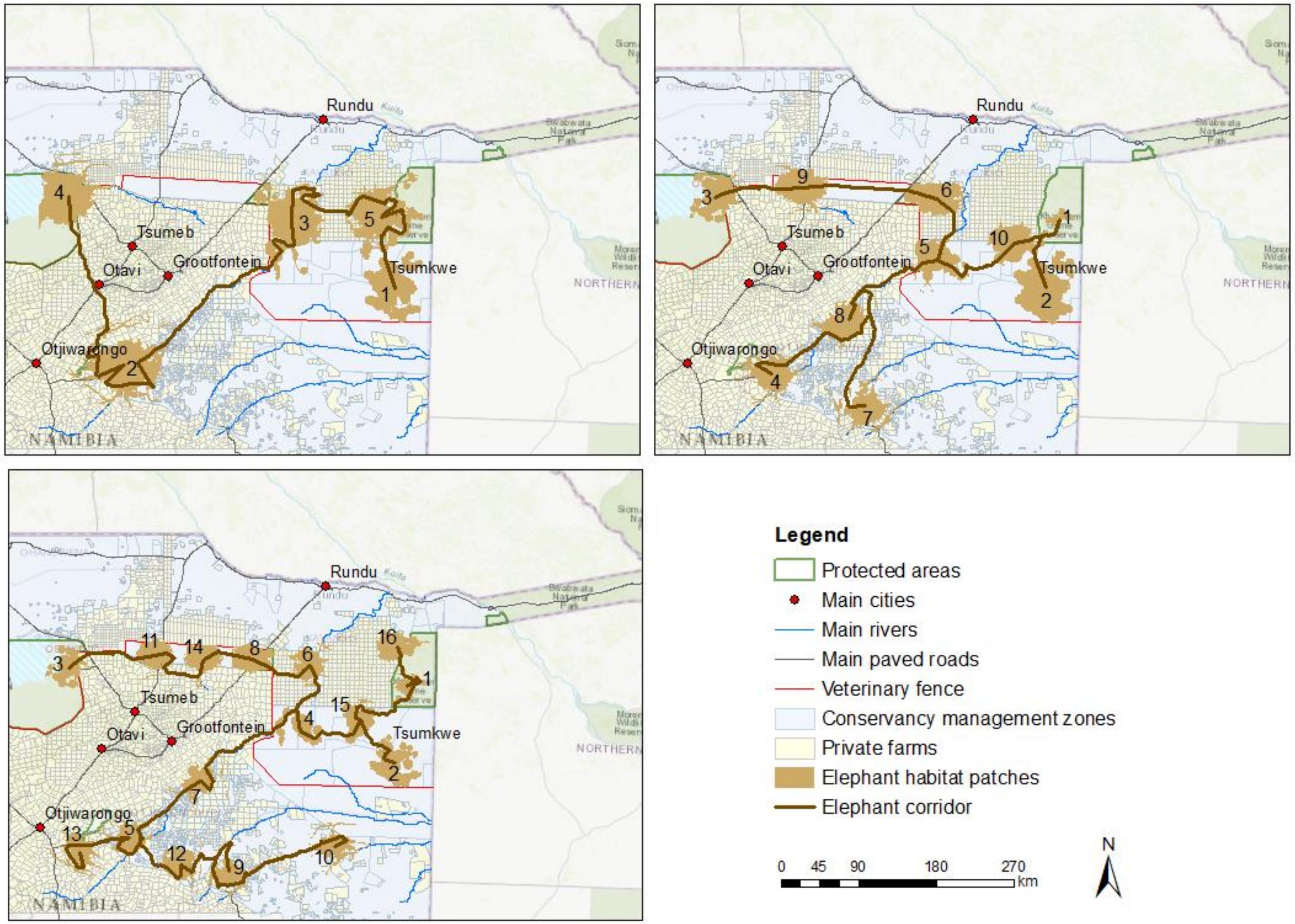


Figure 16. Habitat patches and least-cost paths for elephants with a maximum number of 5 patches (upper left), 10 patches (upper right) and 16 patches (lower left).

5 Discussion

5.1 Factors affecting the distribution and movement of large mammals

The present study demonstrates that Namibian lions and elephants, and likely other large terrestrial mammals, have experienced substantial range contractions and reduced movements due to human activities dominated by land use changes and associated habitat loss and fragmentation. Habitat degradation may further decrease the availability of high-quality forage and affect the quality of migration corridors for elephants and other migratory species (Dejene et al., 2021). Besides, hunting and diseases have threatened the population and distribution of many large mammalian species in the past. The clearing and conversion of natural land to alternative uses are primarily driven by human population growth, agricultural expansion and livestock production, as well as infrastructure development such as settlements and transportation systems. A study from Wingate et al. (2016) found that most land cover changes in north-eastern Namibia occurred within communal land, followed by state protected land, suggesting a reduction in natural habitats available to wildlife. Physical structures such as fences and roads also pose environmental challenges to large terrestrial mammals. These increase competition for space and resources between wild animals and humans, subsequently increase the frequency and intensity of conflicts. Moreover, climate change and variability can induce significant shifts in the distribution of suitable habitats and increase extinction risk for species by exacerbating the impacts of land use and cover changes. Therefore, maintaining and improving habitat connectivity is essential to help large terrestrial mammals persist into the future and lessen the negative effects of land use change, climate change and human-wildlife conflicts. In particular, wildlife corridors allow animals to move between isolated habitat patches, access to larger habitats, reduce the adverse effect on vegetation, minimise interbreeding and improve genetic viability (Ojwang et al., 2017; Osipova et al., 2018).

5.1.1 Increasing human population and urbanisation

The unprecedented growth in human populations and the associated spread of anthropogenic activities have disrupted wildlife populations and interfered with their distributions and movements within and between habitats and ecosystems (Tucker et al., 2021; Tuqa et al., 2014). The loss and fragmentation of natural habitats by rapid land use transformations are the greatest threats to large mammal species, particularly outside protected areas (Baisero et al., 2020; Crooks et al., 2017; Di Minin et al., 2021). For example, increasing unplanned farms and settlements trigger permanent loss of habitats, degrade forage and interrupt the traditional migratory routes of elephants (Shaffer et al., 2019). With the shrinking of dispersal areas and loss of connectivity, competition between wildlife, livestocks and the communities living in adjacent areas may escalate, increasing the likelihood of human-wildlife conflicts and persecution. Additionally, terrestrial mammals are vulnerable to habitat loss and modification by urban development (Lesilau et al., 2021; Magura et al., 2021). Urbanisation can alter the environment available to species by increasing ambient temperature, pollution, the number of barriers preventing wildlife movement and the proportion of impervious surfaces (O'Donnell & delBarco-Trillo, 2020; Ordeñana et al., 2010). It can also impact species through changes in water and nutrient availability, competition and predation rates and increases in disease exposure (O'Donnell & delBarco-Trillo, 2020).

The total human population of Namibia has grown steadily since 1921, from about 229,000 in 1921 to around 1.4 million in 1991 and 2.1 million in 2011 (Namibia Statistics Agency, 2012). The current population is approximately 2.5 million and is projected to reach 3.4 million by 2040 (Namibia Statistics Agency, 2014). Furthermore, the growth rate increased from about 2% per year in the first half of the 20th century to 3% during most of the latter half but dropped to 1.8% more recently (Central Bureau of Statistics, 2010; Namibia Statistics Agency, 2017). According to the Atlas of Namibia's Population (Central Bureau of Statistics, 2010), medical care advancement and immigration have contributed to the national population growth. Due to improved medical care, people's life expectancy has increased. In terms of migration, there were formerly large numbers of Angolans crossing the border into northern Namibia for better economic opportunities and social services, as well as escaping the harsh effects of colonial rule (between 1920s and 1930s) and the more recent civil war during the last two decades of the 20th century. The percentage living in urban areas increased from 28% in 1991 to 33% in 2001 and 43% in 2011, with trend-projections predicting over 60% by 2040 (Namibia Statistics Agency, 2017). As the human population continues to grow and as land use intensifies, specifically in the northern communal areas, the pressure on wildlife and their habitats will be even greater.

5.1.2 Development of land allocation and land use patterns

Land tenure plays an important role in shaping the patterns and changes in land use, as individual tenure systems may be associated with particular economic, political, social and cultural conditions (Farley et al., 2012). Changes in land tenure can furthermore have implications for biodiversity. For instance, deforestation can be accelerated by certain land tenure policy, contributing to biodiversity loss. Unclear ownership, use and access rights to land may also cause uncontrolled land use expansion, resulting in wildlife displacement and flora destruction (Schürmann et al., 2020). In Namibia, the distribution ranges of both lions and elephants have become disconnected and reduced in size over the years, which coincided with the expansion of farming development as a consequence of increased allocation of freehold land since the 1920s. The largest range contraction observed in lions from 1925 to 1975 corroborates the finding by Joubert and Mostert (1975) who reported the absence of lions from all farmland by 1975.

Table 5. Percentage of land allocation in Namibia from 1902-2018 (adapted from Namibia Statistics Agency, 2018)**.**

Year	**State land (km^2)**	**State land (%)**	**Communal land (km^2)**	**Communal land (%)**	**Freehold land (km^2)**	**Freehold land (%)**
1902	526,800	64	249,100	30	48,100	6
1911	575,200	70	77,400	9	171,400	21
1921	515,300	63	67,100	8	241,600	29
1937	385,600	47	143,500	17	294,900	36
1955	219,100	26	221,400	27	383,500	47
Post-1964	128,700	16	332,400	40	362,600	44
2001	150,000	18	317,400	39	356,600	43
2018	194,000	23	287,700	35	342,400	42

Table 5 presents the percentage changes in land allocation in Namibia from colonial times to the present (1902-2018), based on the elaborate data from the Atlas of Namibia (Mendelsohn et al., 2002) and the Namibia Land Statistics Booklet (Namibia Statistics Agency, 2018). In 1902, state land was the largest land class in Namibia at 64%, compared to 30% formally recognised communal land and 6% freehold farmland. A possible explanation for this is that many parcels of land in Namibia were not clearly allocated during the early 20th century and thus fell under government control (Mendelsohn et al., 2002). The percentage of state-owned land continued to increase to 70% by 1911 and later dropped rapidly until 1962-1963, during the initiation of the Odendaal Plan. Since 1964, there has been a slight increase in state land due to the establishment of several national parks and the purchase of freehold farms for resettlement and other purposes (Mendelsohn et al., 2002).

Communal land also decreased from 30% in 1902 to 9% in 1911 and 8 % in 1921. The substantial decline in communal land between 1902 and 1911 was the result of land confiscation during the 1904-1908 war between Germany and the Herero and Nama forces (Mendelsohn et al., 2002). By 1964, communal land expanded steadily from 17% in 1937 to 40% because of the creation of 10 ethnic homelands recommended by the Odendaal Commission but started declining thereafter. Contrastingly, freehold land surpassed communal land to grow to 21% in 1911, as confiscation of land by the 1907 proclamation opened more opportunities for white settler farmers and companies to acquire property (Mendelsohn et al., 2002). The laws enacted in the 1920s by the South African authorities further promoted the growth of white-owned private farmland until around 1955 (47%), followed by a slight decrease from 1964 onwards. The Commission's 1964 report led to numerous freehold farms being purchased by the government and subsequently incorporated into the homelands of Damaraland and Namaland (Mendelsohn et al., 2002). As of 2018, freehold land (43%) still constitutes the largest portion of land in Namibia, followed by communal land (35%) and state land (23%).

Although the extension of white-owned farmland came to a halt in the 1960s, the process of allocating or privately appropriating large, new (private) farms has continued. With the intention of encouraging commercial farming activities in communal areas, the pre-independence administration demarcated and allocated several large farms to individual black farmers during the 1960s, 1970s and 1980s. These original farms were established in the Mangetti Block of Oshikoto (104 farms) and Kavango (44 farms), as well as in the Okamatapati (56 farms) and Rietfontein areas (91 farms) (Mendelsohn, 2006; Ministry of Lands and Resettlement, 2012). More recently, the acquisition of new private farms has rapidly increased, mainly through allocations made by traditional authorities or by claiming land informally. These newly established farms are located in the north-central regions, Kavango and former Hereroland, some of which have been fenced off. Mendelsohn et al. (2002) further noted that many of the farms are used for private ranches and investments, whereas a small proportion is farmed actively and commercially. In addition, the government embarked on the Small-Scale Commercial Farms Development Programme in 2003 (Ministry of Lands and Resettlement, 2012). The first surveyed farms in Caprivi, Kavango and Ohangwena were gazetted in 2007, and Kavango has the majority of these small-scale commercial farms with long-term leasehold agreements (Mendelsohn, 2013; Ministry of Lands and Resettlement, 2012). Apart from small-scale commercial farms on communal land, the Namibian government set up the Green Scheme to encourage the development of irrigation-based agronomic production (Ministry of Lands and

Resettlement, 2015). Currently, seven out of the eleven Green Scheme irrigation farms exist in the Kavango region using the Okavango River. The National Elephant Conservation and Management Plan also suggested that these small-scale commercial farms west of Khaudum and the Green Scheme irrigation farms are more likely to experience increasing human-wildlife conflicts due to the expansion of elephant populations and their distribution (Ministry of Environment, Forestry and Tourism, 2020b).

Besides, multiple studies have investigated the changes in land cover in northern communal areas and found that large tracts of woodland have been cleared for cultivation and settlement, with an increasing trend since past decades. According to Wingate et al. (2016), most deforestations occurred near villages or along rivers and roads, with the Okavango River and western Ohangwena region being the two core areas. Mendelsohn and El Obeid (2003) further reported that the clearing and conversion of woodland to cropland expanded by 3.9% per year between 1943 and 1996 in Kavango. This dramatic increase could relate to the immigration of Angolans both before and during the civil war. Additionally, the construction of the B8 gravel road in 1964 and then the drilling of boreholes nearby has triggered the expansion of settlement and clearing of fields for agriculture along this main road. Another research by Muhoko et al. (2020) observed a similar trend of increasing land clearance in the Kavango East region. While land area covered by forests decreased gradually from 58% in 1990 to 54% in 2016, the cropland had doubled from 3% to 6% by 2016. The study also detected the largest forest conversion within the 2000-2009 period and suggested that a considerable amount of woodland was cleared for commercial farming, such as the Ndonga Linena Green Scheme project (Muhoko et al., 2020). Nevertheless, employment opportunities and the end of the civil war may have slightly slowed down the forest clearance in 2009-2016 period. Owing to the large proportion of natural vegetation clearing, many wildlife species that used to occur along the Okavango River have now disappeared and are mainly concentrated in national parks (Mendelsohn, 2009). With human population growth, the clearing and conversion of woodland persist in the region, which will have further negative implications for wildlife.

5.1.3 Physical barriers – fences and roads

Physical barriers such as fences and roads are growing problems for wildlife and ecosystems. Despite some positive outcomes, fencing can reduce connectivity through landscape fragmentation, restrict dispersal and migration of large terrestrial mammals, prevent access to critical resources and cause injury or death through entanglement or electrocution (Boone &

Hobbs, 2004; Osipova et al., 2018). These effects on large mammals vary depending on the type, maintenance and quality of fences. Furthermore, fencing allow herbivores that reside in protected areas to become overpopulated, resulting in extensive vegetation damage, starvation and increasing incidents of species breaking fences and escaping from the reserves (Boone & Hobbs, 2004; Loarie et al., 2009b; Ministry of Environment, Forestry and Tourism, 2020b).

From the 1920s onwards, the allocation of freehold land to farmers has opened the door for placing fences on commercial farms to demarcate boundaries and control livestock movements, but they have become barriers to wildlife. While attention has focused on commercial farms in the central and south of Namibia, the practice of erecting *illegal* fences has begun in the northern communal areas since the 1970s (Fuller, 2006). The practice expanded rapidly in the 1980s and accelerated thereafter. Massive tracts of land were fenced off by wealthy and politically well-connected individuals, probably due to the lack of clear legislation prior to the Communal Land Reform Act (Fuller, 2006; Mendelsohn et al., 2002; Muduva, 2014). These enclosures further limited free access of other villagers to grazing, water and natural resources, as some of the government boreholes were fenced off (Fuller, 2006; Mendelsohn et al., 2002).

Veterinary cordon fences have also been erected throughout southern Africa to separate large wild mammals and livestock in order to prevent the transmission of infectious diseases, such as Foot-and-Mouth (Naidoo et al., 2022). The intended aim of these vet fences has been achieved, but they have interrupted the migration paths of species and endangered their survival. The Red Line is one of the veterinary cordon fences in Namibia and spans the north-central country parts from the Atlantic Ocean to Botswana. It was constructed in the mid-1960s and had been continually modified — based on the former German Police Zone boundary. This Red Line was not only used to control the spread of (cattle) diseases, but also served as a barrier restricting and containing the mobility of both indigenous peoples and animals from northern Namibia to the central and south sections of the country (Mendelsohn et al., 2002). Between 1965 and 1975, lions had occurred in east-central Namibia but are currently more restricted to protected areas in the north-east (Figure 12a), suggesting the construction of the Red Line may have considerable influence on the lion distribution in north-eastern Namibia. By contrast, the lion range is less affected by the Red Line in the Etosha/Kunene region. This finding is consistent with Stoldt et al. (2020), which have further shown that the Red Line has a significant impact on the ranges of wildebeest and other species along with lions. The Namibia-Botswana border fences along the Khaudum National Park (erected in 1954) as well as along the southern edge of Bwabwata National Park (erected in 1996) are two other veterinary fences that have impaired the movements of elephants to the east and between the Okavango River and the eastern Zambezi region, respectively (Loarie et al., 2009b; Naidoo et al., 2022).

Fencing of national parks and reserves is prevalent in southern Africa. Some parks, such as Etosha National Park in Namibia, have erected electric fences to reduce human-wildlife conflicts, and these fences supposed to have a low permeability for species (Løvschal et al., 2017). However, recent collar data found that elephants have moved in and out of the north-eastern Etosha, as the current condition of the electric perimeter fence is semi-permeable (W. Versfeld, personal communication). The installation and maintenance of electric fences are generally very costly in Africa. Lack of management and continuous upkeep due to insufficient funding can reduce the effectiveness of fencing, leading to a high occurrence of semi-permeable boundaries for large mammalian species (Williams et al., 2021).

In addition to fences, the development and presence of roads pose an imminent threat to the integrity of habitat networks and wildlife through changes in traffic flows (van Strien & Grêt-Regamey, 2016). Paved roads with high speed and high traffic volumes can reduce landscape permeability, impede animal movements, increase population isolation and cause mortality due to collisions (Bennett, 2017). Studies have shown that species with large body size and large home ranges are more likely to suffer the detrimental effects from roads (Gandiwa et al., 2020; Rytwinski & Fahrig, 2012). Railways may also convey similar effects when they run parallel to the existing trunk roads. Besides, road development determines the distribution of human settlements. The construction of new roads can promote the establishment of new settlements and subsequently increase the local population.

Within the study area, the Grootfontein-Rundu trunk road (B8) and Otjiwarongo-Tsumeb-Ondangwa trunk road (B1) can act as movement barriers to large mammal species (P. Beytell, personal communication). Traffic data from 2018 indicated that the B8 trunk road has frequently been used by light and heavy vehicles, with an observed increase in heavy vehicle traffic from 2008 to 2018 (Strauss, 2020). Furthermore, the Namibia Logistics Hub Master Plan (JICA, 2015) demonstrated the existing and future traffic volume on major road sections in 2013 and 2025. As depicted in Table 6, the total daily traffic volumes in the road sections of Grootfontein-Rundu, Otavi-Grootfontein, Otavi-Tsumeb, Otjiwarongo-Otavi and Tsumeb-Ondangwa are expected to increase twofold by 2025.

In the northern communal areas, such as Kavango, people choose to settle along major roads in addition to rivers and dry drainage lines/ omurambas (El Obeid & Mendelsohn, 2001). Many settlements cluster along the Okavango River valley due to the provision of water for animal drinking and crop farming (W. Versfeld, personal communication). Regarding the relationship between roads and settlements, the B8 trunk road provides local people with a well-developed road network and tourism business opportunities (W. Versfeld, personal communication). Future expansions of roads, railways (e.g. Trans-Zambezi Railway Project) and related residential development would further increase the barrier effects on the movements of large, mobile mammal species.

Table 6. Traffic volume on major road sections in 2013 and 2025.

Road sections		**Total traffic volume in 2013 (vehicle/ day)**	**Projected total traffic volume in 2025 (vehicle/ day)**
Grootfontein	Rundu	1,040	2,040
Otavi	Grootfontein	1,190	2,330
Otavi	Tsumeb	3,380	5,750
Otjiwarongo	Otavi	4,570	8,080
Tsumeb	Ondangwa	2,580	4,380

5.1.4 Reduced genetic diversity

Genetic diversity is an important component in supporting the resilience and persistence of populations. Reduced population size and restricted gene flow due to habitat loss and fragmentation can result in decreased genetic diversity and reproductive fitness, lower capacity to adapt to rapidly changing environments and increased risk of local extinction (Bertola et al., 2021; Furlan et al., 2012; Lohay et al., 2020; Schlaepfer et al., 2018; Stevens et al., 2018). In Namibia, there is a rising concern over the long-term viability of the populations of large terrestrial mammals (such as lions and elephants in this study) due to their restricted distributions. They are mostly confined to protected areas, where they can move more freely. Protected areas like national parks not just help provide a refuge for a wide array of different species but also preserve genetic resources for future generations. Yet, existing national parks have become smaller and more isolated, along with increasing vegetation damage, which may not provide sufficient habitats for the species in the long run. For instance, Etosha National Park has shrunk in size for resettlement purposes and has been fenced off, as described in previous chapters. The fencing has disrupted the migration patterns of many animals in Etosha and will increase the isolation of the remaining populations, leading to small population sizes, reduced gene flow and declining genetic diversity (Thouless et al., 2016).

Currently, there is a study on the genetics of lion populations in northern Namibia available, while research on elephants is underway. This recent genetic analysis by Dasch (2021) further provided evidence for the increasing fragmentation of habitats and lion populations in north-central and north-eastern Namibia. The genetic diversity of lion populations was found to be the highest in Zambezi Strip and has decreased with geographical distance from the east (Zambezi Strip) to the west (Skeleton Coast). The study also indicated the infrequent movements of lions between the east and the west by detecting the highest genetic barrier and the lowest genetic admixture between the Zambezi and Etosha National Park based on computational models. In this regard, human-induced habitat loss and fragmentation in north-central and north-eastern Namibia may have contributed to the reductions in gene flow and genetic diversity of lion populations, making the species more vulnerable to environmental disturbances and local extinction.

5.1.5 Climate change

Climate change has significant impacts on species persistence and landscape connectivity. Shifting patterns of rainfall and temperature can influence the abundance and distribution of species and habitat quality, thereby increasing the rates of population declines and extinctions (He et al., 2019; Kapuka & Hlásny, 2021; Tuqa et al., 2014). Climate change can furthermore interact with land use and cover change by amplifying the impact of habitat loss and fragmentation on mammals (Mantyka-Pringle et al., 2015). The loss of connectivity would hinder species movements, along with reducing population size, genetic diversity and adaptive capacity to the changing climate (Ashrafzadeh et al., 2019). Due to their ecology, large mobile terrestrial mammals are more particularly vulnerable to climate change than other species (Hetem et al., 2014). Climate-related extreme events may increase the susceptibility to diseases (e.g. anthrax) in large carnivores and herbivores like lions and elephants (Okello et al., 2016; The Heinz Center, 2012).

According to Namibia's Fourth National Communication Report to the UNFCCC (Ministry of Environment, Forestry and Tourism, 2020a), the average temperature rose at a rate of 0.0123°C annually over the period 1901-2016 and has increased by around 0.2°C every decade. Unlike temperature, it is more difficult to detect rainfall trends in Namibia, and a non-significant precipitation increase of 0.039 mm per year was recorded between 1901 and 2016 (Ministry of Environment, Forestry and Tourism, 2020a). This is because a single rainfall event can contribute to a significant proportion of the annual rainfall in some regions. Climate predictions further indicated that Namibia would become hotter throughout the year, with increased temperatures ranging between 1°C and 3.5°C in summer and 1°C to 4°C in winter in the period 2046-2065 (Ministry of Environment and Tourism, 2011b). In addition, rainfall seasons would be shorter with more intense rainfall, and extreme events such as droughts and floods are likely to become more frequent. A decrease in rainfall of 10-20% by 2045-2065 over the catchments of Zambezi, Kavango, Cuvelai and Kunene Rivers is expected to reduce the runoff and drainage in these shared river systems by +/- 25% (Ministry of Environment and Tourism, 2011b). Moreover, Shrader et al. (2010) studied the impact of reduced rainfall on elephant survivals and estimated that elephants living in enclosed reserves such as Etosha National Park may be the first populations to be effected by climate change, especially the juveniles. Nevertheless, the importance of Etosha as a drought refuge for elephants from further west will continue to increase with climate change (Ministry of Environment, Forestry and Tourism, 2020b).

5.2 Case studies of the influence of land use patterns on species movements

The Khaudum National Park and adjacent areas in north-eastern Namibia are mostly unfenced (except the Namibia-Botswana border) and rich in wildlife habitats with essential migration routes; however, they have different land use patterns and management practices. Many Kavango people (e.g. Gciriku and Shambyu tribes) are the residents of the farming areas west of Khaudum towards the Mangetti area, while San people/bushmen live south of it in the Nyae Nyae Conservancy. The variety of land uses can pose a significant challenge to large mammals' mobility and population viability if adjacent areas often have conflicting and incompatible uses.

5.2.1 Mangetti and west of Khaudum National Park

The vast area west of Khaudum National Park (along the omurambas) has been considered a critical wet season range for many large mammal species (Jones et al., 2009; Ministry of Environment and Tourism, 2013). Some elephant and wild dog populations from Khaudum tend to move westwards into the Kavango West region towards the Mangetti National Park (Ministry of Lands and Resettlement, 2015). However, the development of small-scale commercial farms (mainly for livestock herding and crop cultivation) along the western boundary has severely impeded free wildlife movements and increased human-wildlife conflicts due to fencing and the strong attraction of domestic stock and water points for predators and elephants (Ministry of Environment and Tourism, 2013) (Figure 17). The removal of wet season dispersal areas may further reduce the numbers of some species and the Park's ecological viability, thus requiring more intensive management in and around the Khaudum National Park (Jones et al., 2009). According to the Rapid Survey of Farms (Mendelsohn, 2013), about 622 small scale commercial farms have been allocated by traditional authorities, covering approximately 45% of communal land in the Kavango region. Of these 622 farms, 470 farms are within designated agricultural areas, while 152 farms fall outside the zones. 421 farms also have leaseholds varying in duration between 25 and 99 years. In addition, based on the available information on perimeter fencing, 140 of the 481 farms are fully fenced (29%), and 8 are partially fenced (2%). The survey further noted that most farm owners live in Rundu or elsewhere in the country, and very few people with a population of 1,786 indeed live on the farms.

The Greater Mangetti Complex is regarded as another high conflict zone, although it is home to a small herd of elephants and other species like wild dogs. The complex comprises two main areas: the Mangetti National Park and the Kavango Cattle Ranch, owned and managed by the Namibia Development Corporation (NDC) (Figure 17). The Kavango Cattle Ranch, consisting of 45 farms, was initially started in 1973 (Ministry of Environment, Forestry and Tourism, 2020b; Ministry of Lands and Resettlement, 2012). About 16 farms in the Mangetti West (Oshikoto region) were developed at a later stage. Several of the farms that were part of the Ranch have also been reallocated to the Namibia Defence Force and war veterans or used for other purposes such as resettlement and veterinary quarantine (Ministry of Lands and Resettlement, 2012).

In the Mangetti Complex, elephant movements are mainly within the KCR due to the relatively abundant water sources in the forms of troughs and dams (albeit pumped for cattle) (Ministry of Environment, Forestry and Tourism, 2020b). However, conflicts have occurred between elephants and villagers, particularly on the KCR and southern commercial farmland, when water is limited and difficult for elephants to access (Ministry of Environment, Forestry and Tourism, 2020b). Elephants can cause substantial damage to water installations, fences and occasionally crops, resulting in costly repairs and production losses (Ministry of Environment, Forestry and Tourism, 2020b; Naankuse, 2018). Therefore, many residents of the Mangetti

Complex have negative attitudes toward elephants. As agricultural land expands and the number of elephants inhabiting or entering the KCR increases, human-elephant conflicts are more likely to escalate. Large carnivores may face similar conflict challenges as elephants due to their predation on cattle.

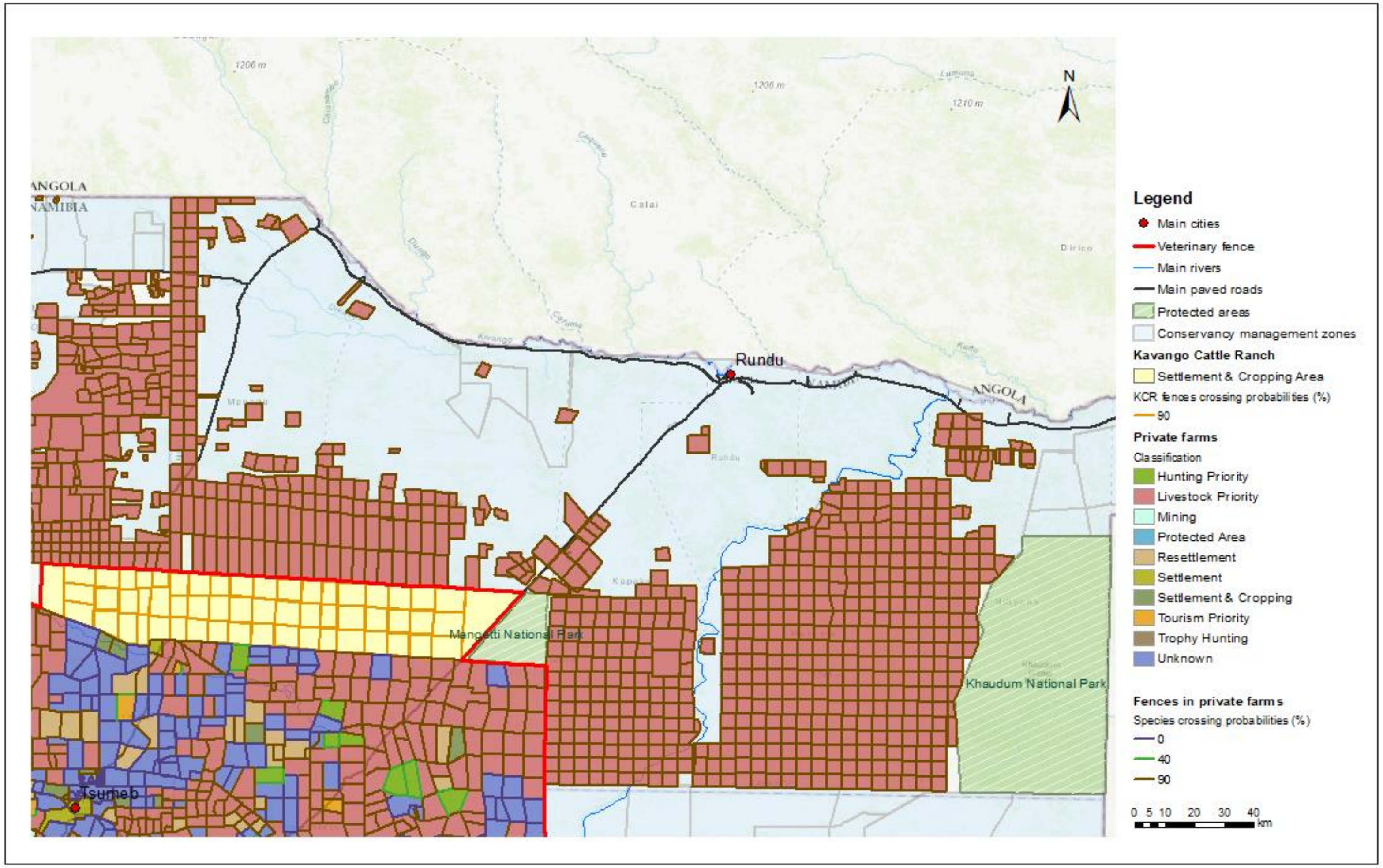


Figure 17. Map showing the area status of the Great Mangetti Complex and west of Khaudum National Park.

5.2.2 Khaudum National Park and Nyae Nyae Conservancy

The situation south of Khaudum National Park is different from the western side. The Park is bordered to the south by the Nyae Nyae Conservancy, a large communal area in which local residents (Ju/'hoansi) are entitled to use wildlife and develop tourism on a sustainable basis (Figure 18). Many large mammals can move freely between Khaudum and Nyae Nyae, and even to the N≠a Jaqna Conservancy without any fencing barriers (Ministry of Environment and Tourism, 2013). In addition, both Khaudum and Nyae Nyae support healthy wildlife populations and form part of the KAZA, allowing species to move across a large landscape between Namibia, northern Botswana and southern Angola. Yet, conflicts between Ju/'hoansi people and wildlife over water access and livestock predation have emerged and been widely reported since the 1980s (Hays & Hitchcock, 2020; Weaver & Skyer, 2005). Matson (2006) further noted that the number of conflicts, particularly with elephants, increased steadily from 2000 to 2003 and started declining in 2004. With improved management and assistance, human-wildlife conflicts (e.g. elephants and lions) in Nyae Nyae have been significantly reduced, making the conservancy one of the most successful CBNRM models (Hays & Hitchcock, 2020; NACSO, 2012).

The Nyae Nyae Conservancy was first gazetted as a communal conservancy in 1998, providing conservancy members with additional rights to utilise and manage forest products and grazing resources. Furthermore, the conservancy is based on a mixed economy system and retains the traditional Ju/'hoansi culture or land management strategy (Hays & Hitchcock, 2020; NACSO, 2012). The Ju/'hoansi have lived in harmony with nature for thousands of years and relied on low-impact hunting and gathering lifestyle; thus, conserving wildlife and plant resources for their own use and tourism is the conservancy's primary objective (Hays & Hitchcock, 2020; Matson, 2006; Weaver & Skyer, 2005). In this regard, Nyae Nyae has been divided into various land-use zones, including exclusive wildlife zones for wildlife utilisation, tourism and (trophy) hunting, and settlement, cropping and community forest zones (NACSO, 2012).

According to Matson (2006), most of the previous human-elephant conflicts in Nyae Nyae took the form of damage to water installations, while other forms included damage to fences, crop-raiding and direct attacks on humans. One of the reasons is that the creation of artificial water points has increased the number of resident elephants in Nyae Nyae, resulting in more competition between people and elephants over scarce water sources (Martin, 2005; NACSO, 2012). The increased livestock activities have also contributed to an increase in predator problems. Nonetheless, the conservancy has been actively mitigating human-wildlife conflicts with support from the Ministry of Environment, Forestry and Tourism (MEFT), the Nyae Nyae Development Foundation and other NGOs. For instance, the conservancy has constructed elephant proof walls around water infrastructure in certain villages, which has substantially reduced conflicts between humans and elephants (Matson, 2006; NACSO, 2012). With mitigation measures such as herding livestock and keeping them in closed enclosures at night, incidents of conflicts with predators (e.g. lions) have also significantly decreased (NACSO, 2012). Importantly, people have a high tolerance for lions and elephants because of their ecological importance and economic value through tourism (NACSO, 2012). In addition to human-wildlife conflicts, community rangers actively monitor the natural resources within the conservancy by conducting patrols and recording data such as game sightings, poaching incidents and game utilisation (NACSO, 2012). Hunting is further managed according to quotas set by the MEFT, mainly based on game counts. Moreover, game reintroductions have taken place in the conservancy to facilitate recoveries of wildlife populations and increase the area value for tourism and trophy hunting (Funston et al., 2017; NACSO, 2012). With the absence of barriers and effective management, the Khaudum/Nyae Nyae system has the greatest potential to recover lion populations in the north-east of Namibia (Funston et al., 2017).

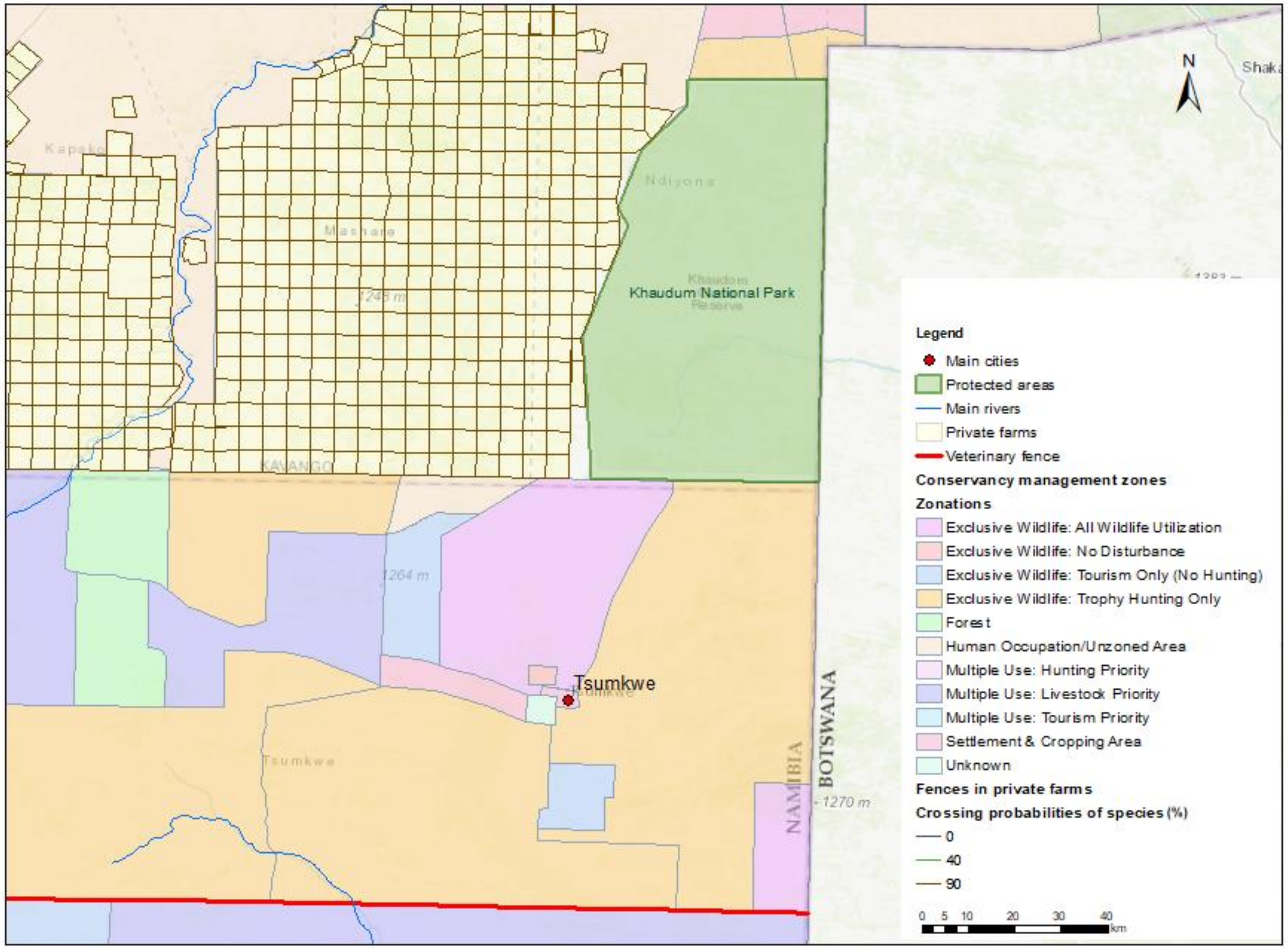


Figure 18. Map showing the area status of the Khaudum National Park and Nyae Nyae Conservancy.

5.3 Model validation

The habitat suitability and connectivity models for lions and elephants developed in this study were based on literature findings, combined with expert knowledge. Validation of the model outputs is therefore essential to ensure their accuracy. Kirchner (2020) also highlighted the use of movement data for model validation, which can highly reduce the uncertainty of a model. In this regard, habitat suitability maps and least-cost corridors for the focal species were validated by expert opinions and using the species' home ranges and core ranges provided by the Ongava Reserve Centre and the Ministry of Environment, Forestry and Tourism. The boundaries of these home ranges and core ranges were computed using kernel density estimation from sample GPS telemetry point locations. Generally, the 95% contour (isopleth) is defined as the entire home range for an individual, while the 50% contour is considered the core area of the home range where the animal spends 50% of its time. Due to limited GPS telemetry data for the species, model validation was focused on the Khaudum and Nyae Nyae area.

5.3.1 Validation of the habitat suitability surface for lions

The habitat suitability surface for lions was verified by comparison with the core ranges determined from the ten lion GPS collars in Khaudum/ Nyae Nyae. Figure 19 shows that the core ranges of all ten lions are mainly concentrated around waterholes and omurambas in the Khaudum National Park and the northern Nyae Nyae Conservancy. Each lion also has a core range that overlaps with at least one core range from another lion. This supports the prediction of the lion suitability model that the areas around the waterholes and omurambas are the most favourable and highly suitable habitat for lions. Although there are no available GPS data for the other parts of the study area, it is assumed that waterholes inside protected areas (e.g. Etosha and Mangetti National Parks) and rivers, including omurambas, are suitable habitats for lions based on their observed space use pattern in the north-east (Figure 13).

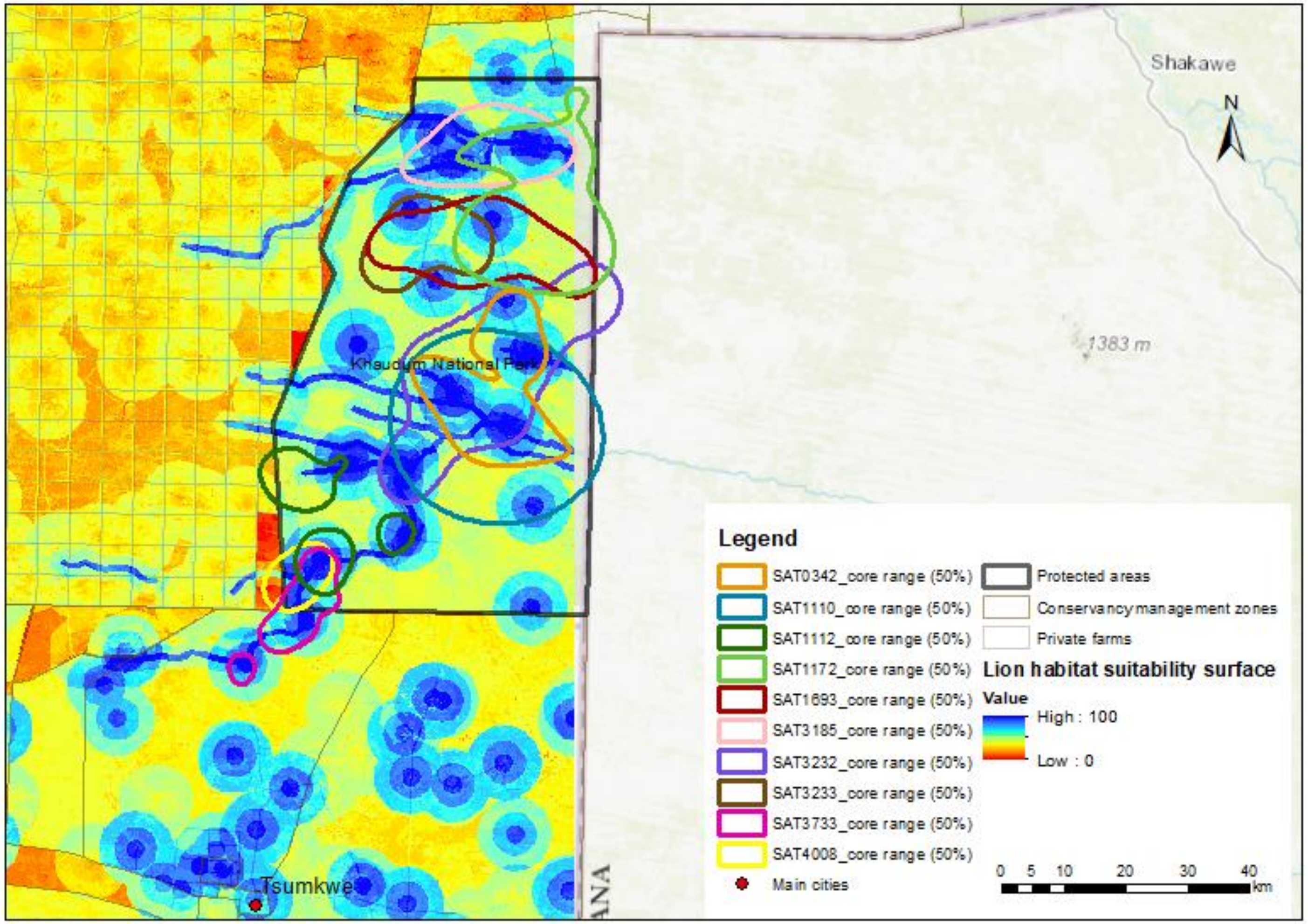


Figure 19. Map showing the comparison of the lion habitat suitability surface and core ranges determined from the lion telemetry data in Khaudum/ Nyae Nyae.

5.3.2 Validation of the habitat patches and corridors for lions

The home range dataset derived from telemetry data of ten collared lions in Khaudum/Nyae Nyae was used to validate the habitat patches and corridors for lions (from the 16-core habitat trial). Areas of home range overlap indicate high habitat quality in the area. As illustrated in Figure 20, the home ranges of lions highly overlap in the south-western (habitat patch 1) and north-western (habitat patch 7) parts of Khaudum National Park. The home range of each lion within this area contains one or both of the two habitat patches. Furthermore, one lion has a home range that includes a third habitat patch (habitat patch 10) on the commercial farms west of Khaudum. Hence, the overlapping of lion habitat patches and home ranges reflects the high reliability of the habitat suitability model and core habitat analysis in this study. By linking the habitat patches 1, 7 and 10, a potential least resistant corridor could be formed between the Khaudum National Park and the northern part of the Nyae Nyae Conservancy. As the core habitats were detected based on the highest average habitat suitability values, the remaining habitat patches (Figure 14 lower left), mainly around waterholes and rivers, could still be suitable for lions even without the validation of lion movement data. With reference to Shortridge (1934), lion footprints were constantly observed along the river bed of the Omatako (Chapter 4.1). As a result, habitat patches 5, 6, 9 and 11 could be connected as a pathway and reused by lions. This Omatako pathway could connect to the previously described corridor between Khaudum and Nyae Nyae. Besides, lion movements have been observed at the Okakarara area where they were thought to have come from Botswana (P. Beytell, personal communication). Historical information also recorded the migration of lions from the west of Waterberg in the Otjiwarongo area to the east (Magistral Papers, 1925/26). Thus, the linkages of habitat patches 6, 9, 12, 14 and 16 could possibly be used by lions. Even though the connectivity model identified a potential route between Etosha to Waterberg via habitat patches 3, 6, 9 and 15, the likelihood that lions use this path is low due to the large number of commercial farms within the area.

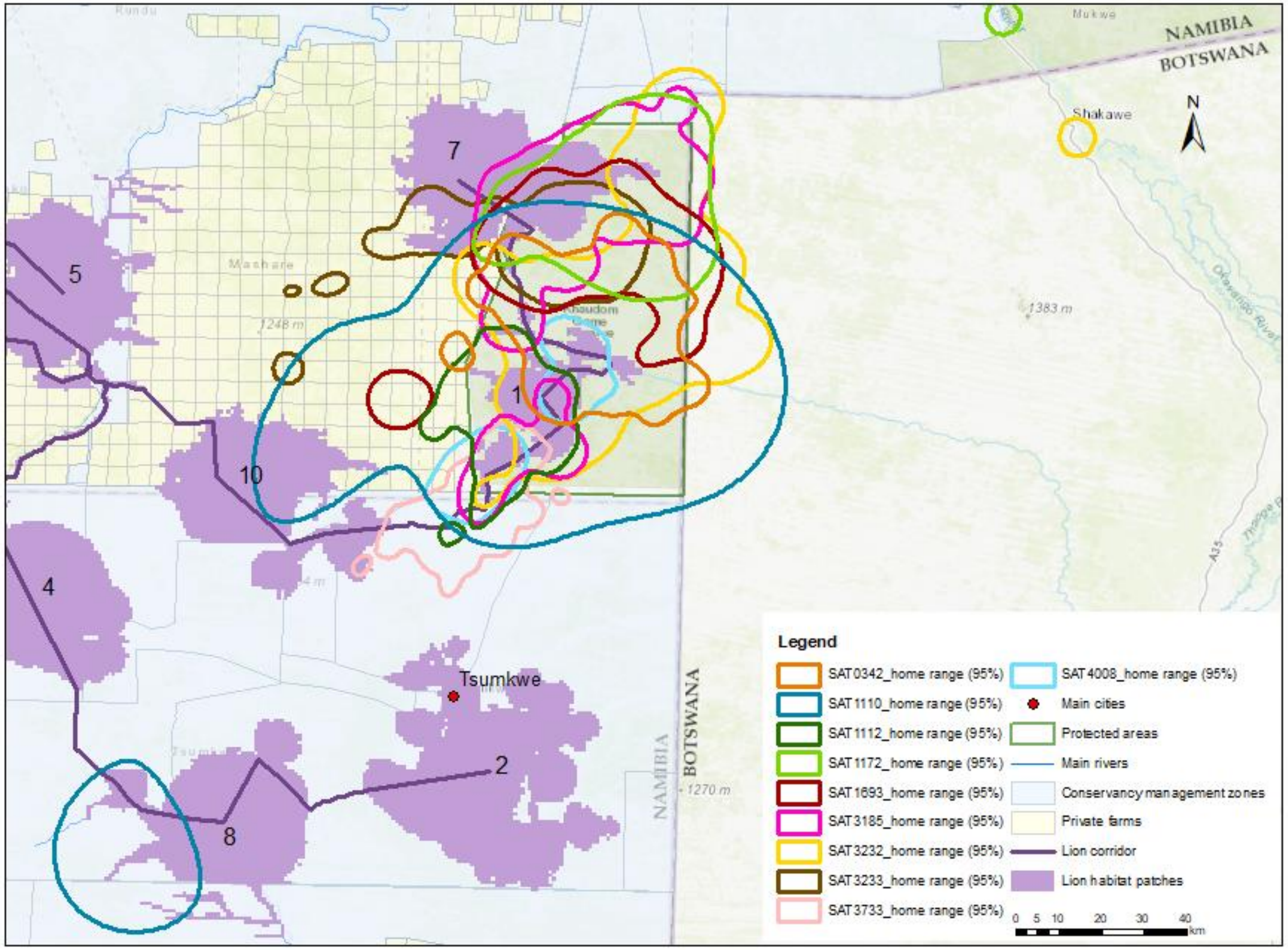


Figure 20. Map showing the comparison of the predicted lion habitat patches and corridors and home ranges determined from the lion telemetry data in Khaudum/ Nyae Nyae.

5.3.3 Validation of the habitat suitability surface for elephants

The elephant habitat suitability surface was validated by the core ranges derived from the eight elephant GPS collars in Khaudum/ Nyae Nyae. Figure 21 shows that much of the elephant core ranges lie within the areas predicted as the most suitable habitats from the elephant habitat suitability model. These core ranges are around and even across waterholes in the Khaudum National Park and the Nyae Nyae Conservancy. Some also contain the omurambas. In addition, there are three sets of overlapping core ranges in Khaudum, one in the north and the other two in the central and south-western parts of Khaudum. One elephant core range further extends into the adjacent commercial farmland from the south-west of Khaudum, even though this farming area was classified as a marginally suitable habitat for elephants in the model. With reference to the observed elephant spatial use patterns in the north-east, it is also assumed that elephants most likely occupy the areas near water sources in the rest of the study area (Figure 15). Moreover, the elephant habitat suitability model predicted lower habitat suitability in the Khaudum area than the lion model. A possible reason for this is that the two models have different parameter weightings and further adjustments are necessary.

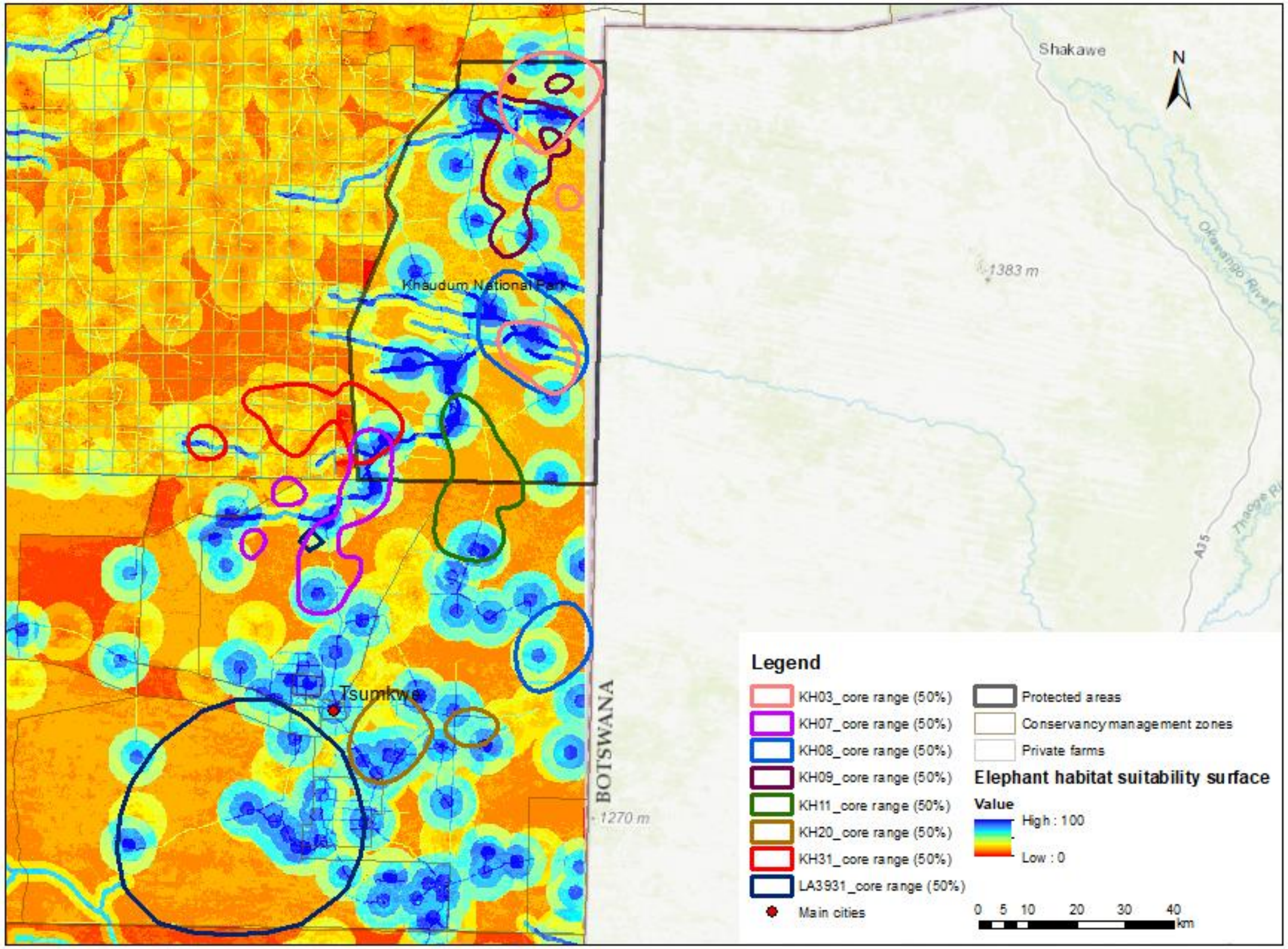


Figure 21. Map showing the comparison of the elephant habitat suitability surface and core ranges determined from the elephant telemetry data in Khaudum/ Nyae Nyae.

5.3.4 Validation of the habitat patches and corridors for elephants

Elephant habitat patches and corridors (from the 16-core habitat trial) were compared with the home ranges of eight collared elephants in Khaudum/ Nyae Nyae. Figure 22 shows a high degree of home range overlap in Khaudum National Park, particularly in the south-western corner (habitat patch 1), and the Nyae Nyae Conservancy (habitat patches 2 and 15). The habitat patch numbered 1 is covered by the home ranges of all eight elephants. Some home ranges contain more than one habitat patch. Further, three home ranges in the south-west of Khaudum extend their coverage to the commercial farms. In addition, one elephant has an extensive home range covering the habitat patches in the south-west of Khaudum, Nyae Nyae and part of the habitat patch in the N≠a Jaqna Conservancy (habitat patch 4). Overall, the overlapping areas of elephant home ranges and habitat patches in Figure 22 fall within the areas classified as suitable habitats, indicating that the elephant habitat suitability and connectivity models used in this study are plausible.

The ideal location for habitat patch 16 would be within the Khaudum National Park. However, according to the model computation, this habitat patch is slightly shifted towards the commercial farming area. This might be partly due to the influence of the dry drainage lines (omurambas) stretching from Khaudum to the commercial farms, which are considered suitable habitats in the elephant suitability model (Figure 21). There have been observed elephant movements between Khaudum and the neighbouring commercial farms (P. Beytell, personal communication). The area is also a former frequently used wet dispersal area by elephants and other mammals (Chapter 5.2.1). Habitat patches 1, 2, 15 and 16 could therefore be connected to form a least-cost corridor to facilitate the movement of elephants from the north-western part of Khaudum to the Nyae Nyae Conservancy. This potential corridor could be further extended to the N≠a Jaqna Conservancy through connecting habitat patch numbered 4.

From the observed elephant space use pattern in the north-east, it can be concluded that the habitat patches elsewhere within the study area are suitable for elephants (Figure 16 lower left). The ephemeral Omatako River has been considered a significant pathway for elephants and other species like wild dogs apart from lions (Chapter 3.4.2). Shortridge (1934) reported that a number of elephants trekked over and wandered the Omatako River in the 1925-1935 period. At present, elephants have still been seen attempting to walk down the Omatako River toward the direction of Waterberg, even with human occupation along the river (P. Beytell, personal communication). Thus, connecting habitat patches 4, 5, 6 and 7 could potentially restore this historically important pathway. Besides, the linkages of habitat patches from south of Waterberg National Park up to the Eiseb River (via habitat patches 5, 9, 10, 12 and 13) might possibly be used by elephants, as sporadic elephant movements have been recorded at the Okakarara and Waterberg area (Ministry of Environment, Forestry and Tourism, 2020b). Another important elephant area is the Mangetti Complex (mainly the KCR), where it hosts a herd of resident elephants. Based on the movement data illustrated in the National Elephant Conservation and Management Plan, the resident elephants have spent most of their time on the Ranch over a year because of many boreholes and water points (Ministry of Environment, Forestry and Tourism, 2020b) (Chapter 5.2.1). This could verify the three habitat patches in KCR (habitat patches 8, 11 and 14) detected from the elephant connectivity model. Moreover, the Mangetti Complex and Etosha National Park could be connected by the habitat patch numbered 3. This potential linkage also matches the historical movement corridor between the north-east Etosha and Mangetti area (via the Omuramba Ovambo), as mentioned in the National Elephant Conservation and Management Plan (Ministry of Environment, Forestry and Tourism, 2020b). In contrast to the 10-and 16- core habitat trials, the trial with 5 core habitats (Figure 16 upper left) detected an alternative linkage to Etosha via the habitat patch in Waterberg area, and it is very unlikely to be used by elephants.

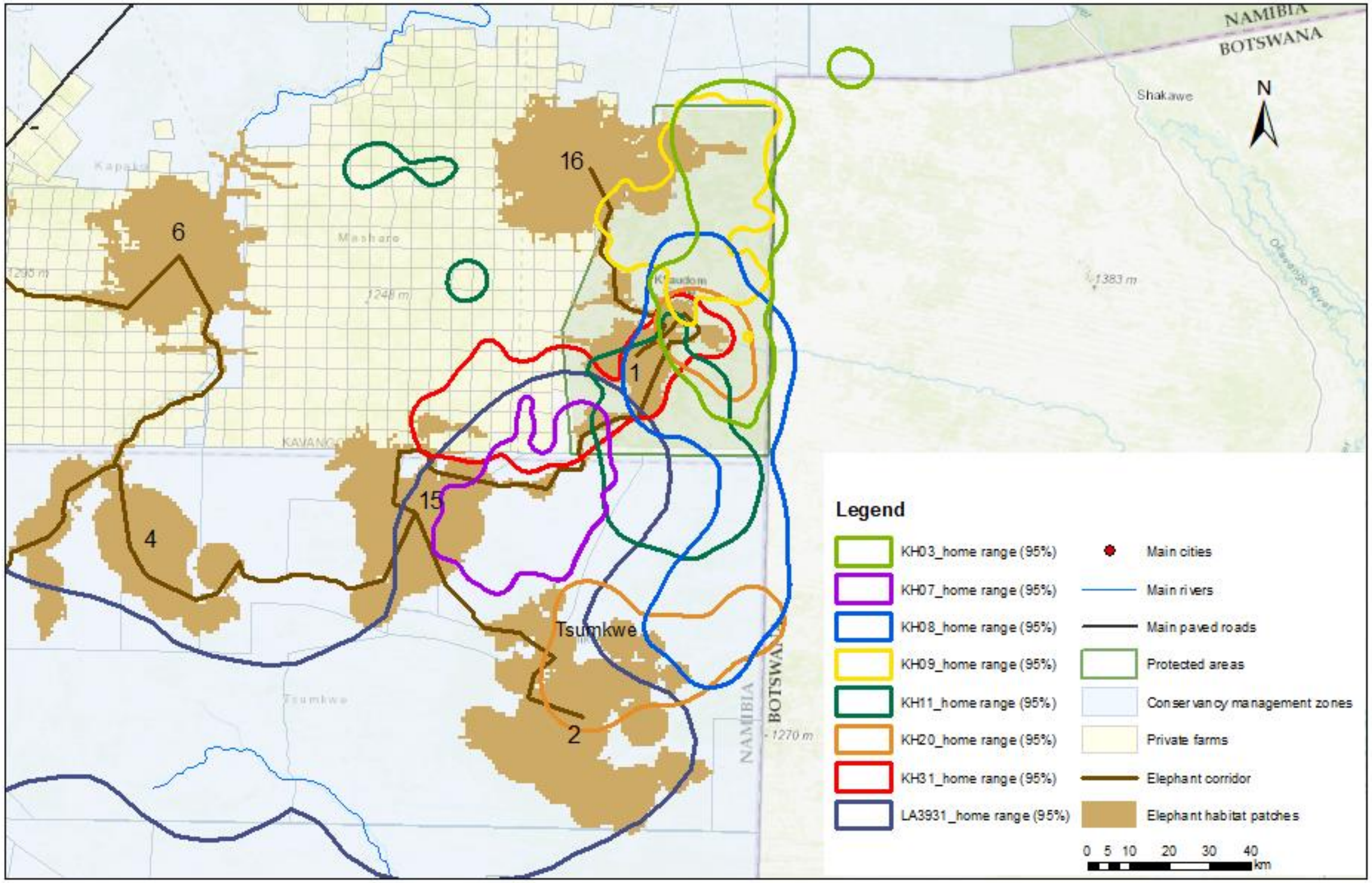


Figure 22. Map showing the comparison of the predicted elephant habitat patches and corridors and home ranges determined from the elephant telemetry data in Khaudum/ Nyae Nyae.

5.4 Considerations for wildlife corridor design and implementation

Wildlife corridors are an important conservation practice that can improve spatial connectivity, facilitate individual movement and increase genetic exchange among populations in fragmented landscapes. Currently, resistance-based connectivity models are the most widely used approach for corridor identification (Osipova et al., 2019; Wade et al., 2015). However, the methods developed for estimating resistance and modelling connectivity are varied, and there is no standardised framework for the appropriate choice of the model parameters and analytical techniques (Lalechère & Bergès, 2021). This may further increase the uncertainties of the model outputs. Several studies have also shown that many of the proposed connectivity models did not undergo a formal validation procedure (Lalechère & Bergès, 2021; LaPoint et al., 2013; Sawyer et al., 2011; Wade et al., 2015). Hence, there is a strong need for empirical validation of connectivity predictions (e.g. with movement data) to prevent misidentification of corridors and misallocation of scarce conservation resources (Lalechère & Bergès, 2021; Naidoo et al., 2018; Osipova et al., 2019).

While empirical-based habitat suitability models are considered more reliable for designing connectivity linkages, expert-based models can be a cost-effective option and perform relatively well when empirical data are sparse and spatially restricted for many species (Beier et al., 2007; Poor et al., 2012; Sawyer et al., 2011). The combination of expert-literature-based habitat suitability model and least-cost path analysis can provide a strong tool for assessing high-quality habitats and identifying potential corridors at larger landscape scales, as used for lions and elephants in this study. A key component of constructing a habitat suitability model is the selection of habitat variables for focal species. Beier et al. (2007) pointed out that many models rely only on relevant habitat factors for species that are available in the form of GIS data. Consequently, insufficient species-specific spatial data with the low accuracy of available land cover data can reduce the success rates of habitat suitability modelling (Beier et al., 2007). To improve the quality of input habitat factors, a clear understanding of species distribution and ecology is essential (LaRue & Nielsen, 2008; Ntukey et al., 2022). The best resources for obtaining this information are wildlife experts and published species-specific literature (Beier et al., 2007; Clevenger et al., 2002; Ntukey et al., 2022). Another point of consideration in the habitat suitability analysis is the weighting of different habitat factors, which is also viewed as the weakest part of the suitability model due to the lack of underlying theory and hard data (Beier et al., 2007). A few studies have suggested to increase the accuracy of the variable ranking by reviewing literature and consulting with experts knowledgeable of the focal species (Beier et al., 2007; Kirchner, 2020; LaRue & Nielsen, 2008; Stevenson-Holt et al., 2014). Nevertheless, the model can still be subject to uncertainties and errors when translating species-specific literature information into numeric values.

For corridor delineation, the least-cost path analysis is one of the simplest techniques based on resistance surface derived from the habitat suitability model. It can also analyse large spatial scales and directly compute the least resistant corridors with the ArcGIS Spatial Analyst toolbox (Esri, 2019). However, this approach assumes that animals have perfect knowledge of the entire landscape and select the routes with the minimal travel cost (Wade et al., 2015). Besides, the least-cost connectivity model does not identify barriers or other risks that could impede movement in the corridor (Krause & Gogol-Prokurat, 2014). In some cases, the least-cost path may still be very costly or even unsuitable for wildlife movement. Given the myriad sources of uncertainties and errors in the modelling process, from habitat suitability to least-cost connectivity analyses, validations of habitat suitability surfaces and least-cost corridor maps should be performed by comparing them with GPS telemetry data to improve model accuracy. Apart from GPS telemetry data, genetic distance data can be used to validate the resistance surface as well as the potential linkages predicted by connectivity models (Lalechère & Bergès, 2021; Wade et al., 2015). Additionally, numerous studies have recommended performing uncertainty or sensitivity analyses to better account for errors and variability when conducting least-cost connectivity assessments (Beier et al., 2008; Sawyer et al., 2011; Stevenson-Holt et al., 2014; Wade et al., 2015). Beier et al. (2008) further advocated the use of uncertainty analysis in linkage design, which could guide conservation decisions by illustrating the effects of model uncertainty to stakeholders and managers.

Moreover, the least-cost path generated with the ArcGIS Spatial Analyst toolbox (Esri, 2019) is a single cell width linear feature, which is unlikely to represent the actual path taken by animals (Kirchner, 2020; Riggio & Caro, 2017; Wade et al., 2015). Hence, Kirchner (2020) proposed an additional use of the Linkage Mapper toolbox (McRae & Kavanagh, 2011) for corridor modelling. The corridor output with the Linkage Mapper can be more realistic as the least-cost corridors are illustrated as the gradient of suitability rather than a line feature. The tool can also identify potential pathways between all core habitat patches, giving a more complete picture.

5.5 Conservation management recommendations

This study provides a preliminary overview of potential corridors for lions and elephants in north-central and north-eastern Namibia, which could reconnect the three wildlife important areas, namely Etosha, Mangetti and Khaudum National Parks (Chapter 4.3 and Chapter 4.5). Some of the corridor segments also include historical migration paths used by the species, for instance, the Omatako River for both species and the Etosha-Mangetti route for elephants. However, the implementation of the proposed corridors would be challenging due to heavy human influence around the linkages, such as expanding settlements and agricultural farms, placement of fences, major road barriers and other urban development. Ryan and Hartter (2012) also highlighted the need to consider land use history and local livelihoods for the success of corridor establishment in areas of high human population density.

There are some alternative strategies possible to recover large mammal movements and maintain the viability of their populations in the study area. Firstly, with reference to the success story of wildlife conservation in Nyae Nyae, promoting the development of wildlife- and tourism-based land uses in communal conservancies with constant monitoring could increase mammals' space use and minimise human-wildlife conflicts (Chapter 5.2.2). It could bring additional economic benefits to local communities by generating substantial revenues and employment opportunities. This approach has been suggested in the Human-Lion Conflict Management Plan and the National Elephant Conservation and Management Plan as part of an effective and appropriate land use planning strategy (Ministry of Environment, Forestry and Tourism, 2020b; Ministry of Environment and Tourism, 2017). As wildlife populations on freehold land continue to increase, the promotion of wildlife and related tourism activities may need to be extended to commercial farms in order to improve human-wildlife coexistence and tolerance. Although it would be much more complicated to convince private farms to switch from livestock farming to wildlife uses, there is still a potential for the transition with clear guidance and adequate incentives and resources.

The removal of fences, such as veterinary fences and boundary fences, could be another movement recovery strategy for large mammals. There are also some successful examples of removing boundary fences in the southern African region, such as the fences between Kruger National Park in South Africa and its neighbouring private game reserves (Ministry of Environment and Tourism, 2010). In addition, fence removal combined with the creation of new artificial water points could increase the range of elephant movements and reduce fence damage by elephants (Kapuka & Hlásny, 2021; Shrader et al., 2010). Nevertheless, this approach has been a controversial topic for wildlife conservation in Namibia and remains difficult to implement. If fencing is unavoidable, careful planning for fences, including the materials and location, would be necessary to reduce negative effects on species (O'Neill et al., 2022).

In recent decades, a variety of innovative fences, such as chilli and beehive fences, have been developed to reduce conflicts between humans and wildlife, particularly with elephants. These fences have been used in various African and Asian countries and have been proven effective in preventing elephants from entering farms and crop-raiding when appropriately applied (Branco et al., 2020; Chang'a et al., 2016). They are also relatively simple and cheap compared to electric fences and could be considered for application in north-central and north-eastern Namibia. Chilli fences are constructed with sisal strings and flags soaked in motor oil mixed with ground chilli and work as olfactory deterrents (Kiffner et al., 2021). In contrast, beehive fences are composed of interlinked live beehives and use bee sounds and stings to deter elephants (Kiffner et al., 2021). Beehive fencing could further benefit local farmers by providing pollination services and valuable bee products such as honey and wax (Branco et al., 2020). Another novel fencing system is real-time virtual fencing or geo-fencing, which uses GPS positioning and wireless mobile network to monitor and control the movements and locations of animals within an area. This approach has been incorporated into the management of large mammalian populations that come into conflict with or are disturbed by human activities, such as African elephants in Kenya and South Africa (Jachowski et al., 2014). It has also been used to alert humans to the presence of susceptible species, as in the case of lions in northern Botswana (Wall et al., 2014; Weise et al., 2019). In north-west Namibia, early warning systems have effectively practised on the desert lions (Desert Lion Conservation Trust, 2022). Despite high installation costs and limited effectiveness testing, the potential for geo-fencing could be the alleviation of human-wildlife conflict focusing on individual problem animals, fewer physical maintenance, along with the creation of job opportunities (Jachowski et al., 2014). Lion lights, an invention from Kenya, have been successfully applied in the north-west of Namibia and could be considered a potential approach for mitigating conflicts with lions and other predators on the north-eastern side (Lesilau et al., 2018; Namibian Lion Trust, 2019).

To enhance tolerance and peaceful coexistence with large mammals, it is of great importance to acquire an understanding of their vital needs and how to live with the species. For example, elephants are highly water-dependent, and conflicts with humans are centered around the damage to water facilities in the semi-arid Namibia. This has further led to the establishment of Elephant Human Relations Aid (EHRA), a Namibian NGO that aims at protecting elephants through monitoring and providing practical conflict solutions. EHRA has built stone walls around water points on farms and within communities and created additional elephant water drinking dams in the north-west of Namibia (EHRA, 2022). The organisation has also initiated an education programme, the PEACE Project, to teach people of all ages the essential facts about elephants (lifestyle and behaviour) and provide safety guidelines for elephant encounters. Through these educational workshops, people might possibly reduce their fears and change their attitudes toward elephants (EHRA, 2022). As the study area contains important habitats for elephants and is also at high risk of conflicts, there is a huge potential for the expansion of EHRA's water point conservation initiative and the PEACE education programme into the north-eastern part of the country with further cooperation and financial support.

Lastly, translocations would play a role in conserving large mammals in the north-eastern part of Namibia, especially in the case of lions, where populations remain low in numbers and have lower genetic diversity than the western ones (Dasch, 2021). This technique could generally bolster species population viability, restore locally extinct species and repair ecosystem integrity (Goldenberg et al., 2019). According to the Status Report Lions of the Kavango and Zambezi Regions (Funston et al., 2017), 11 lions were reintroduced into the southern Khaudum from Ongava in 2015; it could be possible to further recover lion populations in Khaudum/ Nyae Nyae area with this approach. To improve the effectiveness of translocation efforts, it is essential to incorporate the genetic background of populations and disease screening in translocation planning and consider the ecological, behavioural and socio-economic aspects of these interventions (Bertola et al., 2021; Dubach et al., 2013). Dubach et al. (2013) and Dasch (2021) also recommended utilising the populations that are genetically and behaviourally similar for future translocations.

5.6 Further research recommendations

As part of the master's thesis, potential corridors for lions and elephants were successfully identified but only on a year-round basis due to data limitations. The corridors were also partially validated, and thus further corridor analyses are necessary to confirm these preliminary results. It is recommended to develop separate seasonal habitat suitability and connectivity models for each focal species and use the additional Linkage Mapper tool for least-cost corridor detection. In addition, future studies should be conducted on the genetics of Namibian elephants to support the management of elephant populations in the north-central and north-eastern Namibia. Moreover, the success of translating the above-described potential alternative conservation strategies into actions would require further research, planning and cross-sectoral collaboration, including government, environmental agencies, NGOs, private sector and local communities, and even international cooperation.

6. References

Abade, L., Macdonald, D. W., & Dickman, A. J. (2014). Using Landscape and Bioclimatic Features to Predict the Distribution of Lions, Leopards and Spotted Hyaenas in Tanzania's Ruaha Landscape. *PLOS ONE*, *9*(5), e96261. https://doi.org/10.1371/journal.pone.0096261

Adams, T. S. F., Chase, M. J., Rogers, T. L., & Leggett, K. E. A. (2017). Taking the elephant out of the room and into the corridor: can urban corridors work? *Oryx*, *51*(2), 347-353. https://doi.org/10.1017/S0030605315001246

Ament, R., Callahan, R., McClure, M., Reuling, M., & Tabor, G. (2014). *Wildlife Connectivity: Fundamentals for conservation action*. Center for Large Landscape Conservation: Bozeman, Montana.

Ashrafzadeh, M. R., Naghipour, A. A., Haidarian, M., Kusza, S., & Pilliod, D. S. (2019). Effects of climate change on habitat and connectivity for populations of a vulnerable, endemic salamander in Iran. *Global Ecology and Conservation*, *19*, e00637. https://doi.org/https://doi.org/10.1016/j.gecco.2019.e00637

Baisero, D., Visconti, P., Pacifici, M., Cimatti, M., & Rondinini, C. (2020). Projected Global Loss of Mammal Habitat Due to Land-Use and Climate Change. *One Earth*, *2*(6), 578-585. https://doi.org/10.1016/j.oneear.2020.05.015

Barnard, P., Brown, C. J., Jarvis, A. M., Robertson, A., & Rooyen, L. V. (1998). Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. *Biodiversity & Conservation*, *7*(4), 531-547. https://doi.org/10.1023/A:1008831829574

Bauer, H., Packer, C., Funston, P. F., Henschel, P., & Nowell, K. (2016). *Panthera leo. The IUCN Red List of Threatened Species 2016: e.T15951A115130419*. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en

Beier, P., Majka, D., & Jenness, J. (2007). Conceptual steps for designing wildlife corridors. *CorridorDesign, Arizona, USA.*

Beier, P., Majka, D. R., & Spencer, W. D. (2008). Forks in the Road: Choices in Procedures for Designing Wildland Linkages. *Conservation Biology*, *22*(4), 836-851. https://doi.org/https://doi.org/10.1111/j.1523-1739.2008.00942.x

Bennett, V. J. (2017). Effects of Road Density and Pattern on the Conservation of Species and Biodiversity. *Current Landscape Ecology Reports*, *2*(1), 1-11. https://doi.org/10.1007/s40823-017-0020-6

Berry, H. H. (1982). The wildebeest problem in the Etosha National Park: a synthesis. *Madoqua*, *13*(2), 151-157. https://journals.co.za/doi/abs/10.10520/AJA10115498_315 %X The evolutionary time span required to produce specialist grazers such as wildebeest is considered in relation to the effect on the species of rapid, man-induced changes in Etosha such as fencing, constructed water points and abnormal levels of disease and predation. Basic environmental requirements for a viable wildebeest population are examined and related to the situation presently existing in Etosha.

Berry, H. H. (1997). Historical review of the Etosha Region and its subsequent administration as a National Park. *Madoqua*, *20*(1), 3-12.

Bertola, L. D., Miller, S. M., Williams, V. L., Naude, V. N., Coals, P., Dures, S. G., Henschel, P., Chege, M., Sogbohossou, E. A., Ndiaye, A., Kiki, M., Gaylard, A., Ikanda, D. K., Becker, M. S., & Lindsey, P. (2021). Genetic guidelines for translocations: Maintaining intraspecific diversity in the lion (*Panthera leo*). *Evolutionary Applications*, *15*(1), 22-39. https://doi.org/https://doi.org/10.1111/eva.13318

Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, *11*(1), 63-77. https://doi.org/https://doi.org/10.1111/j.1461-0248.2007.01109.x

Boone, R. B., & Hobbs, N. T. (2004). Lines around fragments: effects of fencing on large herbivores. *African Journal of Range & Forage Science*, *21*(3), 147-158. https://doi.org/10.2989/10220110409485847

Branco, P. S., Merkle, J. A., Pringle, R. M., King, L., Tindall, T., Stalmans, M., & Long, R. A. (2020). An experimental test of community-based strategies for mitigating human–wildlife conflict around protected areas. *Conservation Letters*, *13*(1), e12679. https://doi.org/https://doi.org/10.1111/conl.12679

Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P. J., Hanssen, L., Kilian, J. W., Stuart-Hill, G., Taylor, R. D., & Naidoo, R. (2020). Characterizing multispecies connectivity across a transfrontier conservation landscape. *Journal of Applied Ecology*, *57*(9), 1700-1710. https://doi.org/https://doi.org/10.1111/1365-2664.13716

Brown, C. (2017). *The important link between hunting & tourism in Namibia both working for conservation*. Retrieved October 27 from https://n-c-e.org/sites/default/files/2017-04/Hunting_tourism_key_partners_April-2017.pdf

Brown, C. (2019). *Using Namibia's Wildlife to Drive a Green Economy*. Retrieved October 27, 2021 from http://conservationnamibia.com/blog/b2019-green-economy.php

Carroll, K. A., Hansen, A. J., Inman, R. M., Lawrence, R. L., & Hoegh, A. B. (2020). Testing landscape resistance layers and modeling connectivity for wolverines in the western United States. *Global Ecology and Conservation*, *23*, e01125. https://doi.org/https://doi.org/10.1016/j.gecco.2020.e01125

Central Bureau of Statistics. (2010). *An atlas of Namibia's population: monitoring and understanding its characteristics*. Windhoek: Central Bureau of Statistics

Chamaillé-Jammes, S., Mtare, G., Makuwe, E., & Fritz, H. (2013). African Elephants Adjust Speed in Response to Surface-Water Constraint on Foraging during the Dry-Season. *PLOS ONE*, *8*(3), e59164. https://doi.org/10.1371/journal.pone.0059164

Chang'a, A., Souza de, N., Muya, J., Keyyu, J., Mwakatobe, A., Malugu, L., Ndossi, H. P., Konuche, J., Omondi, R., Mpinge, A., Hahn, N., Palminteri, S., & Olson, D. (2016). Scaling-Up the Use of Chili Fences for Reducing Human-Elephant Conflict Across Landscapes in Tanzania. *Tropical Conservation Science*, *9*(2), 921-930. https://doi.org/10.1177/194008291600900220

Chibeya, D., Wood, H., Cousins, S., Carter, K., Nyirenda, M. A., & Maseka, H. (2021). How do African elephants utilize the landscape during wet season? A habitat connectivity analysis for Sioma Ngwezi landscape in Zambia. *Ecology and Evolution*, *11*(21), 14916-14931. https://doi.org/https://doi.org/10.1002/ece3.8177

Christelis, G., & Struckmeier, W. (2011). *Groundwater in Namibia: An explanation to the Hydrogeological Map*. Windhoek: Ministry of Agriculture, Water and Rural Development

Clevenger, A. P., Wierzchowski, J., Chruszcz, B., & Gunson, K. (2002). GIS-Generated, Expert-Based Models for Identifying Wildlife Habitat Linkages and Planning Mitigation Passages. *Conservation Biology*, *16*(2), 503-514. https://doi.org/https://doi.org/10.1046/j.1523-1739.2002.00328.x

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R. B., Marco, M. D., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the National Academy of Sciences*, *114*(29), 7635-7640. https://doi.org/doi:10.1073/pnas.1705769114

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2642-2651. https://doi.org/doi:10.1098/rstb.2011.0120

Cushman, S. A., Chase, M., & Griffin, C. (2010). Mapping Landscape Resistance to Identify Corridors and Barriers for Elephant Movement in Southern Africa. In S. A. Cushman & F. Huettmann (Eds.), *Spatial Complexity, Informatics, and Wildlife Conservation* (pp. 349-367). Springer Japan. https://doi.org/10.1007/978-4-431-87771-4_19

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., & Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PLOS ONE*, *13*(7), e0196213. https://doi.org/10.1371/journal.pone.0196213

Cushman, S. A., Elliot, N. B., Macdonald, D. W., & Loveridge, A. J. (2016). A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecology*, *31*(6), 1337-1353. https://doi.org/10.1007/s10980-015-0292-3

Cushman, S. A., Lewis, J. S., & Landguth, E. L. (2014). Why Did the Bear Cross the Road? Comparing the Performance of Multiple Resistance Surfaces and Connectivity Modeling Methods. *Diversity*, *6*(4), 844-854. https://www.mdpi.com/1424-2818/6/4/844

Dasch, N. (2021). *Population-genetic study to determine the genetic diversity and divergence of lion populations (Panthera leo) in northern Namibia* [Master's thesis, Technical University of Munich].

De Beer, Y., Kilian, W., Versfeld, W., & van Aarde, R. J. (2006). Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments*, *64*(3), 412-421. https://doi.org/https://doi.org/10.1016/j.jaridenv.2005.06.015

De Knegt, H. J., van Langevelde, F., Skidmore, A. K., Delsink, A., Slotow, R., Henley, S., Bucini, G., de Boer, W. F., Coughenour, M. B., Grant, C. C., Heitkönig, I. M. A., Henley, M., Knox, N. M., Kohi, E. M., Mwakiwa, E., Page, B. R., Peel, M., Pretorius, Y., van Wieren, S. E., & Prins, H. H. T. (2011). The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology*, *80*(1), 270-281. https://doi.org/https://doi.org/10.1111/j.1365-2656.2010.01764.x

Dejene, S. W., Mpakairi, K. S., Kanagaraj, R., Wato, Y. A., & Mengistu, S. (2021). Modelling continental range shift of the African elephant (*Loxodonta africana*) under a changing climate and land cover: implications for future conservation of the species. *African Zoology*, *56*(1), 25-34. https://doi.org/10.1080/15627020.2020.1846617

Department of Agriculture and Nature Conservation. (1989). *Annual Report*. Windhoek, South West Africa: Department of Agriculture and Nature Conservation

Desert Lion Conservation Trust. (2022). *NW Human-lion Conflict Management Plan*. Retrieved June 09, 2022 from https://www.desertlion.info/hlc/

Di Minin, E., Slotow, R., Fink, C., Bauer, H., & Packer, C. (2021). A pan-African spatial assessment of human conflicts with lions and elephants. *Nature Communications*, *12*(1), 2978. https://doi.org/10.1038/s41467-021-23283-w

Dieckmann, U. (2007). 100 years of Etosha: An Issue of People and Parks. In O. Bubenzer, A. Bolten, & F. Darius (Eds.), *Atlas of Cultural and Environmental Change in Arid Africa* (Africa Praehistorica 21 ed., pp. 124-127). Köln: Heinrich-Barth-Institut.

Dolrenry, S., Hazzah, L., & Frank, L. (2020). Corridors of tolerance through human-dominated landscapes facilitate dispersal and connectivity between populations of African lions *Panthera leo*. *Oryx*, *54*(6), 847-850. https://doi.org/10.1017/S0030605319000656

Douglas-Hamilton, I., Krink, T., & Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, *92*(4), 158-163. https://doi.org/10.1007/s00114-004-0606-9

Dubach, J. M., Briggs, M. B., White, P. A., Ament, B. A., & Patterson, B. D. (2013). Genetic perspectives on "Lion Conservation Units" in Eastern and Southern Africa. *Conservation Genetics*, *14*(4), 741-755. https://doi.org/10.1007/s10592-013-0453-3

EHRA. (2022). *EHRA's Wildlife Conservation Projects*. Retrieved May 30, 2022 from https://www.ehranamibia.org/what-we-do

El Obeid, S., & Mendelsohn, J. M. (2001). *A preliminary profile of the Kavango region in Namibia*. Windhoek: Namibia Nature Foundation

Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014). The devil is in the dispersers: predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, *51*(5), 1169-1178. https://doi.org/https://doi.org/10.1111/1365-2664.12282

Esri. (2019). *ArcGIS Desktop (Version 10.7.1) [Computer software]* Redlands, CA: Environmental Systems Research Institute.

Everatt, K. T., Moore, J. F., & Kerley, G. I. H. (2019). Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. *Global Ecology and Conservation*, *20*, e00758. https://doi.org/https://doi.org/10.1016/j.gecco.2019.e00758

Farley, K. A., Ojeda-Revah, L., Atkinson, E. E., & Eaton-González, B. R. (2012). Changes in land use, land tenure, and landscape fragmentation in the Tijuana River Watershed following reform of the ejido sector. *Land Use Policy*, *29*(1), 187-197. https://doi.org/https://doi.org/10.1016/j.landusepol.2011.06.006

Ferguson, K., & Hanks, J. (2012). The effects of protected area and veterinary fencing on wildlife conservation in southern Africa. *Parks*, *18*(1), 49-60.

Fuller, B. (2006). *Improving Tenure Security for the Rural Poor: Namibia – Country Case Study/Investing in Rights: Lessons from Rural Namibia*. Commission on Legal Empowerment of the Poor (CLEP) (Working Paper No. 6). Rome: Food and Agriculture Organization.

Funston, P., Beytell, P., Hanssen, L., Singwangwa, M., & Tchadau, B. A. (2017). *Status Report Lions of the Kavango and Zambezi Regions*. Windhoek: Government of the Republic of Namibia

Furlan, E., Stoklosa, J., Griffiths, J., Gust, N., Ellis, R., Huggins, R. M., & Weeks, A. R. (2012). Small population size and extremely low levels of genetic diversity in island populations of the platypus, Ornithorhynchus anatinus. *Ecology and Evolution*, *2*(4), 844-857. https://doi.org/https://doi.org/10.1002/ece3.195

Gandiwa, E., Mashapa, C., Muboko, N., Chemura, A., Kuvaoga, P., & Mabika, C. T. (2020). Wildlife-vehicle collisions in Hurungwe Safari Area, northern Zimbabwe. *Scientific African*, *9*, e00518. https://doi.org/https://doi.org/10.1016/j.sciaf.2020.e00518

Gobush, K. S., Edwards, C. T. T., Balfour, D., Wittemyer, G., Maisels, F., & Taylor, R. D. (2021). *Loxodonta africana (amended version of 2021 assessment). The IUCN Red List of Threatened Species 2021: e.T181008073A204401095*. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T181008073A204401095.en

Goldenberg, S. Z., Owen, M. A., Brown, J. L., Wittemyer, G., Oo, Z. M., & Leimgruber, P. (2019). Increasing conservation translocation success by building social functionality in released populations. *Global Ecology and Conservation*, *18*, e00604. https://doi.org/https://doi.org/10.1016/j.gecco.2019.e00604

Green, S. E., Davidson, Z., Kaaria, T., & Doncaster, C. P. (2018). Do wildlife corridors link or extend habitat? Insights from elephant use of a Kenyan wildlife corridor. *African Journal of Ecology*, *56*(4), 860-871. https://doi.org/https://doi.org/10.1111/aje.12541

Hanssen, L., & Stander, P. (2004). *Namibia Large Carnivore Atlas*. Windhoek: Predator Conservation Trust

Harris, G. M., Russell, G. J., van Aarde, R. I., & Pimm, S. L. (2008). Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx*, *42*(1), 66-75. https://doi.org/10.1017/S0030605308000483

Hays, J., & Hitchcock, R. (2020). Land and resource rights in the Tsumkwe conservancies – Nyae Nyae and N≠ a Jaqna. In W. Odendaal & W. Werner (Eds.), *Neither here nor there: Indigeneity, marginalisation and land rights in post-independence Namibia* (pp. 183-214). Windhoek: Legal Assistance Centre.

He, X., Liang, J., Zeng, G., Yuan, Y., & Li, X. (2019). The Effects of Interaction between Climate Change and Land-Use/Cover Change on Biodiversity-Related Ecosystem Services. *Global Challenges*, *3*(9), 1800095. https://doi.org/https://doi.org/10.1002/gch2.201800095

Hetem, R. S., Fuller, A., Maloney, S. K., & Mitchell, D. (2014). Responses of large mammals to climate change. *Temperature*, *1*(2), 115-127. https://doi.org/10.4161/temp.29651

Hines, C. J. H. (1993). Temporary wetlands of Bushmanland and Kavango, north-east Namibia. *Madoqua*, *18*(2), 57-69. https://doi.org/doi:10.10520/AJA10115498_374

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *74*(3), 559-566. https://doi.org/https://doi.org/10.1111/j.1365-2656.2005.00955.x

Jachowski, D. S., Slotow, R., & Millspaugh, J. J. (2014). Good virtual fences make good neighbors: opportunities for conservation. *Animal Conservation*, *17*(3), 187-196. https://doi.org/https://doi.org/10.1111/acv.12082

Jackson, C. R., Marnewick, K., Lindsey, P. A., Røskaft, E., & Robertson, M. P. (2016). Evaluating habitat connectivity methodologies: a case study with endangered African wild dogs in South Africa. *Landscape Ecology*, *31*(7), 1433-1447. https://doi.org/10.1007/s10980-016-0342-5

JICA. (2015). *Master Plan for the Development of an International Logistics Hub for SADC Countries in the Republic of Namibia*. Windhoek: Government of the Republic of Namibia

Jones, B., Mendelsohn, J., Humphrey, E., & Nott, C. (2009). *Pre-feasibility study for evaluating the potential for diversified Land Uses, including wildlife in the Shambyu and Gciriku Small-Scale Commercial Farms in Kavango Region*. Windhoek: WWF Namibia

Jones, B. T. B. (2007). *Synthesis of the CBNRM policy and legislation in Botswana, Malawi, Mozambique, Namibia, Zambia, and Zimbabwe*. (Occasional Paper No. 16). Harare: WWF-SARPO.

Joubert, E., & Mostert, P. K. N. (1975). Distribution patterns and status of some mammals in South West Africa. *Madoqua*, *9*(1), 5-44.

Kapuka, A., & Hlásny, T. (2021). Climate change impacts on ecosystems and adaptation options in nine countries in southern Africa: What do we know? *Ecosphere*, *12*(12), e03860. https://doi.org/https://doi.org/10.1002/ecs2.3860

Kiffner, C., Schaal, I., Cass, L., Peirce, K., Sussman, O., Grueser, A., Wachtel, E., Adams, H., Clark, K., König, H. J., & Kioko, J. (2021). Perceptions and realities of elephant crop raiding and mitigation methods. *Conservation Science and Practice*, *3*(3), e372. https://doi.org/https://doi.org/10.1111/csp2.372

Kioko, J., Kiffner, C., Jenkins, N., & Collinson, W. J. (2015). Wildlife roadkill patterns on a major highway in northern Tanzania. *African Zoology*, *50*(1), 17-22. https://doi.org/10.1080/15627020.2015.1021161

Kirchner, E. (2020). *Model-based suitability and connectivity analysis of lion and zebra habitats in a wildlife-human interaction region of northern Namibia* [Master's thesis, Technical University of Munich].

Krause, C., & Gogol-Prokurat, M. (2014). *Guidance Document for Fine-Scale Wildlife Connectivity Analysis*. Retrieved May 26, 2022 from https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=93018

Lalechère, E., & Bergès, L. (2021). A Validation Procedure for Ecological Corridor Locations. *Land*, *10*(12), 1320. https://www.mdpi.com/2073-445X/10/12/1320

LaPoint, S., Gallery, P., Wikelski, M., & Kays, R. (2013). Animal behavior, cost-based corridor models, and real corridors. *Landscape Ecology*, *28*(8), 1615-1630. https://doi.org/10.1007/s10980-013-9910-0

LaRue, M. A., & Nielsen, C. K. (2008). Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. *Ecological Modelling*, *212*(3), 372-381. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2007.10.036

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008). Home Range Utilisation and Territorial Behaviour of Lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PLOS ONE*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lesilau, F., Fonck, M., Gatta, M., Musyoki, C., van 't Zelfde, M., Persoon, G. A., Musters, K. C. J. M., de Snoo, G. R., & de Iongh, H. H. (2018). Effectiveness of a LED flashlight technique in reducing livestock depredation by lions (Panthera leo) around Nairobi National Park, Kenya. *PLOS ONE*, *13*(1), e0190898. https://doi.org/10.1371/journal.pone.0190898

Lesilau, F., Verschueren, S., Zelfde, M. v. t., Musters, K. C. J. M., Snoo, G. R. d., & Iongh, H. H. d. (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: the case study of Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198-207. https://doi.org/doi:10.1515/mammalia-2020-0116

Lindsay, K., Chase, M., Landen, K., & Nowak, K. (2017). The shared nature of Africa's elephants. *Biological Conservation*, *215*, 260-267. https://doi.org/https://doi.org/10.1016/j.biocon.2017.08.021

Lindsey, P. (2011). *An analysis of game meat production and wildlife-based land uses on freehold land in Namibia: links with food security*. Harare: TRAFFIC East/Southern Africa.

Lindsey, P. A., Havemann, C. P., Lines, R. M., Price, A. E., Retief, T. A., Rhebergen, T., Van der Waal, C., & Romañach, S. S. (2013). Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. *Oryx*, *47*(1), 41-53. https://doi.org/10.1017/S0030605311001049

Lindsey, P. A., Romañach, S. S., & Davies-Mostert, H. T. (2009). The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. *Journal of Zoology*, *277*(2), 99-105. https://doi.org/https://doi.org/10.1111/j.1469-7998.2008.00529.x

Loarie, S. R., Van Aarde, R. J., & Pimm, S. L. (2009a). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, *142*(12), 3099-3107. https://doi.org/https://doi.org/10.1016/j.biocon.2009.08.021

Loarie, S. R., Van Aarde, R. J., & Pimm, S. L. (2009b). Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, *142*(12), 3086-3098. https://doi.org/https://doi.org/10.1016/j.biocon.2009.08.008

Lohay, G. G., Weathers, T. C., Estes, A. B., McGrath, B. C., & Cavener, D. R. (2020). Genetic connectivity and population structure of African savanna elephants (*Loxodonta africana*) in Tanzania. *Ecology and Evolution*, *10*(20), 11069-11089. https://doi.org/https://doi.org/10.1002/ece3.6728

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Changes in home range size of African lions in relation to pride size and prey

biomass in a semi-arid savanna. *Ecography*, *32*(6), 953-962. https://doi.org/https://doi.org/10.1111/j.1600-0587.2009.05745.x
Løvschal, M., Bøcher, P. K., Pilgaard, J., Amoke, I., Odingo, A., Thuo, A., & Svenning, J.-C. (2017). Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Scientific Reports*, *7*(1), 41450. https://doi.org/10.1038/srep41450
Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature*, *301*(5899), 379-384. https://doi.org/10.1038/301379a0
Magistral Papers. (1925/26). Distribution of Game in South West Africa. *Letters from 1925 and 1926 achieved in the Swakopmund Scientific Society*.
Magura, T., Kiss, E., & Lövei, G. L. (2021). No consistent diversity patterns in terrestrial mammal assemblages along rural-urban forest gradients. *Basic and Applied Ecology*, *52*, 38-45. https://doi.org/https://doi.org/10.1016/j.baae.2021.02.004
Mantyka-Pringle, C. S., Visconti, P., Di Marco, M., Martin, T. G., Rondinini, C., & Rhodes, J. R. (2015). Climate change modifies risk of global biodiversity loss due to land-cover change. *Biological Conservation*, *187*, 103-111. https://doi.org/https://doi.org/10.1016/j.biocon.2015.04.016
Martin, R. B. (2005). *The Transboundary Mammal Project of the Ministry of Environment and Tourism, Namibia*. Windhoek: The Namibia Nature Foundation
Matson, T. K. (2006). *Factors affecting human-elephant conflicts in Nyae Nyae Conservancy and Khaudum National Park, Namibia (Technical Report)*. Windhoek: Ministry of Environment and Tourism and Namibia Nature Foundation
Mbaiwa, J. E., & Mbaiwa, O. I. (2006). The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *International Journal of Wilderness*, *12*(3), 17-23.
McRae, B. H., & Kavanagh, D. M. (2011). *Linkage Mapper Connectivity Analysis Software*. In The Nature Conservancy. https://linkagemapper.org/
MEFT/NACSO. (2021). *The state of community conservation in Namibia*. (Annual Report 2019). Windhoek: MEFT/NACSO
Mendelsohn, J. (2006). *Farming systems in Namibia*. Windhoek: Research and Information Services of Namibia
Mendelsohn, J. (2009). *Land Use in Kavango: Past, Present and Future*. Windhoek: Research and Information Services of Namibia
Mendelsohn, J. (2013). *Rapid Survey of Farms in Kavango*. Windhoek: Ministry of Lands and Resettlement
Mendelsohn, J., & El Obeid, S. (2003). *Sand and Water: A Profile of the Kavango Region*. Cape Town: Struik Publishers
Mendelsohn, J., & El Obeid, S. (2005). *Forests and Woodlands of Namibia*. Windhoek: Research and Information Services of Namibia
Mendelsohn, J., Jarvis, A., & Robert, C. (2002). *Atlas of Namibia: a portrait of the land and its people*. Cape Town: David Philip Publishers.
Mendelsohn, J. M., Shixwameni, L., & Nakamhela, U. (2012). *An overview of communal land tenure in Namibia: Unlocking its economic potential* Paper presented at the Bank of Namiba 14th Annual Symposium, Windhoek, Namibia.
Meyer, N. F. V., Moreno, R., Reyna-Hurtado, R., Signer, J., & Balkenhol, N. (2020). Towards the restoration of the Mesoamerican Biological Corridor for large mammals in Panama: comparing multi-species occupancy to movement models. *Movement Ecology*, *8*(1), 3. https://doi.org/10.1186/s40462-019-0186-0
Ministry of Environment, Forestry and Tourism. (2020a). *Fourth National Communication to the United Nations Framework Convention on Climate Change*. Windhoek: Government of the Republic of Namibia

Ministry of Environment, Forestry and Tourism. (2020b). *National Elephant Management Plan 2021/2022-2030/2031*. Windhoek: Government of the Republic of Namibia

Ministry of Environment and Tourism. (2010). *State of Protected Areas in Namibia: A Review of Progress and Challenges*. Windhoek: Government of the Republic of Namibia

Ministry of Environment and Tourism. (2011a). *National Policy on Climate Change for Namibia*. Windhoek: Government of the Republic of Namibia

Ministry of Environment and Tourism. (2011b). *Second National Communication to the United Nations Framework Convention on Climate Change*. Windhoek: Government of the Republic of Namibia

Ministry of Environment and Tourism. (2013). *Management Plan Khaudum National Park 2013/2014 to 2017/2018*. Windhoek: Government of the Republic of Namibia

Ministry of Environment and Tourism. (2014). *Fifth National Report to the Convention on Biological Diversity*. Windhoek: Government of the Republic of Namibia

Ministry of Environment and Tourism. (2017). *Human-Lion Conflict Management Plan for North West Namibia*. Windhoek: Government of the Republic of Namibia

Ministry of Lands and Resettlement. (2012). *Road Map for the development of small-scale farming areas on communal land in Namibia*. Windhoek: Ministry of Lands and Resettlement/ KfW

Ministry of Lands and Resettlement. (2015). *Regional Development Profile for the Kavango East Region*. Rundu: Ministry of Lands and Resettlement

Movirongo, C. (2021). *Human-wildlife conflict incidents across the country on the rise - Shifeta*. Namibia Economist. Retrieved October 15, 2021 from https://economist.com.na/59826/environment/human-wildlife-conflict-incidents-on-the-rise-locally-shifeta/

Muduva, T. (2014). *Grazing Rights in Communal Areas of a Post-independent Namibia: A case study of a grazing dispute in Western Kavango Region* [Master's thesis, University of the Western Cape].

Muhoko, E., de Wasseige, C., & De Cauwer, V. (2020). Assessing land cover change in Namibia's Kavango East region: a multi-date object approach. *BOIS & FORETS DES TROPIQUES*, *344*(0), 17-32. https://doi.org/10.19182/bft2020.344.a31897

Naankuse. (2018). *Mangetti Cattle Ranch*. Retrieved May 2 from https://naankuse.com/conservation-research/mangetti/

NACSO. (2012). *Living with wildlife – the story of Nyae Nyae conservancy*. Windhoek: NACSO

NACSO. (2013). *Namibia's communal conservancies: a review of progress and challenges in 2011*. Windhoek: NACSO

NACSO. (2018). *Registered communal conservancies in Namibia*. Retrieved November 18, 2021 from http://www.nacso.org.na/resources/map

Naidoo, R., Beytell, P., Brennan, A., Kilian, W., McCulloch, G., Stronza, A., Taylor, R., Tsholofelo, C., & Songhurst, A. (2022). Challenges to Elephant Connectivity From Border Fences in the World's Largest Transfrontier Conservation Area [Brief Research Report]. *Frontiers in Conservation Science*, *3*. https://doi.org/10.3389/fcosc.2022.788133

Naidoo, R., Chase, M. J., Beytell, P., Du Preez, P., Landen, K., Stuart-Hill, G., & Taylor, R. (2016). A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. *Oryx*, *50*(1), 138-146. https://doi.org/10.1017/S0030605314000222

Naidoo, R., Du Preez, P., Stuart-Hill, G., Jago, M., & Wegmann, M. (2012). Home on the Range: Factors Explaining Partial Migration of African Buffalo in a Tropical Environment. *PLOS ONE*, *7*(5), e36527. https://doi.org/10.1371/journal.pone.0036527

Naidoo, R., Kilian, J. W., Du Preez, P., Beytell, P., Aschenborn, O., Taylor, R. D., & Stuart-Hill, G. (2018). Evaluating the effectiveness of local- and regional-scale wildlife corridors using quantitative metrics of functional connectivity. *Biological Conservation*, *217*, 96-103. https://doi.org/https://doi.org/10.1016/j.biocon.2017.10.037

Namibia Statistics Agency. (2012). *Namibia 2011: Population & Housing Census Main Report*. Windhoek: Namibia Statistics Agency

Namibia Statistics Agency. (2014). *Namibia 2011 Census Population Projections 2011 to 2041*. Windhoek: Namibia Statistics Agency

Namibia Statistics Agency. (2017). *Namibia Inter-censal Demographic Survey 2016 Report*. Windhoek: Namibia Statistics Agency

Namibia Statistics Agency. (2018). *Namibia Land Statistics Booklet*. Windhoek: Namibia: Statistics Agency

Namibia Statistics Agency. (2019). *Namibia Labour Force Survey 2018 Report*. Windhoek: Namibia: Statistics Agency

Namibian Lion Trust. (2019). *Livestock Protection*. Retrieved June 09, 2022 from https://namibianliontrust.org/livestock-protection/

Newmark, W. D., Boshe, J. I., Sariko, H. I., & Makumbule, G. K. (1996). Effects of a highway on large mammals in Mikumi National Park, Tanzania. *African Journal of Ecology*, *34*(1), 15-31. https://doi.org/https://doi.org/10.1111/j.1365-2028.1996.tb00590.x

Ngene, S., Okello, M. M., Mukeka, J., Muya, S., Njumbi, S., & Isiche, J. (2017). Home range sizes and space use of African elephants (*Loxodonta africana*) in the Southern Kenya and Northern Tanzania borderland landscape. *International Journal of Biodiversity and Conservation*, *9*(1), 9-26. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en

Ntukey, L. T., Munishi, L. K., Kohi, E., & Treydte, A. C. (2022). Land Use/Cover Change Reduces Elephant Habitat Suitability in the Wami Mbiki–Saadani Wildlife Corridor, Tanzania. *Land*, *11*(2), 307. https://www.mdpi.com/2073-445X/11/2/307

O'Neill, H. M. K., Durant, S. M., Strebel, S., & Woodroffe, R. (2022). Fencing affects African wild dog movement patterns and population dynamics. *Oryx*, *56*(1), 128-136. https://doi.org/10.1017/S0030605320000320

O'Donnell, K., & delBarco-Trillo, J. (2020). Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: a meta-analysis. *Journal of Urban Ecology*, *6*(1). https://doi.org/10.1093/jue/juaa014

Ojwang, G. O., Wargute, P. W., Said M. Y., Worden J. S., Davidson, Z., Muruthi, P., Kanga, E., Ihwagi, F., & Okita-Ouma, B. (2017). *Wildlife Migratory Corridors and Dispersal Areas: Kenya Rangelands and Coastal Terrestrial Ecosystems*. Nairobi: Government of the Republic of Kenya

Okello, M. M., Kenana, L., Maliti, H., Kiringe, J. W., Kanga, E., Warinwa, F., Bakari, S., Ndambuki, S., Massawe, E., Sitati, N., Kimutai, D., Mwita, M., Gichohi, N., Muteti, D., Ngoru, B., & Mwangi, P. (2016). Population density of elephants and other key large herbivores in the Amboseli ecosystem of Kenya in relation to droughts. *Journal of Arid Environments*, *135*, 64-74. https://doi.org/https://doi.org/10.1016/j.jaridenv.2016.08.012

Okita-Ouma, B., Koskei, M., Tiller, L., Lala, F., King, L., Moller, R., Amin, R., & Douglas-Hamilton, I. (2021). Effectiveness of wildlife underpasses and culverts in connecting elephant habitats: a case study of new railway through Kenya's Tsavo National Parks. *African Journal of Ecology*, *59*(3), 624-640. https://doi.org/https://doi.org/10.1111/aje.12873

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., Haas, C. D., Harris, S., Hathaway, S. A., Turschak, G. M., Miles, A. K., & Van Vuren, D. H.

(2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy*, *91*(6), 1322-1331. https://doi.org/10.1644/09-mamm-a-312.1
Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2018). Fencing solves human-wildlife conflict locally but shifts problems elsewhere: A case study using functional connectivity modelling of the African elephant. *Journal of Applied Ecology*, *55*(6), 2673-2684. https://doi.org/https://doi.org/10.1111/1365-2664.13246
Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Validating movement corridors for African elephants predicted from resistance-based landscape connectivity models. *Landscape Ecology*, *34*(4), 865-878. https://doi.org/10.1007/s10980-019-00811-0
Pekor, A., Miller, J. R. B., Flyman, M. V., Kasiki, S., Kesch, M. K., Miller, S. M., Uiseb, K., van der Merve, V., & Lindsey, P. A. (2019). Fencing Africa's protected areas: Costs, benefits, and management issues. *Biological Conservation*, *229*, 67-75. https://doi.org/https://doi.org/10.1016/j.biocon.2018.10.030
Pinheiro, I., Gabaake, G., & Heyns, P. (2003). Cooperation in the Okavango River Basin: the OKACOM perspective. In A. Turton, P. Ashton, & E. Cloete (Eds.), *Transboundary rivers, sovereignty and development: Hydropolitical drivers in the Okavango River Basin* (pp. 105-118). Pretoria and Geneva: AWIRU and Green Cross International.
Poor, E. E., Loucks, C., Jakes, A., & Urban, D. L. (2012). Comparing Habitat Suitability and Connectivity Modeling Methods for Conserving Pronghorn Migrations. *PLOS ONE*, *7*(11), e49390. https://doi.org/10.1371/journal.pone.0049390
Pulsford, I., Lindenmayer, D., Wyborn, C., Lausche, B., Vasilijević, M., Worboys, G. L., & Lefroy, T. (2015). Connectivity Conservation Management. In I. Pulsford, G. L. Worboys, M. Lockwood, A. Kothari, & S. Feary (Eds.), *Protected Area Governance and Management* (pp. 851-888). ANU Press.
Purdon, A., Mole, M. A., Chase, M. J., & van Aarde, R. J. (2018). Partial migration in savanna elephant populations distributed across southern Africa. *Scientific Reports*, *8*(1), 11331. https://doi.org/10.1038/s41598-018-29724-9
Reid, H., Sahlen, L., Stage, J., & MacGregor, J. (2007). *The economic impact of climate change in Namibia. How climate change will affect the contribution of Namibia's natural resources to its economy*. (Environmental Economics Programme Discussion Paper 07-02). London: International Institute for Environment and Development.
Riggio, J., & Caro, T. (2017). Structural connectivity at a national scale: Wildlife corridors in Tanzania. *PLOS ONE*, *12*(11), e0187407. https://doi.org/10.1371/journal.pone.0187407
Robson, A. S., Trimble, M. J., Purdon, A., Young-Overton, K. D., Pimm, S. L., & van Aarde, R. J. (2017). Savanna elephant numbers are only a quarter of their expected values. *PLOS ONE*, *12*(4), e0175942. https://doi.org/10.1371/journal.pone.0175942
Roever, C. L., van Aarde, R. J., & Leggett, K. (2013). Functional connectivity within conservation networks: Delineating corridors for African elephants. *Biological Conservation*, *157*, 128-135. https://doi.org/https://doi.org/10.1016/j.biocon.2012.06.025
Rudnick, D., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenbach, F., Epps, C., Gerber, L. R., Hartter, J. N., Jenness, J. S., Kintsch, J., Merenlender, A. M., Perkl, R. M., Perziosi, D. V., & Trombulack, S. C. (2012). The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology.
Rust, N. A., & Marker, L. L. (2014). Cost of carnivore coexistence on communal and resettled land in Namibia. *Environmental Conservation*, *41*(1), 45-53. https://doi.org/10.1017/S0376892913000180

Rust, N. A., Tzanopoulos, J., Humle, T., & MacMillan, D. C. (2016). Why Has Human–Carnivore Conflict Not Been Resolved in Namibia? *Society & Natural Resources*, *29*(9), 1079-1094. https://doi.org/10.1080/08941920.2016.1150544

Ryan, S., & Hartter, J. (2012). Beyond Ecological Success of Corridors: Integrating Land Use History and Demographic Change to Provide a Whole Landscape Perspective. *Ecological Restoration*, *30*, 320-328. https://doi.org/10.3368/er.30.4.320

Rytwinski, T., & Fahrig, L. (2012). Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation*, *147*(1), 87-98. https://doi.org/https://doi.org/10.1016/j.biocon.2011.11.023

Sach, F., Dierenfeld, E. S., Langley-Evans, S. C., Watts, M. J., & Yon, L. (2019). African savanna elephants (*Loxodonta africana*) as an example of a herbivore making movement choices based on nutritional needs. *PeerJ*, *7*, e6260. https://doi.org/10.7717/peerj.6260

Sargent, R., Deere, N. J., McGowan, P. J. K., Bunnefeld, N., & Pfeifer, M. (2021). Room to roam for African lions *Panthera leo*: a review of the key drivers of lion habitat use and implications for conservation. *Mammal Review*, *52*(1), 39-51. https://doi.org/https://doi.org/10.1111/mam.12262

Sawyer, S. C., Epps, C. W., & Brashares, J. S. (2011). Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *Journal of Applied Ecology*, *48*(3), 668-678. https://doi.org/https://doi.org/10.1111/j.1365-2664.2011.01970.x

Schalkwyk, D. L. v., McMillin, K. W., Witthuhn, R. C., & Hoffman, L. C. (2010). The Contribution of Wildlife to Sustainable Natural Resource Utilization in Namibia: A Review. *Sustainability*, *2*(11), 3479-3499. https://www.mdpi.com/2071-1050/2/11/3479

Schlaepfer, D. R., Braschler, B., Rusterholz, H.-P., & Baur, B. (2018). Genetic effects of anthropogenic habitat fragmentation on remnant animal and plant populations: a meta-analysis. *Ecosphere*, *9*(10), e02488. https://doi.org/https://doi.org/10.1002/ecs2.2488

Schürmann, A., Kleemann, J., Fürst, C., & Teucher, M. (2020). Assessing the relationship between land tenure issues and land cover changes around the Arabuko Sokoke Forest in Kenya. *Land Use Policy*, *95*, 104625. https://doi.org/https://doi.org/10.1016/j.landusepol.2020.104625

Shaffer, L. J., Khadka, K. K., Van Den Hoek, J., & Naithani, K. J. (2019). Human-Elephant Conflict: A Review of Current Management Strategies and Future Directions [Review]. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00235

Shepard, D. B., Kuhns, A. R., Dreslik, M. J., & Phillips, C. A. (2008). Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation*, *11*(4), 288-296. https://doi.org/https://doi.org/10.1111/j.1469-1795.2008.00183.x

Shortridge, G. C. (1934). *The Mammals of South West Africa - A Biological Account of the Forms occurring in that Region* (Vol. 1 and 2). Namibia Scientific Society (William Heinemann Ltd.).

Shrader, A. M., Pimm, S. L., & van Aarde, R. J. (2010). Elephant survival, rainfall and the confounding effects of water provision and fences. *Biodiversity and Conservation*, *19*(8), 2235-2245. https://doi.org/10.1007/s10531-010-9836-7

Smith, J. A., Duane, T. P., & Wilmers, C. C. (2019). Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape. *Landscape and Urban Planning*, *183*, 50-58. https://doi.org/https://doi.org/10.1016/j.landurbplan.2018.11.003

Snyman, A., Raynor, E., Chizinski, C., Powell, L., & Carroll, J. (2018). African Lion (*Panthera leo*) Space Use in the Greater Mapungubwe Transfrontier Conservation Area. *African Journal of Wildlife Research*, *48*(2), 1-12, 12. https://doi.org/10.3957/056.048.023001

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioral Ecology and Sociobiology*, *52*(4), 303-307. https://doi.org/10.1007/s00265-002-0515-x

Stander, P. E. (1991). Demography of lions in the Etosha National Park, Namibia. *Madoqua*, *18*(1), 1-9. https://doi.org/doi:10.10520/AJA10115498_339

Starik, N., Mbango, O. K., Bengsch, S., Göttert, T., & Zeller, U. (2020). Landscape Transformation Influences Responses of Terrestrial Small Mammals to Land Use Intensity in North-Central Namibia. *Diversity*, *12*(12), 488. https://www.mdpi.com/1424-2818/12/12/488

Stein, A. B., Aschenborn, O., Kastern, M., Andreas, A., & Thompson, S. (2012). *Namibia Large Carnivore Atlas*. Windhoek: Ministry of Environment and Tourism

Stevens, K., Harrisson, K. A., Hogan, F. E., Cooke, R., & Clarke, R. H. (2018). Reduced gene flow in a vulnerable species reflects two centuries of habitat loss and fragmentation. *Ecosphere*, *9*(2), e02114. https://doi.org/https://doi.org/10.1002/ecs2.2114

Stevenson-Holt, C. D., Watts, K., Bellamy, C. C., Nevin, O. T., & Ramsey, A. D. (2014). Defining Landscape Resistance Values in Least-Cost Connectivity Models for the Invasive Grey Squirrel: A Comparison of Approaches Using Expert-Opinion and Habitat Suitability Modelling. *PLOS ONE*, *9*(11), e112119. https://doi.org/10.1371/journal.pone.0112119

Stoldt, M., Göttert, T., Mann, C., & Zeller, U. (2020). Transfrontier Conservation Areas and Human-Wildlife Conflict: The Case of the Namibian Component of the Kavango-Zambezi (KAZA) TFCA. *Scientific Reports*, *10*(1), 7964. https://doi.org/10.1038/s41598-020-64537-9

Strauss, S. (2020). *Environmental Assessment for the Preservation and Rehabilitation of Trunk Roads 8/2 and 8/3 (TR0802 and TR0803): Taranaki, Mururani Gate to Rundu in the Kavango East, Kavango West and Otjozondjupa Regions.* Windhoek: GCS Namibia

The Heinz Center. (2012). *Climate-change vulnerability and adaptation strategies for Africa's charismatic megafauna*. Washington, DC: The H. John Heinz III Center for Science, Economics and the Environment

Thomson, G. R., Penrith, M.-L., Atkinson, M. W., Atkinson, S. J., Cassidy, D., & Osofsky, S. A. (2013). Balancing Livestock Production and Wildlife Conservation in and around Southern Africa's Transfrontier Conservation Areas. *Transboundary and Emerging Diseases*, *60*(6), 492-506. https://doi.org/https://doi.org/10.1111/tbed.12175

Thouless, C. R., Dublin, H. T., Blanc, J. J., Skinner, D. P., Daniel, T. E., Taylor, R. D., Maisels, F., Frederick, H. L., & Bouché, P. (2016). *African Elephant Status Report 2016: an update from the African Elephant Database*. (Occasional Paper Series of the IUCN Species Survival Commission No. 60). Gland: IUCN.

Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J. R. M., Midgley, G. F., & Corsi, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology*, *12*(3), 424-440. https://doi.org/https://doi.org/10.1111/j.1365-2486.2006.01115.x

Trinkel, M. (2013). Climate variability, human wildlife conflict and population dynamics of lions *Panthera leo*. *Naturwissenschaften*, *100*(4), 345-353. https://doi.org/10.1007/s00114-013-1034-5

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population.

Animal Conservation, *13*(4), 374-382. https://doi.org/https://doi.org/10.1111/j.1469-1795.2009.00344.x
Tsalyuk, M., Kilian, W., Reineking, B., & Getz, W. M. (2019). Temporal variation in resource selection of African elephants follows long-term variability in resource availability. *Ecological Monographs*, *89*(2), e01348. https://doi.org/https://doi.org/10.1002/ecm.1348
Tucker, M. A., Santini, L., Carbone, C., & Mueller, T. (2021). Mammal population densities at a global scale are higher in human-modified areas. *Ecography*, *44*(1), 1-13. https://doi.org/https://doi.org/10.1111/ecog.05126
Tuqa, J. H., Funston, P., Musyoki, C., Ojwang, G. O., Gichuki, N. N., Bauer, H., Tamis, W., Dolrenry, S., Van't Zelfde, M., de Snoo, G. R., & de Iongh, H. H. (2014). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*, *2*, 1-10. https://doi.org/https://doi.org/10.1016/j.gecco.2014.07.006
Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., & Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, *49*(1), 73-81. https://doi.org/https://doi.org/10.1111/j.1365-2664.2011.02099.x
Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, *25*(3), 337-351. https://doi.org/10.1007/s10980-009-9425-x
van Aarde, R. J., Pimm, S. L., Guldemond, R., Huang, R., & Maré, C. (2021). The 2020 elephant die-off in Botswana. *PeerJ*, *9*, e10686. https://doi.org/10.7717/peerj.10686
Van Der Wulp, C., & Hebinck, P. (2021). Fighting fences and land grabbers in the struggle for the Commons in N ≠ a Jaqna, Namibia. *African Affairs*, *120*(480), 417-443. https://doi.org/10.1093/afraf/adab017
van Strien, M. J., & Grêt-Regamey, A. (2016). How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. *Ecological Modelling*, *342*, 186-198. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2016.09.025
Viljoen, P. J. (1987). Status and past and present distribution of elephants in the Kaokoveld, South West Africa/Namibia. *South African Journal of Zoology*, *22*(4), 247-257. https://doi.org/10.1080/02541858.1987.11448054
Viljoen, P. J. (1989). Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib Desert, South West Africa/Namibia. *African Journal of Ecology*, *27*(3), 227-240. https://doi.org/https://doi.org/10.1111/j.1365-2028.1989.tb01016.x
Wade, A. A., McKelvey, K. S., & Schwartz, M. K. (2015). Resistance-surface-based wildlife conservation connectivity modeling: Summary of efforts in the United States and guide for practitioners. *Gen. Tech. Rep. RMRS-GTR-333. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 93 p.*, *333*.
Wall, J., Douglas-Hamilton, I., & Vollrath, F. (2006). Elephants avoid costly mountaineering. *Current Biology*, *16*(14), R527-R529. https://doi.org/10.1016/j.cub.2006.06.049
Wall, J., Wittemyer, G., Klinkenberg, B., & Douglas-Hamilton, I. (2014). Novel opportunities for wildlife conservation and research with real-time monitoring. *Ecological Applications*, *24*(4), 593-601. https://doi.org/https://doi.org/10.1890/13-1971.1
Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., Henley, M., Vollrath, F., Maisels, F., Ferwerda, J., & Douglas-Hamilton, I. (2021). Human footprint

and protected areas shape elephant range across Africa. *Current Biology*, *31*(11), 2437-2445.e2434. https://doi.org/10.1016/j.cub.2021.03.042

Wato, Y. A., Prins, H. H. T., Heitkönig, I. M. A., Wahungu, G. M., Ngene, S. M., Njumbi, S., & van Langevelde, F. (2018). Movement Patterns of African Elephants (*Loxodonta africana*) in a Semi-arid Savanna Suggest That They Have Information on the Location of Dispersed Water Sources [Original Research]. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00167

Weaver, L. C., & Skyer, P. (2005). Conservancies: integrating wildlife land-use options into the livelihood, development, and conservation strategies of Namibian communities. In S. A. Osofsky, S. Cleaveland, W. B. Karesh, M. D. Kock, P. J. Nyhus, L. Starr, & A. Yang (Eds.), *Conservation and Development Interventions at the Wildlife/Livestock Interface. Implications for Wildlife, Livestock and Human Health* (pp. 89-104). Gland and Cambridge: IUCN.

Weise, F. J., Hauptmeier, H., Stratford, K. J., Hayward, M. W., Aal, K., Heuer, M., Tomeletso, M., Wulf, V., Somers, M. J., & Stein, A. B. (2019). Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence [Original Research]. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00242

Williams, K. S., Williams, S. T., Welch, R. J., Marneweck, C. J., Mann, G. K. H., Pitman, R. T., Whittington-Jones, G., Balme, G. A., Parker, D. M., & Hill, R. A. (2021). Assumptions about fence permeability influence density estimates for brown hyaenas across South Africa. *Scientific Reports*, *11*(1), 620. https://doi.org/10.1038/s41598-020-77188-7

Wingate, V. R., Phinn, S. R., Kuhn, N., Bloemertz, L., & Dhanjal-Adams, K. L. (2016). Mapping Decadal Land Cover Changes in the Woodlands of North Eastern Namibia from 1975 to 2014 Using the Landsat Satellite Archived Data. *Remote Sensing*, *8*(8), 681. https://www.mdpi.com/2072-4292/8/8/681

Yiu, S. W., Karczmarski, L., Parrini, F., & Keith, M. (2019). Resource selection in reintroduced lions and the influence of intergroup interactions. *Journal of Zoology*, *307*(2), 111-124. https://doi.org/https://doi.org/10.1111/jzo.12620

Young, K. D., Ferreira, S. M., & Van Aarde, R. J. (2009). Elephant spatial use in wet and dry savannas of southern Africa. *Journal of Zoology*, *278*(3), 189-205. https://doi.org/https://doi.org/10.1111/j.1469-7998.2009.00568.x

Zeller, K. A., Jennings, M. K., Vickers, T. W., Ernest, H. B., Cushman, S. A., & Boyce, W. M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Diversity and Distributions*, *24*(7), 868-879. https://doi.org/https://doi.org/10.1111/ddi.12742

Ziółkowska, E., Ostapowicz, K., Radeloff, V. C., Kuemmerle, T., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Śmietana, W., & Selva, N. (2016). Assessing differences in connectivity based on habitat versus movement models for brown bears in the Carpathians. *Landscape Ecology*, *31*(8), 1863-1882. https://doi.org/10.1007/s10980-016-0368-8

Declaration of Authorship

I declare that this thesis is my own work and that, to the best of my knowledge, it contains no material previously published, or substantially overlapping with material submitted for the award of any other degree at any institution, except where due acknowledgment is made in the text.

Munich, 13.06.2022 ……………………………….

(Corsa Lok Ching Liu)