

**THE IMPACT OF LINEAR BARRIERS ON THE MOVEMENT
ECOLOGY OF UNGULATES IN THE GREATER SOSSUSVLEI-
NAMIB LANDSCAPE, NAMIBIA**

Stefanie Kim Urban (Student number: 216042992)

Thesis submitted in partial fulfillment of the requirements for the degree of
Master of Natural Resource Management at the Namibia University of Science
and Technology



**NAMIBIA UNIVERSITY
OF SCIENCE AND TECHNOLOGY**

Supervisor: Prof. Morgan Hauptfleisch (NUST)

September 2021

Declaration

I, *Stefanie Kim Urban*, hereby declare that the work contained in the thesis entitled: *The impact of linear barriers on the movement ecology of ungulates in the Greater Sossusvlei-Namib Landscape, Namibia* is my own original work and that I have not previously in its entirety or in part submitted it at any university or higher education institution for the award of a degree.

Signature:.......... Date: 30 September 2021

Retention and Use of Thesis

I, *Stefanie Kim Urban*, being a candidate for the degree of *Master of Natural Resource Management* accept the requirements of the Namibia University of Science and Technology relating to the retention and use of theses deposited in the Library and Information Services.

In terms of these conditions, I agree that the original of my thesis deposited in the Library and Information Services will be accessible for purposes of study and research, in accordance with the normal conditions established by the Librarian for the care, loan or reproduction of theses.

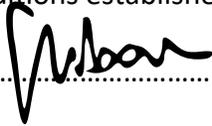
Signature:.......... Date: 30 September 2021

Table of Contents

<i>List of Figures</i>	<i>vi</i>
<i>List of Tables</i>	<i>viii</i>
<i>List of Acronyms</i>	<i>ix</i>
<i>Acknowledgements</i>	<i>x</i>
<i>Abstract</i>	<i>xi</i>
Chapter 1: Introduction and literature review	1
1.1 Background.....	1
1.2 The applications and benefits of fences.....	2
1.3 The negative aspects of fences.....	5
1.4 The negative aspects of roads.....	8
1.5 The move towards open systems.....	10
1.6 Movement ecology and movement in arid environments.....	12
1.7 Home range studies.....	15
1.8 Study species.....	16
1.8.1 Hartmann’s mountain zebra <i>Equus zebra hartmannae</i>	17
1.8.2 Gemsbok <i>Oryx gazella gazella</i>	20
1.8.3 Springbok <i>Antidorcas marsupialis</i>	23
1.9 Research motivation and problem statement.....	25
1.10 Research Objectives.....	28
Chapter 2: Methods and study area	29
2.1 Description of the study area.....	29
2.2 Animal collaring.....	32
2.3 Data screening and preparation.....	34
2.4 Home range analysis.....	35
2.5 Modelling of barrier effects on animal distribution.....	36
2.6 Hotspot analysis.....	38
Chapter 3: Results	40
3.1 Home range analysis.....	40
3.1.1 Hartmann’s mountain zebra.....	45
3.1.2 Gemsbok.....	51

3.1.3	Springbok	57
3.2	The impact of barriers on animal distribution.....	61
3.2.1	Hartmann’s mountain zebra	63
3.2.2	Gemsbok	63
3.2.3	Springbok	64
3.3	<i>The barrier effect on ungulate movements</i>.....	64
3.3.1	Hartmann’s mountain zebra	64
3.3.2	Gemsbok	67
3.3.3	Springbok	70
3.4	Hotspot analysis related to topography	73
3.4.1	Hartmann’s mountain zebra	73
3.4.2	Gemsbok	73
3.4.3	Springbok	74
Chapter 4:	<i>Discussion</i>.....	78
4.1	Home range sizes	78
4.1.1	Hartmann’s mountain zebra	78
4.1.2	Gemsbok	80
4.1.3	Springbok	81
4.2	The barrier effect of roads and fences.....	84
4.2.1	Home ranges as related to barriers	84
4.2.2	Ungulate distribution in relation to barriers	86
4.2.3	Movement restrictions in relation to barriers.....	89
4.3	Hotspots of occurrence.....	92
Chapter 5:	<i>Conclusion</i>	93
Chapter 6:	<i>Management implications & future research opportunities</i>.....	94
References		100
Appendices		121
Appendix 1	Information on the capture and tracking of ungulates in the GSNL.....	121

List of Figures

Figure 1: Map of the Greater Sossusvlei-Namib Landscape, including the NamibRand Nature Reserve, and the Namib-Naukluft Park.	30
Figure 2: Box and whisker plot of estimated home range sizes of Hartmann’s zebra, gemsbok and springbok.	44
Figure 3: Comparison of estimated home range sizes (km ²) between Hartmann’s mountain zebra, gemsbok and springbok.	44
Figure 4: a - o: Estimated home ranges of Hartmann’s zebra (km ²).	50
Figure 5: a - m: Estimated home ranges of gemsbok (km ²).	56
Figure 6: a - l: Estimated home ranges of springbok (km ²).	60
Figure 7: a) The distances to the nearest barriers for the north region of the study area. b) a scale map of the north region with geographical features for orientation.	61
Figure 8: a) The distances to the nearest barriers for the mid region of the study area. b) a scale map of the mid region with geographical features for orientation.	62
Figure 9: a) The distances to the nearest barriers for the south region of the study area. b) a scale map of the south region with geographical features for orientation.	62
Figure 10: a) Relationship between distance to nearest barrier and the density of Hartmann’s zebra locations, with upper and lower confidence intervals (universal barrier relationship). b) Proportion of estimated Hartmann’s zebra locations that lie a certain distance from the nearest barrier, with upper and lower confidence intervals.	63
Figure 11: a) Relationship between distance to nearest barrier and the density of gemsbok locations, with upper and lower confidence intervals (universal barrier relationship). b) Proportion of estimated gemsbok locations that lie a certain distance from the nearest barrier, with upper and lower confidence intervals.	63
Figure 12: a) Relationship between distance to nearest barrier and the density of springbok locations, with upper and lower confidence intervals (universal barrier relationship). b) Proportion of estimated springbok locations that lie a certain distance from the nearest barrier, with upper and lower confidence intervals.	64
Figure 13: a - e: Estimated number of Hartmann’s zebra telemetry locations per cell.	66
Figure 14: a - f: Estimated number of gemsbok telemetry locations per cell.	69
Figure 15: a - f: Estimated number of springbok telemetry locations per cell.	72

Figure 16: a - c: Hartmann's mountain zebra hotspots.	75
Figure 17: a - c: Gemsbok hotspots.	76
Figure 18: a - c: Springbok hotspots.	77
Figure 19: The identified barriers to ungulate movements in the GSNL.....	95

List of Tables

Table 1: Summary of collared animals in the Greater Sossusvlei-Namib Landscape.....	33
Table 2: Home range and core area sizes along with 95% confidence intervals and the minimum convex polygon (MCP) home range of fifteen collared Hartmann’s zebra	41
Table 3: Home range and core area sizes along with 95% confidence intervals and the minimum convex polygon (MCP) home range of thirteen collared gemsbok	42
Table 4: Home range and core area sizes along with 95% confidence intervals and the minimum convex polygon (MCP) home range of eleven collared springbok	43

List of Acronyms

AWT	Africa Wildlife Tracking
GSNL	Greater Sossusvlei-Namib Landscape
LMC	Landscape Management Committee
MCP	Minimum Convex Polygon
MEFT	Ministry of Environment, Forestry and Tourism
NAMPLACE	Namibia Protected Landscape Conservation Areas Initiative
NCE	Namibia Chamber of Environment
NNP	Namib-Naukluft National Park
PLCA	Protected Landscape Conservation Area
ST	Savannah Tracking

Acknowledgements

My special thanks go out to my supervisor Professor Morgan Hauptfleisch for guiding this thesis and giving his valued input, and to Lindesay Scott-Hayward, Senior Research Fellow at the Centre for Research into Ecological & Environmental Modelling at the University of St Andrews for the time and effort she put into assisting me with the statistical analysis part of the thesis. I could not have done it without them. I would like to acknowledge the Namibia Chamber of Environment (NCE) for the substantial financial assistance towards tuition fees, the GSNL initiative for permitting me to use the collar data, Murray Tindall, Control Warden, and Lee Tindall, Environment Warden of the NamibRand Nature Reserve and coordinators of the Greater Sossusvlei-Namib Landscape for all the collar-related information, insight and assistance throughout this study, which originally started as an Honours mini-thesis in 2016. And most importantly, my husband, mother, sister and friends who provided me with loving support throughout.

Abstract

Ungulate movements in arid environments are driven by rain events, food resources and surface water availability. In hyper arid areas such as the Namib desert these are patchily distributed, fluctuating and overall sparse. As a result, animals living in these environments are often highly mobile to exploit the ephemeral and spatiotemporally variable resources. In the past few decades, there has been growing recognition of the importance of habitat connectivity, and the detrimental effects of linear infrastructure on wildlife and their movements. One objective of the Greater-Sossusvlei Namib Landscape (GSNL) is to create a fence-free Namib and thereby facilitate the movement of wildlife between the Namib desert and the less arid Great Western Escarpment, which lies to its east. As mitigation measures are costly, identifying problematic road and fence segments where such measures could be applied effectively is a challenge. The movements of 40 ungulates were tracked in the GSNL, including 12 springbok (*Antidorcas marsupialis hofmeyri*), 13 gemsbok (*Oryx gazella gazella*) and 15 Hartmann's mountain zebra (*Equus zebra hartmannae*). The impact of linear barriers (including fences and roads) on their distributions and home ranges was investigated, and movement-limiting fence segments and roads were identified. In general, ungulate home range sizes were smaller in areas where there were physical barriers, including either roads or fences around land units. Roads and fences impacted ungulate movements considerably in some areas: these included the main roads C14 and C19 that run from the coast to Maltahöhe and from Solitaire to Maltahöhe respectively, several district roads, sections of the Namib-Naukluft fence, as well as livestock farm fences. While Hartmann's mountain zebra were able to cross some fences, springbok and gemsbok were not as successful, their movements sometimes being completely restricted within farms or along fences. Barriers had differential effects on ungulate distributions: gemsbok location densities and proportions were greatest approximately 3 to 5 km from any barrier. Hartmann's zebra location densities were generally close to barriers, and decreased with distance from the barrier, with the largest proportion of locations located within 1 km of the nearest barrier with another peak at 2 km. Springbok location densities and proportions were greatest less than 1 km, as well as between 3 to 5 km from barriers. These findings show that roads and fences play a substantial role in shaping animal distributions, and restrict the movements of individuals of all three species to varying degrees. The consequences of movement limitations are likely to worsen due to the effects of climate change in increasing rainfall variability.

Keywords: wildlife telemetry, range distribution, ungulates, linear infrastructure, barrier effect, arid environments, Greater Sossusvlei Namib Landscape, springbok, gemsbok, Hartmann's mountain zebra

Chapter 1: Introduction and literature review

1.1 Background

The Greater Sossusvlei-Namib Landscape (GSNL), located in the south-west of Namibia, is one of five Protected Landscape Conservation Areas (PLCAs) in Namibia, which were established under the Namibia Protected Landscape Conservation Areas Initiative (NAMPLACE). The project was initiated in 2011 by Namibia's Ministry of Environment, Forestry and Tourism (MEFT), and co-financed by the Global Environment Facility through the United Nations Development Programme (Smith 2016, Global Environment Facility n.d.). The objective of the project, which was completed in January 2019, was to establish the PLCAs, ensure that areas adjacent to existing protected areas are compatible with biodiversity conservation goals, and to establish corridors for wildlife populations (Global Environment Facility n.d.). The intention was that, after completion of the NAMPLACE initiative, the PLCAs should be able to continue their activities.

The PLCAs provide a platform for landscape members and stakeholders to address issues of common concern. Each PLCA is comprised of a State Protected Area at its core and adjacent areas with compatible land uses and shared biodiversity objectives. The management of each conservation area is achieved through collaborative management of landscape members and stakeholders (both private and public), which are represented by the Landscape Management Committee (LMC). The committee members are elected from the various stakeholder groups, including land owners and custodians, line ministries, tour operators, service providers and NGOs. The LMC oversees the implementation of landscape strategic management plans and annual workplans (Nam-Place Project n.d.).

The PLCAs extend the land that is under protection with an additional 15,550 km², of which the GSNL covers 5,730 km² (Nam-Place Project n.d.). The GSNL encompasses the state-owned Namib-Naukluft National Park (NNP) at its core and the adjacent freehold farms. Small-stock farming was the main land use before the freehold land was increasingly dedicated to biodiversity and landscape conservation (Ministry of Environment and Tourism n.d.). The majority of farms in this area now practice conservation and tourism land uses, which are compatible with the land uses of the national park (Southern African Institute for Environmental Assessment 2014). The NNP is one of the flagship and most visited parks in Namibia, with Sossusvlei constituting the main tourist attraction (Global Environment Facility n.d.).

The purpose of the GSNL is to enhance collaborative management between its members at a landscape level in order to strive towards ecological and biodiversity conservation goals, as well as to improve socio-economic development (Ministry of Environment and Tourism n.d.). One objective of the GSNL is to create a fence-free Namib and thereby facilitate the movement of wildlife between the Namib desert and the Great Western Escarpment, which lies to its east (Odendaal and Shaw 2010, Ministry of Environment and Tourism n.d.). This is currently achieved by the active removal of fences or by not maintaining the fences (Southern African Institute for Environmental Assessment 2014). The goal is to enable wildlife movements in response to rainfall events and food availability. When rainfall in the Namib plains is low or non-existent, wildlife can move towards to escarpment in the east and when there is good rainfall, they are able to move towards the Namib plains in the west (Ministry of Environment and Tourism n.d.). Freedom of movement will become all the more important in the light of climate change and the predicted increase in surface temperatures (James and Washington 2013, Engelbrecht *et al.* 2015). Wildlife will respond by shifting their distribution along climatic gradients (Schloss *et al.* 2012, Lawler *et al.* 2013), such as tracking shifts in suitable temperatures (Nuñez *et al.* 2013), and beyond currently established protected areas (Tabor *et al.* 2018, Malakoutikhah *et al.* 2020).

A baseline survey carried out by NAMPLACE in 2013 showed that 52% of farms in the GSNL were connected to the NNP due to removed or breached fences (Southern African Institute for Environmental Assessment 2014). A substantial portion of the landscape is already fence-free due to ongoing fence removals.

1.2 The applications and benefits of fences

The use of fences, which have benefits but at the same time can be detrimental to conservation efforts, is a matter of contention (Boone and Hobbs 2004, Creel *et al.* 2013, Packer *et al.* 2013, Jakes *et al.* 2018). Fences have been used since the Neolithic to separate resources, such as food and goods, from threats, including humans and predators (Hayward and Kerley 2009). Nowadays, fences are present almost everywhere and are continuing to proliferate (Cumming *et al.* 2015) due to anthropogenic activities (Løvschal *et al.* 2017). The benefit of fences is clear in some cases, such as in the management of publicly-owned resources in light of the “tragedy of the commons” (Hardin 1968).

There are many examples of extensive fences that have been built mainly in the twentieth century (Bradby *et al.* 2014), each with a specific application, including border, barrier, conservation, reserve, agricultural exclusion, road and veterinary cordon fences (refer to Smith *et al.* (2020) for definitions). Border fences are used for security purposes, for example to control the illegal movement of people (Linnell *et al.* 2016), such as at the USA-Mexico border or the fences erected in the EU to stem the influx of refugees (Linnell *et al.* 2016, Smith *et al.* 2020) and to curb wildlife and livestock movements (Gadd 2012). The boundaries of Botswana, South Africa, Mozambique, Zimbabwe and Namibia comprise vast stretches of fencelines made up of razor wire or electrified fencing (Gadd 2012).

Veterinary cordon fences (VCFs) are a characteristic feature of southern Africa's landscapes (Gadd 2012), and are constructed to limit the spread of diseases between wildlife and domestic animals, such as Foot-and-Mouth Disease (FMD) carried by the buffalo African buffalo *Syncerus caffer* (Boone and Hobbs 2004, Miguel *et al.* 2013, Thomson *et al.* 2013). Veterinary fences afford livestock producers in Africa the opportunity to access European markets by exporting disease-free beef (Boone and Hobbs 2004, Thomson *et al.* 2013). Examples of VCFs comprise the Northern and Southern Buffalo Fences for FMD control, and the Setata, Samochima, and Ikoga veterinary fences, constructed to halt the spread of Contagious Bovine Pleuropneumonia (CBPP) in the Okavango Delta of Botswana (Mbaiwa and Mbaiwa 2006); the 80 km veterinary fence along the southern boundary of Gonarezhou National Park, Zimbabwe (Dube *et al.* 2010); and the VCF or "red line" in northern Namibia, which separates areas free of FMD in the south from those that experience occasional outbreaks of the disease to the north of the fence, and is made up of a double game proof and stock proof fence (van Schalkwyk *et al.* 2010, Mannetti *et al.* 2019). Although VCFs are primarily a feature on the African continent, there are also a few examples of VCFs employed elsewhere, such as in New Zealand to halt the spread of bovine tuberculosis from brushtail possums *Trichosurus vulpecula* (Cown and Rhodes 1992), and in Canada to prevent the spread of bovine tuberculosis from wild elk *Cervus elaphus* and deer *Odocoileus virginianus* to cattle (Brook 2010).

Livestock and game fences are used to achieve management objectives and to increase productivity in the livestock farming (but see Salomon *et al.* 2013) and game ranching industry (Bothma and du Toit 2010, Oberem and Oberem 2016). In Namibia approximately 43% of the land is used for cattle and small-stock (sheep and goat) production in the country's centre and southern areas (Barnes and de Jager 1996, Erb 2004), with an estimated amount of 3,500 commercial farms (Lindsey 2011). Although the

exact extent of fences in Namibia is not known, this points towards an extensive network of fences due to commercial farming activities. In Namibia, the increased conversion of traditional livestock farms to wildlife-based land uses, such as ecotourism, hunting and wildlife production, was brought about by a change in legislation in the late 1960s giving landowners full ownership over huntable game (with the exception of protected game) (Joubert *et al.* 1983, Erb 2004, Lindsey 2011). This has resulted in an increased prevalence of wildlife-proof fences, which due to their height and/or electrification are much less permeable to wildlife than livestock fences (which are shorter and made up of five horizontal wires) (Weise *et al.* 2011). The Namibian Nature Conservation Ordinance 4 of 1975 confers private ownership over wildlife only if the piece of land in question is enclosed by a game-proof fence. Since this ownership and use right over huntable game requires the land to be enclosed with game-proof fencing, there is an increased move towards the division of freehold land (Lindsey 2011). This poses a problem for landscape-level conservation and counters MEFT's own policy to drive landscape conservation.

Fences are used to mitigate human-wildlife conflict (Lindsey *et al.* 2012), although they can also have the opposite effect. For example, when access to water is restricted by fences, animals may be forced to access water resources close to humans and their livestock (Gadd 2012). Barrier fences to exclude perceived pests, such as the so-called "vermin barrier fences" to restrict dingo and emu movements into farmlands in Australia (Bradby *et al.* 2014), are widespread (Smith *et al.* 2020). Other examples include the wire-mesh jackal-proof fences used by small-stock farmers in Namibia to control black-backed jackal movements (Cunningham 2019); and fences preventing wildlife, such as elephants and other herbivores, such as zebra and common eland from raiding crops in Asia and Africa (Davies *et al.* 2011, Gross *et al.* 2019). Japan (Huygens and Hayashi 1999) and North America (Geisser and Reyer 2004) also make use of so-called pest exclusion fencing. The objective of these fences is to prevent predation on livestock (Chardonnet *et al.* 2010, Cunningham 2019) and crop damage (Davies *et al.* 2011), which can constitute a considerable loss of income to landowners (Kerley *et al.* 2017), and to limit grazing competition between livestock and wildlife (Waters *et al.* 2020). Legal requirements, such as South Africa's Fencing Act of 1912 (Act 17 of 1912) and its Amendment of 1922 (Act 11 of 1922), made it mandatory for landowners to erect fences around their properties and to make these impermeable to so-called pests (Salomon *et al.* 2013), thereby contributing to an increase in impermeable barriers. By law, the construction of jackal-proof fences is a requirement in certain areas of Namibia (Erb 2004).

Reserve and conservation fences (Smith *et al.* 2020) are erected to protect wildlife and natural resources from human activities, by preventing disturbance, ecosystem degradation and harvesting (Lindsey *et al.* 2012) and to protect endangered species from the threats posed by humans, such as poaching (Hayward and Kerley 2009, Smith *et al.* 2020). Furthermore, the fencing of roads and highways is often suggested as an effective tool in preventing wildlife-vehicle collisions (Clevenger *et al.* 2001), although they can have the opposite effect of trapping wildlife within the road reserve (Eloff and van Niekerk 2005). Road fences also channel wildlife towards road under- or overpasses (Bissonette and Rosa 2012). As a result of these benefits, the monitoring and mitigation of fence impacts has not been a priority in the past (Ferguson *et al.* 2012) and even nowadays, the requirements for environmental impact assessments and the consultation of the public and environmental agencies are sometimes bypassed due to political interest and pressure (Gadd 2012, Bradby *et al.* 2014). In general, the increasing pressure for land and the increased development of rural and natural landscapes are contributing to a proliferation of fences (Linnell *et al.* 2016, Li *et al.* 2017, Løvschal *et al.* 2017).

1.3 The negative aspects of fences

As Smith *et al.* (2020) so aptly articulate, whether a fence is deemed good or bad is dependent on its intended purpose and which effects are examined. While the economic (especially agricultural) and ecological uses and benefits of fences are clear in some cases, there are several costs, either intended or unintended, associated with fences (Smith *et al.* 2020). These effects are experienced by both target species (i.e. those species whose movement fences are intended to restrict) and non-target species. Common intended effects of fences include separation (e.g. to prevent disease spread), exclusion of predators and pests, and redirection (e.g. of wildlife towards over- or underpasses), while unintended effects are numerous (see Smith *et al.* 2020 for a global review, and Lindsey *et al.* 2012 for a review of Africa).

Fences have several direct and indirect ecological effects (Taylor and Martin 1987, Jakes *et al.* 2018), which are either immediate or occur over long time spans (Gadd 2012). Direct negative impacts include injury and mortality due to entanglement of wildlife in fence wires (Rey *et al.* 2012). Fence entanglement has been reported for various ungulate species, including most African medium and large ungulates (Gadd 2012), North American ungulates, such as mule deer *Odocoileus hemionus*, pronghorn

Antilocapra americana and elk *Cervus elaphus* in (Harrington and Conover 2006) as well as other taxa such as reptiles (Ferronato *et al.* 2014) and birds (Ley and Tynan 2008).

Indirect effects on wildlife result in alterations to biology and behaviour (Jakes *et al.* 2018), at the individual or population level (Gadd 2012). If not planned according to conservation objectives, fences can fragment and isolate wildlife populations, thereby constituting a barrier to gene flow, and resulting in inbreeding, reduced individual and population fitness, and possibly population extinction (Jaeger and Fahrig 2004, Hilty *et al.* 2006, Ito *et al.* 2013, Ottewell *et al.* 2014, White *et al.* 2018, Smith *et al.* 2020). Fenced-off areas can lead to increased population density and overpopulation of species (Slotow *et al.* 2005, Welch and Parker 2016), with negative effects on resource availability as well as land degradation (Sinclair and Fryxell 1985, Taylor and Martin 1987), resulting in a decrease in carrying capacity and population declines, if not managed correctly (Hayward *et al.* 2007, Apio *et al.* 2015, Welch and Parker 2016, Moseby *et al.* 2018). Fences can also lead to changes in animal distribution, impacting the competitive balance of species in a guild and thus affecting community structures (Cozzi *et al.* 2013).

Fencing off parcels of land in heterogeneous landscapes decreases the variety of resources and thus the range of options that are available to herbivores, hence affecting herbivores in low quality or resource-poor patches negatively and decreasing the carrying capacity of land (Boone and Hobbs 2004). Fences can have ecosystem-level effects, as was the case in eastern Qinghai-Tibetan plateau region of China, where land use shifts and the construction of fences resulted in changed grazing behaviour of yaks *Bos grunniens* with knock-on effects to vegetation communities and ecological functioning (Li *et al.* 2017). Behavioural changes of wildlife as a result of fences have also been reported, for example the alteration of hunting behaviours by predators (Davies-Mostert *et al.* 2013). Examples are wolves' *Canis lupus* use of forestry fences in Poland to capture their prey (Bojarska *et al.* 2017) and the use of the Pilanesberg National Park boundary fence by wild dogs *Lycaon pictus* as an aid in trapping and capturing their prey (van Dyk and Slotow 2003).

Fence design (including height), fence type (e.g. use of electrification), alignment and extent are the main factors that influence the permeability of fences and provide challenges to wildlife movements (Gadd 2012, Dean *et al.* 2018, Jakes *et al.* 2018). In general, the degree of impenetrability of a fence has an impact on the severity of negative impacts on wildlife (Dean *et al.* 2018). Fences have different designs depending on the intended application and can be adapted to the animal they intend to keep in

or out, as species exhibit different fence behaviours (Bothma and du Toit 2010, Lindsey *et al.* 2012, Wilkinson *et al.* 2021). Some jump over fences (kudu, impala, eland), while others prefer to crawl underneath (warthog, duiker, springbok, gemsbok) or even break fences (African savanna buffalo, giraffe, blue wildebeest) (Bothma and du Toit 2010). Hence, the success of an animal moving across a fence is dependent on the fence design and the species in question (Boone and Hobbs 2004). This also means that fences have differential effects on species due to different fence behaviours: while a fence may constitute an impermeable barrier to some species, it may be permeable to other species (Cozzi *et al.* 2013). The life stage of the individual also plays a role. Harrington and Conover (2006) found that juvenile ungulate mortalities as a result of fencing were eight times more likely than adult mortalities.

Most fences are designed to restrict the movement of one or more target species, but may also have knock-on effects on the movement of other (non-target) species, such as the effects of veterinary fences on elephant movements (Cushman *et al.* 2010) or the effects of pest exclusion fences on reptiles (Ferronato *et al.* 2014). Fence height is a key risk factor (Rey *et al.* 2012). Furthermore, fence effects depend on the adaptability and learning ability of wildlife. For example, there is evidence that some animals are able to adapt their movement to fence constructions and are able to circumvent linear barriers, such as elephants (O'Connell-Rodwell *et al.* 2000). Another frequent phenomenon is that animals get funneled and trapped in fences that join at acute angles (Gadd 2012).

Another major issue is the extent of fencing. In Botswana alone, 5,000 km of fence line (including border fences) have been constructed for the cattle industry (Gadd 2012). Lastly, the alignment of fences is an issue, as it is often based on human, and not ecological, needs (Gadd 2012, Beale *et al.* 2013). The uses of fences to fulfil human needs have been discussed above, and include political boundaries (e.g. country borders) and national security, disease control, and existing land uses. In the same vein, protected areas, and even parks as large as the Kruger National Park (19,500 km²), frequently do not include the entire range of an animal and all its resource requirements (Bolger *et al.* 2008, Fynn and Bonyongo 2011, Beale *et al.* 2013). This is especially the case with migratory ungulates, where both the dry and wet season ranges, including the migration routes along which stop-overs take place, must be conserved and managed.

The emergence of linear anthropogenic barriers, including pipelines, railways, roads and fences has been identified as one of the major causes for the decline in large-scale movements of ungulates over the

past two centuries (Bolger *et al.* 2008). Fences obstruct the traditional seasonal migration of wildlife between rangelands and water, which is of utmost importance to their survival (Boone and Hobbs 2004, Mbaiwa and Mbaiwa 2006). Globally, large-scale movements of ungulates are at risk (Berger 2004, Harris *et al.* 2009) and as they are often transboundary, they present challenges to conservation (Middleton *et al.* 2020). The effects of fences as barriers to wildlife movements are the subject of various research articles and have been studied worldwide on a wide variety of ungulate species (Ellington 2007, Harris *et al.* 2009, Bartlam-Brooks *et al.* 2011, Bennitt *et al.* 2016, Ekernas and Berger 2016, Jones *et al.* 2019, Middleton *et al.* 2020). According to a study on equid migrations in Asia and Africa, extirpation of migrations was best explained by full or partial fencing of protected areas (Ekernas and Berger 2016).

Countless observations of negative fence effects on animal movements originate from the African continent. Anecdotal evidence exists for historical springbok *Antidorcas marsupialis* migrations in South Africa's Karoo, and the decline of these, which has been partly attributed to the construction of fences to protect grazing and water resources for domestic livestock (Roche 2008). It is especially in times of drought that negative effects on wildlife become evident (Boone and Hobbs 2004), as was the case in Botswana during the drought in the 1980s, which exacerbated the effects of veterinary cordon fences on migratory wildlife such as wildebeest (Parry 1987, Spinage 1992). The accelerated proliferation of fences in the Greater Mara ecosystem of Kenya, East Africa is threatening the migrations of animals, such as wildebeest, in this region (Løvschal *et al.* 2017), while the residency of subpopulations of Cape buffalo *Syncerus caffer caffer* in the Okavango Delta has been linked to VCFs (Bennitt *et al.* 2016).

1.4 The negative aspects of roads

Roads can have impacts on ungulates for various reasons, including ungulate-vehicle collisions (Seiler 2004), associated exclusion fences (Seiler 2004) and due to constituting semi-permeable barriers to animal movements (Sawyer *et al.* 2013). The field of road ecology, which is concerned with the ecological effects of roads and vehicles (Forman *et al.* 2003), has been playing an increasingly important role in conservation over the past three decades (Bullock *et al.* 2011, Bennett 2017). The negative impacts of roads have been shown to affect most classes of terrestrial animals due to collisions with vehicles, and the resultant mortalities have been quantified at local and regional scales in several papers (Caro *et al.* 2000, Hell *et al.* 2005, Bullock *et al.* 2011, Mkanda and Chansa 2011, Kambourova-Ivanova *et*

al. 2012, Collinson *et al.* 2015, Kioko *et al.* 2015, Chyn *et al.* 2019, Gandiwa *et al.* 2020, Rendall *et al.* 2021). Few road-related studies originate from the African continent compared to the rest of the world (most studies stemming from North America and Europe) (Bennett 2017).

The “road effect zone” describes the area adjacent to roads over which ecological effects and traffic are experienced (Forman and Deblinger 2000), which in turn influences the abundance and distribution of individuals inhabiting neighbouring areas (Bennett 2017). The size of the road effect zone and its severity is influenced by road characteristics (width and surface type i.e. paved or unpaved), traffic (intensity and speed), the environment of the adjacent landscape (including topography, vegetation, water), and the species characteristics and behaviour (van der Ree *et al.* 2015). The ecological effects on wildlife are not static, and can change with the seasons (Gagnon *et al.* 2007), as resources fluctuate and in turn affect daily and seasonal movements.

Roads block or filter the movement of wildlife, and lead to wildlife mortality or road avoidance (van der Ree *et al.* 2015), known as the barrier effect. The barrier effect of roads stems from several factors, including disturbances (due to noise and other pollution, anthropogenic activities, vehicle movement), the physical barrier and mortality due to collisions, all of which interact to reduce the number of successful crossings or to deter movement across the linear infrastructure altogether (Seiler 2003). Sawyer *et al.* (2013) highlight the effects of semi-permeable barriers on the behaviour of migratory animals. They found that migratory behaviour of mule deer was altered by the intensity and size of semi-permeable barriers associated with gas development in Wyoming. Notably, in areas with more intensive development, deer took detours from established migration routes, increased the rate of movement, and decreased stop-over use, while the surface area of the migration route and its use was reduced.

Barrier-related effects often work in unison: animals that avoid roads (and rarely cross them) experience low rates of wildlife-vehicle collisions and mortality, but are potentially affected by barriers to movement. On the other hand, species that are attracted to roads may be affected by higher mortality rates due to wildlife-vehicle collisions (or not, depending on how mobile they are) (van der Ree *et al.* 2015). The interplay between both proximity avoidance and low barrier permeability reduces the crossing frequency of roads substantially and together, makes roads an effective barrier to movement (Beyer *et al.* 2016). At the population level, roads can either result in the decline of genetic diversity due

to reduced gene flow (as a result of road avoidance) and reduced population size (caused by mortality) (Forman *et al.* 2003, Fahrig and Rytwinski 2009), with the latter having been identified as the main impact on genetic variation (Jackson and Fahrig 2011).

1.5 The move towards open systems

In the past few decades, there has been growing recognition of the importance of habitat connectivity, and the negative impacts of fences on wildlife movements (Linnell *et al.* 2016). In a workshop conducted by conservation practitioners from southern and eastern Africa, two of the ten lessons identified for management of savanna ecosystems was the importance of buffer zones and the conservation of movement corridors (Beale *et al.* 2013). Buffer zones are areas of compatible land use surrounding protected areas, such as the wildlife management areas in Botswana (Parry and Campbell 1990, Perkins 2019). These zones serve (among other purposes) as corridors for movement between suitable habitat patches (Caro *et al.* 2009, Beale *et al.* 2013).

An increased awareness of the importance of wildlife movement corridors (Riggio and Caro 2017, Naidoo *et al.* 2018) and landscape connectivity has resulted in increased efforts to reconnect landscapes (Linnell *et al.* 2016) and a shift of focus away from protected areas as the sole solution to conserve biodiversity (Belote *et al.* 2017). Protected areas on their own are often inadequate to sustain wildlife populations, as is the case with “gap species” (whose range does not overlap with protected areas) and “ecological refugee species” that are confined to unsuitable or poor quality habitat in conservation areas (Lea *et al.* 2016).

Globally, progress in restoring habitat connectivity for wildlife has been achieved through increased transboundary cooperation between neighbouring countries (Linnell *et al.* 2016), as observed in Europe with its European Green Belt conservation initiative (Schindler *et al.* 2011) and the Waterton-Glacier International Peace Park (between America and Canada) (Pouya and Pouya 2018). In Australia, conservation actions to increase connectivity have resulted in regional as well as sub-continental initiatives towards the establishment of corridors, such as the Gondwana Link initiative (Fitzsimons *et al.* 2013, Bradby *et al.* 2016). Several transfrontier conservation initiatives exist in Africa, such as the Great Limpopo Transfrontier Park (between Mozambique, South Africa and Zimbabwe), and the Kavango-

Zambezi Transfrontier Conservation Area (KAZA) (between Namibia, Angola, Botswana, Zambia and Zimbabwe) which spans over 444,000 km² (Pouya and Pouya 2018).

The move towards open systems has also occurred on more regional scales. The establishment of larger conservation areas by removing internal farm fences and cooperatively manage properties in order to enable wildlife movements and to achieve other ecological objectives has increased in southern Africa (Lindsey *et al.* 2008). The same has been observed in Namibia with its NAMPLACE initiative (Global Environment Facility n.d.). This has been fuelled by a move towards ecotourism and wildlife-based land uses due to their economic and ecological benefits, and the global comparative advantage that southern Africa enjoys related to these alternative land uses (Cumming *et al.* 2015). Solutions towards an increased landscape connectivity also include making fences more permeable, for example by creating fence gaps to enable animals to cross safely (Dupuis-Desormeaux *et al.* 2018).

The success of increased connectivity depends on how wildlife responds to the removal of fences and if newly accessible areas will be utilised (Druce *et al.* 2008, Dupuis-Desormeaux *et al.* 2018). For example, a study on elephant response to fence removal showed that they were slow in moving into new areas and their ranges only expanded slightly into new habitat after a year (Druce *et al.* 2008). After removal of a large section of fence line (1.5 km) and fence modification to make it more permeable to most species, a fence gap created prior to this removal/modification was still used extensively, demonstrating the high level of pathway fidelity displayed by wildlife (Dupuis-Desormeaux *et al.* 2018). Some evidence suggests that fence effects on wildlife movement behaviour may not be permanent and can be reversed, such as in the case of the zebra *Equus burchelli antiquorum* in Botswana (Bartlam-Brooks *et al.* 2013). A veterinary cordon fence, which existed between 1968 and 2004, bisected the historical migration route from the Okavango Delta to the Makgadikgadi area. Within a few years after the removal of the fence, the migrations of the younger zebra generations resumed, either due to the re-establishment of historical migrations or due to exploratory movements leading to renewed migrations into these novel area. However, although this means that animals may be flexible in deciding whether or not to migrate (as was the case with the zebra in Botswana), they may be less flexible in the choice of the migration route (Bracis and Mueller 2017). Flexibility depends on whether the knowledge of the migration route stems from plastic social learning or from genetically inherited memory.

1.6 Movement ecology and movement in arid environments

Movement, defined as a change in the spatial position of an organism over time, is a basic characteristic of life (Nathan *et al.* 2008). It can manifest itself in various ways: actively, passively, locally or over large distances. An animal's movement is linked to fitness outcomes (Liedvogel *et al.* 2013) in response to short-term goals, such as gaining energy, reproduction, and survival, including escaping predators and avoiding unfavourable environmental conditions, as well as long-term goals, such as inbreeding avoidance and population survival (Holyoak *et al.* 2008).

Movement not only determines the fate of the individual itself, but also that of entire populations, communities, ecosystems, and ultimately the diversity of life (Nathan *et al.* 2008). Nathan *et al.* (2008) developed a conceptual framework for movement ecology, with the goal of providing an integrative approach to understanding the causes and consequences of movement. The authors suggested four principal contributing factors to movement, each of these characterised by questions that are fundamental to movement studies, including i) the internal state (*why move?*), which includes an organism's physiological state and the proximate and ultimate goals of movement (energy acquirement, survival, reproduction), ii) motion capacity (*how to move?*), which entails the type of locomotion (self-propelled or externally influenced) and related biomechanics, (iii) the navigation capacity (*where to move?*), the ability of an organism to choose a direction and to know its location relative to its destination, and responding to information from direct or indirect cues or memory (from previous experiences or in some cases without previous experiences), and (iv) *which external factors affect the movement and how*, which includes biotic and abiotic environmental factors. These include resource distribution, landscape and physical factors, meteorological factors, as well as the relationship with other organisms (e.g. conspecifics, predators, interspecific competitors). External factors should also include anthropogenic impacts on the environment (Nandintsetseg 2019), such as fences. According to Nathan *et al.* (2008), an organism's movement path is controlled by the motion and navigation capacity relative to its internal state, and all three of these factors can be altered by external influences. Ultimately, all of these components interact and produce the observed movement path.

Understanding the driving factors and underlying processes of movement are central to addressing conservation concerns (Nathan *et al.* 2008). For example, individual-based simulation models showed that zebra migrations between the Okavango Delta and the Makgadikgadi grasslands are accurately

described by the use of memory and the utilisation of long-term averages of past resource conditions to predict future conditions (Bracis and Mueller 2017). The study suggested that these zebra migrations are controlled by genetically inherited memory and hence migration routes may be inflexible and fixed. Migratory animals relying on inherited directional information may not be able to take into consideration changed conditions caused by, for example, fences. Contrary to this, a reliance on information obtained and updated through social learning would allow the animal to adapt its route or destination. The findings of the zebra study show that conserving existing migration routes is all the more important for the protection of migratory species, especially in the face of habitat fragmentation and climate change, as they may be unlikely to use alternative routes.

Various types of movement exist - some are local in scale and are related to the daily activities of an organism to exploit resources (e.g. food, shelter and mates) while others occur on larger scales. Often one species can exhibit several types of movement in their lifetime (Dingle 2014). Although movement patterns are sometimes difficult to distinguish (Dingle 2014) and the utilisation of movement terms is often variable among movement ecologists (Nathan *et al.* 2008), several categories can be identified. Range residency (Mueller *et al.* 2011) or station-keeping (Dingle 2014) occurs when an animal resides in its home range. This includes foraging (movement in search of resources), commuting (movement in search of resources on a regular short term basis, and territoriality (Dingle 2014). An exploratory movement that takes place when an animal leaves its current home range in search of a suitable new home range within its habitat is called ranging. Ranging (in some literature referred to as “dispersal”), much like migration, may in some cases cover large distances (Dingle 2014). All the aforementioned movements are stimulated by a shortage of a resource, are proximately triggered and cease as soon as the resource has been located.

Migration occurs when an animal pre-emptively moves out of its current habitat into a new habitat, usually at some distance. The key characteristic is a suppression of responses to resources while migration is taking place, as opposed to ranging, where such responses are not inhibited (Dingle 2014). Animal populations can be partially migratory, where some individuals migrate while others are sedentary, or differentially migratory, where individuals (often of different ages or sex) migrate different distances. Another movement pattern, nomadism, is long-distance, but occurs in an uncoordinated fashion among individuals and is unpredictable in timing and direction (Mueller and Fagan 2008).

While migratory movements are characterised by predictable seasonal movements, nomadic movements are temporally and geographically unpredictable (Mueller and Fagan 2008, Jonzén *et al.* 2011). Nomadism occurs in environments with unpredictable and spatiotemporally variable resources, where animals track patchily distributed resources over large distances (Fryxell *et al.* 2004, Roshier *et al.* 2008, Mueller *et al.* 2011). Although nomadism is not as well studied as other types of movement (Olson *et al.* 2010), several examples of nomadic ungulates around the world have been suggested in literature. These include Arabian sand gazelle *Gazella marica* (Cunningham and Wronski 2011), Arabian oryx *Oryx leucoryx* (Tear *et al.* 1997), Mongolian gazelle *Procapra gutturosa* (Olson *et al.* 2010), Thomson's gazelle *Gazella thomsoni thomsoni* (Fryxell *et al.* 2004), as well as gemsbok *Oryx gazella gazella* (Furstenburg 2016a).

Nomadism has been suggested as the primary movement type in arid environments with spatially and temporally variable resources (Olson *et al.* 2010, Mueller *et al.* 2011). Nandintsetseg (2019) contrasts water-dependent nomadic movements from forage-dependent nomadism. The author suggests that the former is driven by temporal changes in spatially static water resources, where animals revisit previously visited areas frequently, while the latter is driven by spatiotemporal variations in forage availability, where animals move long distances and infrequently visit previously visited areas.

The primary influencing factors on wildlife movements in arid environments are rain events, food resources and surface water availability (Fennessy 2009). Arid environments, commonly classified as areas receiving less than 250 mm annual rainfall (Ward 2016), are controlled by water input as a key factor in stimulating biological processes (Noy-Meir 1973). These water inputs or rain events occur as infrequent and discrete events that have a large unpredictable component (Noy-Meir 1973) and food resources in these environments are likewise patchily distributed, fluctuating and overall sparse (Rubenstein 1989, Dingle 2014) due to the strong correlation between primary productivity and precipitation (Seely 1978a). As a result, animals living in arid environments are often highly mobile to exploit the ephemeral and spatiotemporally variable resources (Noy-Meir 1973, Dingle 2014). Furthermore, factors such as runoff, slope and aspect, temperature, soil texture and groundwater seepage and their interactions influence vegetation growth (Noy-Meir 1973, Laity 2008) and hence can be expected to influence ungulate movements. Although the effect of rainfall pulses act on a local scale, they are in turn driven by global events, such as the El Niño-Southern Oscillation (ENSO) (Goudie and

Viles 2015, Ward 2016). Further nutrition-related drivers of spatial distributions of ungulates include plant mineral and nutrient content (McNaughton 1988).

1.7 Home range studies

Animals that are tracked serve as proxies for monitoring the impacts of anthropogenic activities and modified landscapes on animal populations (Loarie *et al.* 2009). An animal's position in space can provide insights into the animal's adaptations to its environment and give reasons as to why an animal has chosen to be more active in certain areas (Cagnacci *et al.* 2010). Cagnacci *et al.* (2010) highlight the importance of using GPS-based radio-telemetry to understand key theories of animal ecology, including the concept of home ranges.

Burt (1943) defines a home range as the area over which an animal travels in order to obtain resources required for survival, to carry out reproductive activities and to rear its offspring. He suggests that occasional exploratory ventures outside the area should not be viewed as part of the home range and that areas used as home ranges can change within an animal's lifetime. This also applies to migratory animals that can have different home ranges depending on the season (Burt, 1943). Burt's definition of the term has been criticised as it is difficult to evaluate and quantify (Powell 2000, Mitchell *et al.* 2012). Powell (2000) highlights that different species display diverse ways of using an area with different behaviours, yet in all cases the area can be recognised as a home range. Nevertheless, Burt's definition prevails as the basis of many home range estimators (Powell and Mitchell 2012) and is the most commonly used in the literature on home ranges (McLoughlin and Ferguson 2000, Börger *et al.* 2006, Jerina and Leslie 2012).

A home range is a spatial expression of the decisions taken by an animal in order to gain resources necessary for survival (van Moorter *et al.* 2009). Studying an animal's home range gives important insights into mating patterns, social structures, and feeding habits (Powell 2000). As home ranges encompass all the resources utilised by their occupants, studying them improves knowledge on the ecological needs of an animal, as well as the influence of a variety of factors on animal spacing and movements (Seaman and Powell 1990). This knowledge can feed directly into management and conservation decisions for the animal under study (e.g. Linnell *et al.* 2001).

A variety of determinants influences the size and location of an animal's home range, including the animal's body size which corresponds to its metabolic rate (McNab 1963, Swihart *et al.* 1988), sex (Burt 1943), food availability (Brown and Orians 1970, Tufto *et al.* 1996), water availability (McKee *et al.* 2015), climate (Lindstedt *et al.* 1986), topographical constraints due to costs of locomotion (Powell and Mitchell 1998), landscape heterogeneity and structure (Saïd and Servanty 2005, Massé and Côté 2012), reproductive status of females (van Beest *et al.* 2011) and population density and risk of predation (Desy *et al.* 1990).

Great strides in movement research have been made with the advent of telemetry (the remote measurement of data) and the tracking of animal movement by collecting time-indexed data of an animal's location (Cooke *et al.* 2004). This progress is reflected in the massive influx of high-resolution movement data (Fagan *et al.* 2013) and the enormous amount of research papers and literature focusing on movement (Holyoak *et al.* 2008). Technological advances in telemetry studies, such as global positioning system (GPS) transmitters, have enabled movement studies across a range of taxonomic groups (Holyoak *et al.* 2008), giving rise to location datasets that are more precise than those collected using very high frequency (VHF) technology (Walter *et al.* 2015).

The collection of location data at high sampling frequencies, which is enabled by GPS-based technology, gives rise to highly autocorrelated datasets (Kays *et al.* 2015). Serial autocorrelation poses one of the greatest challenges pertaining to home range estimation methods (Noonan *et al.* 2019), as it results in negatively biased home range sizes (Swihart and Slade 1985). The most commonly used home range estimators, including the kernel density estimation (KDE) and minimum convex polygon (MCP) methods, make the critical assumption of statistical independence of location data (Worton 1989, Noonan *et al.* 2019). This assumption of independence is violated if location data are collected at short time intervals. Due to the importance of home range studies to management decisions and towards ecological studies, it is important to take into account serial autocorrelation in order to avoid possible negative implications stemming from biased range estimates.

1.8 Study species

In the following section, the current knowledge regarding Hartmann's mountain zebra (*Equus zebra hartmannae*), gemsbok (*Oryx gazella gazella*) and springbok (*Antidorcas marsupialis hofmeyri*) will be

explored, with particular focus on their distribution, adaptations, diet and water requirements, home ranging and movement behaviour, as well as the drivers of their movement.

1.8.1 Hartmann's mountain zebra *Equus zebra hartmannae*

The mountain zebra belongs to the family Equidae in the order Perissodactyla (Skinner and Chimimba 2005). Two subspecies of mountain zebra are recognised: the Cape mountain zebra *Equus zebra zebra* (Linnaeus 1758) and the Hartmann's mountain zebra *Equus zebra hartmannae* (Matschie 1898) (Novellie *et al.* 2002, Skinner and Chimimba 2005). The Hartmann's mountain zebra still occurs throughout much of its historical range (Novellie *et al.* 2002), which is confined to Namibia, with a marginal extension into Angola (in the Iona National Park) and the Northern Cape, South Africa (Skinner and Chimimba 2005, Gosling *et al.* 2019). In addition, the range of this water-dependent species has expanded into previously unsuitable habitat due to the proliferation of artificial water points as well as some introductions outside of their range (Novellie *et al.* 2002).

The largest proportion of the Hartmann's zebra population in Namibia occurs on commercial farms, followed by communal conservancies, while only a quarter of the population is present in protected areas (Novellie *et al.* 2002, Moodley and Harley 2005). One of the largest sub-population occurs in the Naukluft area of the Namib-Naukluft National Park, making it an important protected area for this species (Novellie *et al.* 2002, Gosling *et al.* 2019). Hartmann's zebra on commercial farms are more vulnerable during droughts than those in other land ownership type, due to direct competition with livestock and human-wildlife conflict (Joubert 1973, Gosling *et al.* 2019). They are considered as "problem animals" by farmers and hence have been subject to persecution, especially during past droughts (Joubert 1973, 1974).

The Hartmann's zebra is listed as vulnerable on the IUCN Red List of Threatened Species and is classified as Specially Protected Game under the Nature Conservation Ordinance 4 of 1975 of Namibia, its consumptive utilisation being subject to permit control (Gosling *et al.* 2019). It is also listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Gosling *et al.* 2019). Hartmann's zebra populations have recovered steadily due to increased protection and community- and private-based conservation of the subspecies (Moehlman *et al.* 2016), as well as due to their economic value as a result of their consumptive (trophy hunting and sale of tanned skins) and non-consumptive (ecotourism) use (Novellie *et al.* 2002). Nevertheless, a catastrophic drought and

resulting mortalities in combination with over-harvesting, especially on freehold conservancies and commercial farms, is identified as the main threat to the persistence of future populations (Gosling *et al.* 2019).

Hartmann's zebra primarily inhabit the escarpment that separates the dry Namib desert and coastal plain in the west and the wetter inland plateau to the east (Gosling *et al.* 2019). Their habitat is the ecotone of this mountainous escarpment region and the adjoining plains (Skinner and Chimimba 2005), with a preference for the foot slopes of mountains (Bothma and du Toit 2010). It has been suggested that, along with vegetation type, the presence of permanent water (artificial waterholes and natural springs) is a contributing factor to the distribution and preference of Hartmann's zebra for the escarpment zone (Joubert 1973, Gosling *et al.* 2019).

There is some anecdotal evidence that Hartmann's zebra are affected by fences, such as the veterinary cordon fence in the north of Namibia along which large mortalities of the Hartmann's zebra occurred during a drought in the 1980s (Gosling *et al.* 2019). Nevertheless, it is able to use permanent openings or gaps created by other animals or by rivers to cross fences (Gosling *et al.* 2019).

Hartmann's zebra are water-dependent (Skinner and Chimimba 2005, Bothma and du Toit 2010) and thus, as for all equids, the distribution of water has a strong influence on movement patterns and space use of this species (Schoenecker *et al.* 2016). Muntifering *et al.* (2019) found that Hartmann's zebra usually stayed within 4 km to permanent water sources, and even closer during the dry season, which emphasises the importance of being able to access permanent water sources. In areas where Hartmann's zebra are undisturbed, they drink at any time of the day, while they usually drink in the late evening or early morning in areas where they are hunted (Joubert 1972a). They drink daily, sometimes twice daily, especially during the hot, dry summer months (Joubert 1972a). They dig for water in areas where surface water is not available (Skinner and Chimimba 2005). Observations of Hartmann's zebra showed that they display several behavioural adaptations to avoid water loss, including aligning the bulk of grazing activities in summer to times of the day where temperatures are lowest; orienting their bodies in a way that reduces the exposure of their dark stripes to the sun; and using trees for shade intermittently (Joubert 1972a).

Hartmann's zebra are short-grass, non-selective grazers and bulk roughage feeders (Skinner and Chimimba 2005, Bothma and du Toit 2010), and need to consume large quantities of grass (Gosling *et al.* 2019). The daily distance covered by the zebra subspecies is variable and depends on availability of grazing and season (Joubert 1972a). They have been reported as being sedentary in some areas, only traveling an average of 1 to 3 km daily to graze and a maximum of 5 km to water points (Joubert 1972a). On the other hand, some literature refers to the migratory nature of Hartmann's zebra movements, and that separate summer and winter ranges are observable (Joubert 1972b, Gosling *et al.* 2019). This type of movement is apparent in areas where their movement is not entirely restricted (Joubert 1972b) and is in response to resource availability: in the dry season, the Hartmann's zebra range in the mountains where they follow ancient trails to rainwater pools, and move back to the plains in the rainy season until the grazing deteriorates (Joubert 1972a, P.J. Viljoen as cited in Skinner and Chimimba 2005). In the Otjovasandu area, which lies at the extreme west of the Etosha National Park, summer and winter areas were 120 km apart (Joubert 1972b). The seasonal movement of Hartmann's zebra was also observed in the Naukluft area, where they ranged in the northern part of the Naukluft mountains when seasonal pans formed during the rainy season (Joubert 1972b). Once the water in the pans dried up, they dispersed again over the entire mountain range to areas where perennial waterholes exist. Due to some individuals moving long distances to separate seasonal ranges, Gosling *et al.* (2019) maintain that Hartmann's zebra should be classified as a migratory species.

A study of collared Hartmann's zebra in the Kunene region of Namibia showed that mean seasonal home range sizes were larger in the wet season (681 km²) than in the dry season (256 km²) (Muntifering *et al.* 2019). Hartmann's zebra moved approximately 5 km per day, with no significant differences between seasons. There was a distinctive shift in home ranges in response to seasons, but the degree of seasonal home range overlap was variable among different individuals. Hartmann's zebra were found to select for areas with high primary productivity and hence high-quality grazing. The authors also found that Hartmann's zebra selected areas close to permanent water sources, usually not ranging more than 4 km from water sources and even less (2 km) in the dry season. They were also found to select for areas closer to roads. Joubert (1972b) reports winter home range sizes of 6 – 10 km² in the Daan Viljoen Game Reserve, and 10 – 20 km² in the Etosha National Park. Summer home range sizes were reported to be considerably smaller. The author also found that breeding units displayed a preference for specific areas in the summer and winter, to which they returned repeatedly, and Hartmann's zebra tended to be

sedentary on these summer and winter ranges. In Etosha, seasonal ranges were 120 km apart. Range sizes are as large as 200 km² where unrestricted (Bothma and du Toit 2010).

The social organisation of Hartmann's zebra is based on two distinct herd structures: the breeding unit (harem), composed of one adult stallion having exclusive dominance over a number of females with or without foals, and the bachelor group, which consists of immature males that become sexually mature during the time of association with the group (Joubert 1972b). The bachelor groups are a reservoir of sexually mature males for replacement of dominant males in harem groups, while some may also form their own harem groups. Mountain zebra are not territorial (Penzhorn 2013).

1.8.2 Gemsbok *Oryx gazella gazella*

The gemsbok *Oryx gazella gazella* (Linnaeus 1758) belongs to the tribe Hippotragini and, like springbok, form part of the subfamily Antilopinae (Skinner and Chimimba 2005). The ungulate is restricted to the southern African subregion, including Namibia, Botswana and South Africa, with a marginal extension into western Zimbabwe (Skinner and Chimimba 2005), but absent from its former range in Angola (East 1999). In Namibia, they are still widespread in their former range, with large populations occurring on private lands as well as in protected areas, but naturally absent from the north and north-east of Namibia (Skinner and Chimimba 2005). *Oryx gazella* is genetically distinct from the Beisa Oryx (*O. beisa*) from East Africa (Osmers *et al.* 2012).

Gemsbok are primarily grazers (van Zyl 1965, Leuthold 1977, Bothma and du Toit 2010), occasionally feeding on dicotyledons (Leuthold 1977), and are classified as highly selective grazers (Bothma and du Toit 2010) or selective grass and roughage feeders (Skinner and Chimimba 2005). They show flexibility in their diets, evidenced by an increased consumption of browse material when grass cover is minimal (Dieckmann 1980), especially in dry spells (Hamilton *et al.* 1977) or when they are restricted to marginal habitats characterised by limited grass resources (Dieckmann 1980). They are non-migratory (Skinner and Chimimba 2005) and opportunistically utilise vegetation that is patchily distributed, an important strategy in desert environments (Kreulen 1985, Kilian 1995). The antelope travels long distances to areas with a green flush of vegetation after rainfall (Coetzee 1969).

Gemsbok are water-independent (Bothma and du Toit 2010). A study on gemsbok in the Kalahari region of Botswana showed that they were frequently active in areas more than 20 km away from potential

sources of water (Boyers *et al.* 2019). In the Namaqualand, which is characterised by winter rainfall, gemsbok were not observed at water points during winter, nor were their tracks found around waterpoints (Dieckmann 1980).

They are well adapted to arid regions characterised by high temperatures and low precipitation (Knight 2013). Behavioural adaptations are the key to their ability to survive in these desert environments (Knight 2013) and include being more active during the night in the hot seasons than in the cooler seasons and avoiding the heat of the day by seeking out cool microclimates (Boyers *et al.* 2019). Furthermore, gemsbok feed on roots, tsama melons and underground tubers that have a high moisture content to supplement their water intake (Williamson 1987). Morphological adaptations include a pelage that reflects heat (Knight 2013). Based on experiments on captive gemsbok, it is widely held that the species employs adaptive heterothermy, the prevention of water loss during evaporative cooling by raising the body temperature, and selective brain cooling due to the carotid rete when exposed to high temperatures (Taylor 1969). Studies on free-ranging gemsbok do not support the findings (Maloney *et al.* 2002, Fuller *et al.* 2004). It is hypothesised that the phenomenon of fluctuating body temperatures occurs as a result of hyperthermia induced by dehydration, while selective brain cooling serves a thermoregulatory function while resting (Maloney *et al.* 2002, Mitchell *et al.* 2002).

Gemsbok habitat comprises mainly open arid to semi-arid grasslands (Knight 2013). Similar to springbok, gemsbok occupy all habitat types of the Namib desert, including the Pro-Namib, gravel plains and sand dunes (Coetzee 1969). However, they frequent rocky outcrops and the slopes of canyons more commonly than springbok do. They are the only large herbivores that are resident in dunes, where they browse on the dominant succulent shrub *Trianthema hereroensis* at the base of dunes and on the coarse grass *Stipagrostis sabulicola* higher up the dune slope during the dry season (Nott and Savage 1985). Gemsbok commonly occur on the gravel plains when there is vegetation after localised rainfall events (Coetzee 1969).

Aerial surveys carried out by Kilian (1995) showed that the Haiber plains of the Pro-Namib support a large gemsbok population, where their distribution is influenced by the vegetation on sandslope substrates mainly occurring along large granite outcrops or mountains. Kilian (unpublished data, as cited in Kilian 1995) found that gemsbok in the Koichab plains of the Namib-Naukluft Park disperse north to the shrub-coppice dunes and south to the winter rainfall region in prolonged dry periods. These

movements are in response to the availability of perennial grasses in the former and dicotyledonous vegetation in the latter habitats (Kilian pers obs, as cited in Kilian 1995). In the Namaqualand, gemsbok frequented features such as drainage lines and ephemeral streams during the dry season, where green vegetation was available longer, while concentrating on the plains and flatter areas due to the appearance of ephemerals in the wet season (Dieckmann 1980).

During March to August, gemsbok in the central Namib graze on the patchily distributed grasses on the plains and dunes in the Namib desert after scattered seasonal rains, and subsequently retreat to ephemeral rivers, such as the Kuiseb, in the dry season (when food on the plains and dunes is depleted) to browse on the *Acacia albida* leaves and consume *A. albida* pods when browse becomes limited (Hamilton *et al.* 1977). This movement pattern may be enhanced in periods of limited rainfall on the plains and dunes (Hamilton *et al.* 1977). The dietary change to foods with less moisture content is accompanied by an increased need for free water, resulting in the excavation of waterholes (and intraspecific competition) in the dry Kuiseb riverbed. Tarr and Tarr (1989) noticed a similar movement pattern of wildlife from the plains to river beds, especially of gemsbok into the Hoanib river in search for shelter from the heat and for *Acacia albida* pods. Gemsbok in the Kgalagadi and Gemsbok National Park displayed a more resident pattern of movement, with relatively stable ranges, although females in the waterless Gemsbok National Park did shift their movement towards water sources in the dry season (Knight 1991).

Gemsbok occur in mixed herds, nursery herds, and as territorial males, some being solitary and others occurring along with mixed or nursery herds (Dieckmann 1980). Herd sizes differ depending on the availability and nutritional value of food resources (Dieckmann 1980). They congregate in large numbers after rainfall, and as food resources become less abundant and more unevenly dispersed, the large gemsbok herds break up into smaller herds (Dieckmann 1980). Territorial males show a degree of tolerance towards other males, but have absolute dominance over non-territorial males in the social hierarchy of mixed herds. They display herding behaviour, and mating is performed by the territorial males, while rarely carried out by bachelor males (Dieckmann 1980).

Territory and home range sizes of gemsbok vary according to environmental factors and the carrying capacity of the veld (Dieckmann 1980). Territory sizes ranged between 14 – 30 km² in the Southern Kalahari (Knight 1991). The minimum territory sizes of five males in the Namaqualand (Northern Cape,

South Africa) ranged between 4 to 10 km² (Dieckmann 1980). The territory boundaries were not well defined, but were delineated by natural and artificial features, such as koppies, drainage lines and roads. It was found that the core activity areas of territories were sandy and open with sparse vegetation and at least one water point, either natural or artificial. Males eventually leave their territories and join mixed herds after periods of solitude (Skinner and Chimimba 2005). However, according to observations, one gemsbok individual retained its territory for three years (Knight 1991). Non-territorial bulls range over large areas, up to 3,600 km² (Knight 2013).

1.8.3 Springbok *Antidorcas marsupialis*

The springbok *Antidorcas marsupialis* (Zimmermann 1780), a medium-sized antelope is found in the arid regions and grasslands of southern Africa (Skinner and Chimimba 2005, Skinner 2013, Castelló 2016). Its distribution is confined to Namibia, Botswana and South Africa, with a narrow extension into southwestern Angola. It is wide-spread in Namibia, only being absent from the country's north-eastern region (Skinner and Chimimba 2005, Skinner 2013). The order Ruminantia includes both oryx and springbok from the tribes Hippotragini and Antilopini respectively, both of which form part of the subfamily Antilopinae in the Bovidae family (Skinner and Chimimba 2005). Although the classification of springbok into subspecies is debated (Robinson 1975, Peters and Brink 1992, Oberem and Oberem 2016), three subspecies are generally recognised, of which *A. m. hofmeyri* is found in the study area (Skinner and Chimimba 2005, Bothma and du Toit 2010).

Springbok habitat choice is influenced by the availability of nutritious vegetation, mineral content of food and height and density of vegetation (Bigalke 1972). Its habitat comprises the semi-desert scrub of the Kalahari, Karoo and open pan veld, dune pathways, dry river beds and grassy plains (Skinner and Chimimba 2005, Bothma and du Toit 2010, Oberem and Oberem 2016). Springbok are ubiquitous in all habitat types of the Namib desert, including the pro-Namib and gravel plains, along dune streets and river beds, and to a lesser extent the rocky outcrops and canyons (Coetzee 1969). Classified as intermediate feeders (Hofmann *et al.* 1995) with a tendency to becoming concentrate selectors in optimal forage conditions (Skinner and Chimimba 2005), the springbok diet consists of browse, short grasses, forbs and succulents (Bothma and du Toit 2010, Oberem and Oberem 2016). They consume mainly grasses and forbs in summer and browse more in winter and during droughts (Bigalke 1972, Hofmann and Stewart 1972, Davies *et al.* 1986, Hofmann 1989, Apps 2012).

Springbok can survive, at least temporarily, in areas lacking surface water (Bigalke 1972). They are generally water-independent (Bothma and du Toit 2010), provided that they can obtain sufficient moisture from their diet (Nagy and Knight 1994). In a study on captive springbok, Greenwald (1967) established that food moisture content must be greater than 10% in order for a springbok to be water independent, while Nagy and Knight (1994) found that free-ranging springbok in the Kalahari desert required a diet containing at least 67% water in order to survive without drinking. Some desert plants in habitat occupied by springbok can adsorb moisture when conditions are humid and cool (even when the air is unsaturated) (Louw and Seely 1982). Therefore it is possible that springbok (as well as gemsbok) increase their water intake when feeding at night or the early morning. Despite their water independence, springbok will drink if free water is available. Based on field observations in the Etosha National Park in Namibia, as well as in the Kalahari Gemsbok Park and on farms in South Africa, Bigalke (1972) found that drinking occurred indiscriminately of time of day and season, but that it stopped after rain and during cold weather. Observations in the Kalahari Gemsbok National Park showed that springbok drink once every 1 – 2 days, and sometimes more frequently (Bigalke 1972).

Springbok have several morphological and physiological adaptations that aid in conserving water, including an efficient digestive system and kidney function, as well as a low field metabolic rate (Hofmeyr and Louw 1987, Nagy and Knight 1994, Hofmann *et al.* 1995). Springbok supplement their moisture requirements by selecting foods with a high moisture content, such as wild melons and cucumbers, fruits, succulents, roots and bulbs (Nagy and Knight 1994, Bothma and du Toit 2010, Apps 2012). However, these adaptations may not be sufficient to maintain a water balance at all times, especially in confined areas like game camps (Skinner *et al.* 1986), and during droughts, which can cause high mortality rates in springbok (Bothma and du Toit 2010).

Springbok are fine-tuned to rain events and display opportunistic mobility, travelling to areas where rain has occurred and feeding on the actively growing, green vegetation that they show a preference for (Skinner and Louw 1996, Bothma and du Toit 2010), and then dispersing or moving elsewhere when resources are depleted (Bigalke 1972, Skinner and Chimimba 2005, Bothma and du Toit 2010). Springbok are gregarious, assembling in large numbers in summer to feed on the patchily distributed green vegetation that appears after localised rainfall events (Bigalke 1972). In the drier winter months, springbok form smaller, dispersed herds (Bigalke 1972). Herds can either be mixed, consisting of adults and juveniles of both sexes, or bachelor herds of mostly mature adult males (Bigalke 1970). Females

break away from mixed herds at the onset of lambing (Skinner *et al.* 1974). The home range sizes of ewe herds are variable, and depend on the season and food availability (Bothma and du Toit 2010). According to Furstenburg (2016b), family herds stay in fixed home ranges between 300 – 800 hectares in size.

Only territorial springbok rams are sedentary and do not respond to rainfall events in the same way (Skinner and Chimimba 2005). Rams are territorial in late summer and autumn and remain on their territories for as long as sufficient food is available, abandoning their territories at the end of the dry season when resources are depleted or in periods of extreme resource scarcity (Bothma and du Toit 2010, Skinner 2013). However, they show great fidelity, returning to their territories after the first summer rains (Skinner 2013). Territories are chosen according to the best available grazing (Bothma and du Toit 2010), thereby attracting ewes (Skinner and Chimimba 2005). The territory sizes of territorial males vary in the literature, and evidently depend on the region as well as on resource availability. According to Bothma and du Toit (2010), the sizes can vary between 2 – 6 ha (0.02 – 0.06 km²). Kingdon and Hoffman (2013) report territory sizes in the Kgalagadi Transfrontier Park as being 0.2 km² (20 ha) during times with sufficient food availability, but up to five times larger during dry spells, while Apps (2012) reports the territory sizes of breeding rams as being between 1 – 17 ha in the same area. Territories are much larger in the North West Province of South Africa (25 – 70 ha) (Apps 2012).

Springbok sporadically moved in mass migrations or so-called “treks”, a phenomenon that largely seized by the end of the nineteenth century, most likely due to anthropogenic factors and the spread of rinderpest (Skinner and Louw 1996, Skinner and Chimimba 2005). The trigger for these mass movements is disputed, but was likely a combination of high population density and lack of resources due to overgrazing or drought (Skinner and Louw 1996).

1.9 Research motivation and problem statement

An assessment of the first set of collar data was conducted by Mendelsohn (2014), and Mendelsohn and Mendelsohn (2014). This study was limited in scope and geography, and therefore by combining these data with the data collected under my study, a better picture of movement across the entire southern Namib was possible.

Only seven extant species of wild equids can be found today, including the mountain zebra (Moehlman *et al.* 2016, Ransom and Kaczensky 2016). Although populations of the Hartmann's mountain zebra subspecies have shown a marked recovery in their numbers in the last decade and harvesting is currently at sustainable levels, the effects of future droughts could lead to a reduction of a third of the future population within the next three generations, especially if harvesting numbers are not adjusted accordingly (Gosling *et al.* 2019). This effect is exacerbated by fragmentation of habitats as a result of barriers, such as roads and fences, which can cause a decline in populations, by eliminating access to forage and water (Moehlman *et al.* 2016). Nevertheless, their ranging behaviour and the effects of barriers on Hartmann's zebra have been little researched. Springbok and gemsbok are economically important to the wildlife industry in southern Africa (Skinner and Chimimba 2005, Relton *et al.* 2016) due to their trophy value (Humavindu and Barnes 2003) and for their meat (Bothma and du Toit 2010, Lindsey *et al.* 2013). Both species are classified as "least concern" with an increasing population trend for the former (IUCN SSC Antelope Specialist Group 2016) and stable for the latter (IUCN SSC Antelope Specialist Group 2020). Yet, a step-wise decline in gemsbok numbers in the GSNL following successive dry periods has been reported (Global Environment Facility n.d.). This decline has been attributed to the strong fence that was built along the eastern boundary of the NNP in the 1980s, resulting in the inability of wildlife to pursue their historical east-west movements (Global Environment Facility n.d.). Despite this, so far very few studies have attempted to quantify the effect of roads and fences on gemsbok and Hartmann's zebra movements (Muntiferung *et al.* 2019, Lehmann *et al.* 2020), with no known studies conducted with springbok.

Roads and fences entertain a wide range of ecological effects. The study of the former has given rise to the field of road ecology (Forman *et al.* 2003, Coffin 2007), which has been at the receiving end of much empirical research. While the direct mortality of wildlife due to wildlife-vehicle collisions is the most widely acknowledged impact of roads, as it relates to public safety (Bennett 2017), other more indirect effects on animal movements are much less studied (Seiler 2003), especially on a landscape scale (Bennett 2017) and where it pertains to road avoidance or the "road effect zone" (Forman *et al.* 2003). The ecological impacts of fences have received far less attention than those of roads, despite being more ubiquitous in some landscapes, and despite posing unique challenges to wildlife movements due to their vertical structure (Jakes *et al.* 2018). This research project seeks to contribute to empirical research of fence ecology particularly for dryland ecosystems (Durant *et al.* 2015). Furthermore, not much has been done in terms of fence research in Namibia, whereas its neighbouring countries South

Africa and Botswana have received the bulk of research on fence ecology in Africa (McInturff *et al.* 2020).

Lastly, most literature related to anthropogenic impacts on wildlife movements focuses on migratory animals and large scale wildlife migrations (Harris *et al.* 2009, Bartlam-Brooks *et al.* 2011, Poor *et al.* 2012, Seidler *et al.* 2015, Naidoo *et al.* 2016, Sawyer *et al.* 2016, Middleton *et al.* 2020). Few studies focus on animals that are not necessarily migratory and display movements that are less predictable in time and space, such as those of nomadic animals in arid and hyper-arid environments (Ito *et al.* 2013, Nandintsetseg *et al.* 2019).

The GSNL is ecologically important as a transitional zone between the Namib desert and the adjacent escarpment. Known as the Pro-Namib ecotone, wild ungulates utilise its grazing resources (and that of the Namib) when rainfall allows for sufficient grass production. This grazing is normally insufficient to sustain large herds or ungulates, forcing them into the adjacent escarpment, where they compete with domestic livestock for grazing, are persecuted by farmers and are impeded by a dense fence network. As a result, the GSNL initiated a research project to investigate the movement patterns by wildlife in response to barriers.

The conservation of animal movements and the mitigation of barrier effects can be partly achieved by identifying solutions that can be controlled. These include, but are not limited to, reducing the amount of fences by removal, making fences wildlife-friendly and hence more permeable, constructing wildlife crossings at roads, and by adapting these solutions to be local and site-specific (Ekernas and Berger 2016). In order to apply these solutions, which are often costly and resource-intensive (Huijser *et al.* 2009), it is essential to identify the problem fences or roads to ensure effectiveness as was revealed by previous studies (Burkholder *et al.* 2018, Jones *et al.* 2020) and to target problematic barriers for a cost-effective use of available financial resources/funds. Animal tracking via GPS telemetry is an invaluable tool to rise up to this challenge faced by land and wildlife managers.

1.10 Research Objectives

The overall aim of the study was to quantify the effect of fences around landholdings and along roads on the movement patterns of Hartmann's mountain zebra (*Equus zebra hartmannae*), gemsbok (*Oryx gazella gazella*) and springbok (*Antidorcas marsupialis hofmeyri*) in the GSNL.

This was achieved through completion of the following objectives:

- Carry out home range analyses and compare home range sizes between individuals and between species;
- Investigate if hotspots of animal occurrence are identifiable and relatable to barriers; and
- To model and quantify the effect of linear barriers (including fences around landholdings and along roads, as well as roads) on the distribution of the study species' (the so-called "barrier effect")

Based on the results, a map, which shows the problematic fence and road segments for which mitigation measures could be prioritised, was produced and recommendations for the mitigation of barrier effects were made.

Chapter 2: Methods and study area

2.1 Description of the study area

The Greater Sossusvlei-Namib Landscape is located in the Hardap and Erongo regions of Namibia (Fig. 1) and includes the large 49,768 km² Namib-Naukluft National Park (NNP) at its core as well as a number of neighbouring farming and tourism establishments (Global Environment Facility n.d.). The landscape focal area, which encompasses the landholdings adjoining the NNP and is the area where most of the collared animals occur, is wedged between the Great Western Escarpment to the east and the Namib Sand Sea to the west, in the so-called Pro-Namib (Coetzee 1969, Odendaal and Shaw 2010, Seely and Pallett 2012). The landholdings constitute various types of land uses, including tourism, commercial livestock farming (both cattle and small-stock), and game farming, as well as private reserves, including the Tsondab Valley Scenic Reserve to the north and the NamibRand Nature Reserve in the south of the GSNL (Landscape Members n.d.). The NamibRand Nature Reserve extends over an area of 172,200 ha (Odendaal and Shaw 2010). The reserve, which is made up of former livestock farms rehabilitated into a continuous fence-free area, is bordered by the NNP in the west and the Nubib mountains in the east.

The study area incorporates primarily the Namib plains and the adjoining escarpment, with some animal ranges extending into the Nama-Karoo Basin and Namib-Naukluft mountains (Mendelsohn *et al.* 2002). Four zebra individuals range in the Central-Western Plains north of the Kuiseb river (between the Kuiseb and Swakopmund rivers). Habitats include vegetated dune belts, sand and gravel plains, mountains, and isolated inselbergs with wind-blown vegetated sand along their margins (Seely and Pallett 2012, Global Environment Facility n.d.). The Central-Western plains are made up of gypsum and gravel covered areas, with hills and rocky outcrops (Goudie and Viles 2015). The Great Escarpment, which runs along southern Africa from Mozambique to southern Angola, includes mountain ranges such as the rugged and deeply dissected Naukluft (Goudie and Viles 2015) and Zaris mountains (Seely and Pallett 2012). It forms the western boundary of the adjoining interior plateau (Lancaster 2002). The main soil types linked to the study area include lithic Leptosols and poorly developed eutric Regosols to the east of the Namib Sand Sea, as well as petric Calcisols and rocky outcrops primarily in the central Namib desert (Mendelsohn *et al.* 2002).

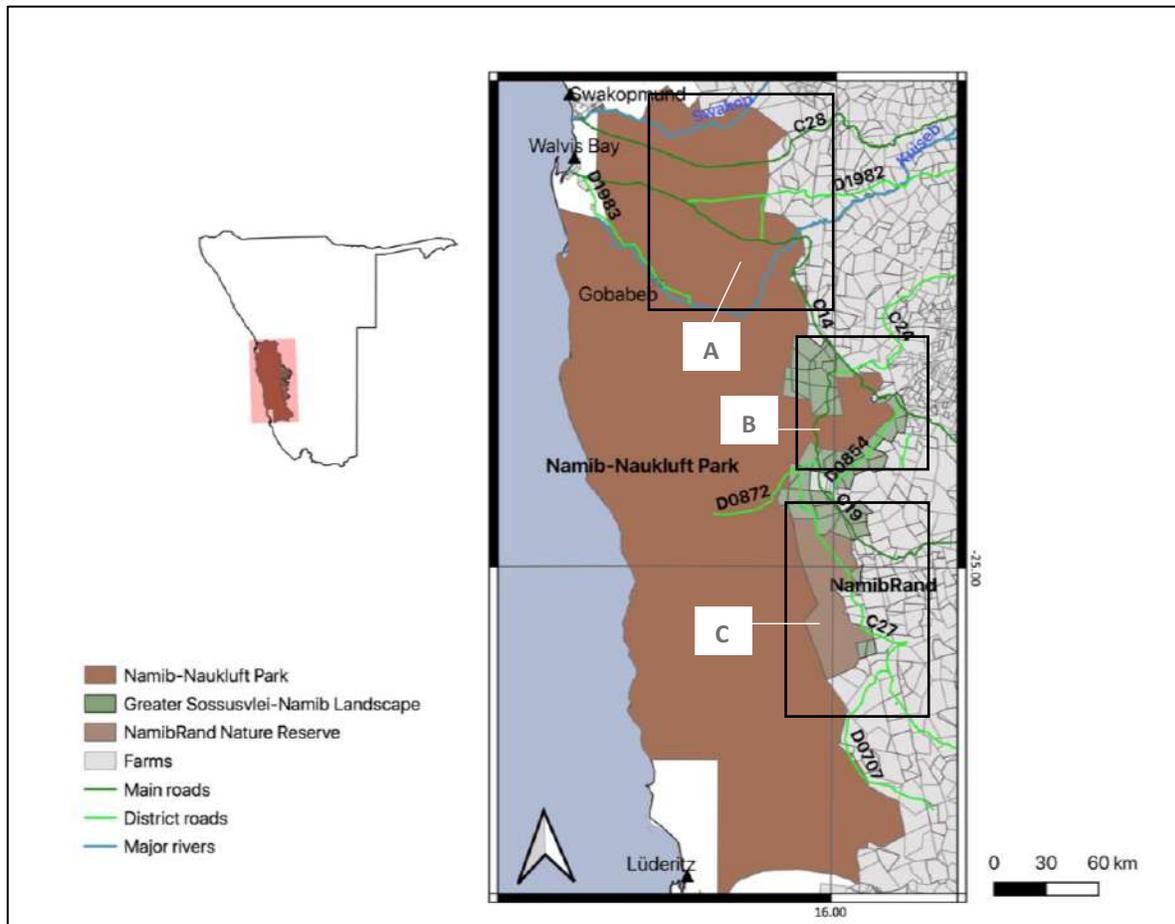


Figure 1: Map of the Greater Sossusvlei-Namib Landscape, including the NamibRand Nature Reserve, and the Namib-Naukluft Park. The study area was divided into three regions: north (A), mid (B) and south (C).

Some collared individuals penetrate into the extensive dune fields of the Namib desert. The desert occurs as a narrow coastal strip, about 120 - 200 km wide, that is bounded by mountain ranges of the Great Escarpment to the east and the Atlantic ocean on the west (Goudie and Viles 2015). It extends over a distance of 2,000 km along the Atlantic coast of southern Africa (Laity 2008). The Namib is a coastal desert (Laity 2008), which has primarily formed as a result of the cold offshore Benguela current and its cooling effect on air masses (Ward 2016). This cooling effect reduces the capacity of air masses to hold moisture and hence results in little or no rainfall (Ward 2016). The extensive dune field of the Namib Sand Sea, which is a UNESCO World Heritage Site, covers an area of approximately 34,000 km² (Goudie and Viles 2015) and stretches for 400 km south of the Kuisseb river to Lüderitz (Laity 2008).

The Namib desert gradually changes from hyper-arid to arid in a west to east direction (Lancaster 2002, Rohde *et al.* 2019). The study area primarily lies below the 100 mm median annual rainfall isopleths,

excepting the Naukluft mountains that lie between the 100 - 150 mm isopleths (Global Environment Facility n.d.). Coastal areas of the Namib receive little rainfall (e.g. 15 mm annually at Walvis Bay) while annual rainfall towards the base of the escarpment may exceed 200 mm (Goudie and Viles 2015). Thus, a rainfall gradient that generally increases from west to east is apparent (Seely 1978b) with some exceptions such as the Haiber plains, which are located south and east of the Sesriem and Awasib shrub-coppice dunes respectively (Kilian 1995). The observed lack of an east-west rainfall gradient is likely due to the topographical features of granite outcrops and mountains in this area, which have an impact on the distribution of rainfall and runoff (Günster 1995).

Rain in the central Namib falls mainly in late summer (January to April) (Lancaster 2002). This summer rainfall pattern continues southwards to Sesriem, and gradually changes to a combination of both summer and winter rainfall at Aus (Kilian 1995). The summer rainy season is followed by a dry season (May to August) (Henschel *et al.* 2005). Nevertheless, rainfall is extremely erratic (Seely and Pallett 2012), and occurs in discontinuous pulses of relatively short duration, which are variable in time and space, as well as in magnitude and duration (Noy-Meir 1973, Henschel *et al.* 2005, Goudie and Viles 2015). Fog is the main source of moisture in the hyper-arid coastal areas of the Namib and shows an inverse trend to rainfall, as it decreases from the coast inland (Lancaster *et al.* 1984, Laity 2008). It constitutes an important source of moisture for some plants, for example the endemic grass *Stipagrostis sabulicola*, which grows on dunes and harvests fog to supplement its water requirements (Ebner *et al.* 2011), and animals (such as the tenebrionid beetle) living in the Namib desert (Whitford and Duval 2020). Fog seldom penetrates into the study area and hence does not play a major role.

The GSNL focal area, situated mainly in the Nama-Karoo biome, is characterised by the desert/dwarf shrub transition with sparse annual and perennial grass cover interspersed with occasional shrubs, while the area between the Kuiseb and Swakop rivers is dominated by Namib grasslands of the central desert, as well as sparse shrubland of the central western escarpment and inselbergs (Mendelsohn *et al.* 2002, Harper-Simmonds *et al.* n.d.). Vegetation cover is generally sparse, except along ephemeral rivers and shallow washes, which support taller plants and trees (Joubert 1973, Goudie and Viles 2015, Harper-Simmonds *et al.* n.d.), as well as in the proximity of rocky outcrops which have a higher grass cover (Günster 1995). However, flushes of annual grasses briefly cover the gravel plains after sufficient rain has fallen (Laity 2008, Global Environment Facility n.d.).

Several ephemeral rivers occur in the study area and constitute important linear oases for flora and fauna (Jacobson *et al.* 1995). They flow only sporadically, their flooding being caused by rainfall over the inland mountain ranges (Jacobson *et al.* 1995, Jacobson and Jacobson 2013). The Tsauchab and Tsondab rivers drain endorheically into the Sossusvlei and Tsondabvlei pans in the Namib Sand Sea respectively (Seely and Pallett 2012, Goudie and Viles 2015). Both of these rivers do not penetrate further west, while the Kuiseb river reaches the Atlantic occasionally following sufficient rains over the Khomas Hochland. The Tsauchab, which originates to the east of the Naukluft mountains and passes through the Sesriem Canyon, only reaches the Sossusvlei in exceptionally wet years (Goudie and Viles 2015). Perennial sources of surface water due to groundwater discharge, including seeps and pans, (Viles and Goudie 2013), several hypersaline springs on the gravel plains of the central Namib desert, such as Hosabes and Ubib (Day and Seely 1988, Brain and Koste 1993, Day 1993, Eckardt *et al.* 2013) exist in the study area, as well as springs in the Naukluft mountains (Global Environment Facility n.d.). Several artificial water sources and permanent waterholes are located in the GSNL, in the mountainous escarpment zone, and in the central Namib gravel plains, which are utilised extensively by wildlife (Coetzee 1969, Joubert 1973, Kok and Grobbelaar 1985, Mendelsohn *et al.* 2002).

The study area was divided into three regions (north, mid and south). The north region encompasses the fenceless central area of the Namib-Naukluft Park, bound by the Swakop and Kuiseb rivers. The mid region encompasses the Naukluft area of the Namib-Naukluft Park (also fenceless), as well as landholdings to the north, and the Sesriem area to the south. The south region includes the NamibRand Nature Reserve and adjacent national park to the west, which do not contain any fences. The mid and south regions of the study area contain frequent barrier encounters, mostly due to cattle and sheep farm inner and outer fences adjacent to the national park and private nature reserve. Main roads and district roads run across the study site, the majority to the east of the national park.

2.2 Animal collaring

Forty-one animals were collared between November 2013 and May 2018, including 12 springbok, 14 gemsbok (of which one collar did not transmit any data) and 15 Hartmann's zebra (Table 1, Appendix A). The majority of collars were sourced from Africa Wildlife Tracking (AWT) (www.awt.co.za), while six collars used on springbok were manufactured by Savannah Tracking (ST) (www.savannahtracking.com). AWT collars fitted on springbok, gemsbok and zebra weighed approximately 500 g, 900 g and 1.2 kg

respectively (S. Haupt, personal communication, 25 August, 2016) and contained both GPS and VHF features. The ST collars fitted on six springbok weighed 400 g (Dr. H. Rasmussen, personal communication, 11 February, 2020).

The deployment of collars was performed by a wildlife veterinarian from the Ministry of Environment, Forestry and Tourism (MEFT) under a valid research permit. Only gemsbok females were collared, to attempt the tracking of herds and not just individuals. However, both Hartmann’s zebra males and females were collared as males do not display territoriality. Even though springbok males can be territorial, mostly males were collared as they are physically more robust and therefore better suited for collaring. Only one springbok female was collared. The choice of individuals was based on size and body condition of the animals. Hence, only fully grown, adult animals were collared (M. Jago, personal communication, 6 February 2020). Although not an ideal situation, the difficulty to access many parts of the landscape, and the infrequency of sightings of wildlife led to the collaring being less selective than if only one sex was collared for comparison. However, since the movement patterns following resources are expected to outweigh social and territorial behaviour, the selection of individuals was considered adequate.

Animals were darted and immobilised using thiafentanil and ketamin in different dosages, administered by a pneudart RDD 3cc 1 ¼ inch barbed needle through a model 389 projector from a helicopter, and reversed with naltrexone (M. Jago, personal communication, 6 February 2020). The collaring procedure was kept to a minimum of 15 minutes. Permissions to deploy collars and enter the Namib-Naukluft Park were provided by MEFT. After immobilisation, the animals recovered fully.

*Table 1: Summary of collared animals in the Greater Sossusvlei-Namib Landscape (F = Female / M = Male).**

Species	No. of individuals			Tracking duration (days)	No of signals
	F	M	Total		
Springbok	1	11	12	3124	11242
Gemsbok	13	0	13	9106	27526
Hartmann's zebra	5	10	15	8452	31331
Total	19	21	40	20682	70099

*Note: The collar of one gemsbok was faulty and did not transmit data.

All collars used the iridium satellite system to collect and transfer location data. The end of data collection was determined by either the failure of the collars due to a depleted battery, or the mortality of the individual. The collection of location data for nine individuals was terminated due to mortality, of which seven were springbok. Collar 1767 was faulty from the beginning and no data were available for that gemsbok. The data set from collar 132 was divided into two data sets, as this collar was re-fitted on another springbok after the collar was retrieved. The data set was renamed to collar ID SAT132.2. Satellite collars SAT1107 and SAT1769 belonged to the same individual (i.e. the same gemsbok was collared twice), with an eight-month interruption between collaring. Each of the collars was equipped with a VHF transmitter which aided collar recovery at the end of the GPS/Iridium lifespan.

2.3 Data screening and preparation

As the data sets gathered from AWT and ST collars were in different formats, the data sets were transformed to an identical format by using the same column headings for each variable collected. The columns “sex” and “species” were added to the data sets and populated. Any extraneous columns representing variables that were not analysed were removed. After all data sets were in an identical format, the excel files were re-saved in a csv format for further analysis.

Based on the recommendation of Dechen Quinn *et al.* (2012), the first two weeks of post capture data were removed from the data sets, in order to take into account the effects of capturing, handling and collaring on animal behaviour and post capture movement rates. Fixes that continued to be collected after a mortality occurred were removed from the data sets. Each data set was visually inspected to determine whether a mortality had occurred or if the collar battery had reached its end of life. If towards the end of the data set several location fixes overlapped, a mortality was assumed and all overlapping fixes but the first were removed.

Further cleaning of collar data was undertaken in the software R version 3.6.2 (R Core Team 2019). Each data set was plotted and outliers (i.e., location points located outside of the study area) were identified and removed. The package T-LoCoH (Lyons *et al.* 2019) was used to remove duplicate fixes. The data sets were subsequently reprojected from the World Geodetic System (WGS) coordinate system EPSG:4326 WGS 84 to the Universal Transverse Mercator (UTM) coordinate system EPSG:32733 – WGS 84 / UTM zone 33 South to convert the coordinate units to meters.

The shapefile of farm boundaries was obtained from the NUST shapefile archive. Topological errors in the farm shapefile were cleaned in the open source GIS application QGIS version 3.10.3 (QGIS development team 2021) in the following steps: i) the features in the attribute table with areas equal to zero were removed ii) the tool “snap geometries to layer” in the Processing Toolbox was used to remove sliver polygons and invalid geometries (with a tolerance of 15 m and behaviour set to “snap to anchor mode (single layer only)”) and iii) to check if all topological errors had been removed, the core plug-in “Check Geometries” was used and remaining errors (overlaps and gaps) were cleaned using a value of 30 map units squared. A map was provided by the GSNL in which the status of fences in the landscape were indicated. All fences that have been taken down were removed from the shapefile, using the “Aggregate” tool in the Processing Toolbox. The output was a layer with merged polygons, which was subsequently combined with the original farm layer, and used for further analysis.

2.4 Home range analysis

The method as outlined by Estevinho Santos Faustino (2020) was used for home range analysis and all models were fitted using the R package MRSea v1.02 (Scott-Hayward *et al.* 2017). This method was used as it accounts for the autocorrelation in sequential location data (Estevinho Santos Faustino 2020). The data for each tag were turned into presence-absence data by randomly selecting absence locations from the bounding box of the tag locations plus 2 km in every direction. These pseudo-absences were selected at a ratio of 5 absences : 1 presence.

The model fitted to the data was a binary generalised additive model with presence as the response and smooth covariate relationships (B-splines) for altitude, distance to water and distance to barrier. In addition, a spatially adaptive two-dimensional smooth of coordinates (Gaussian radial basis) was used to mop up any unmodelled patterns from the environmental covariates. The flexibility of the 1D and 2D smooths was chosen using SALSA with Bayesian Information Criterion (BIC) as the fitness measure. As the location points are correlated in time, a panel structure (year-month), was used to calculate robust standard errors.

Predictions were made to a 500m x 500m grid in the region specific to each tag. Owing to the pseudo-absence generation, the predictions are relative probabilities of presence. The uncertainty of the predictions was estimated using a parametric bootstrap of the model coefficients (1,000 replicates) and

the robust variance-covariance matrix. The bootstrap predictions were used to get 95-percentile-based confidence intervals for the home range and core areas. Springbok st2010-2800 was tracked for 15 days only and hence its home range and core area size of 4 km² and 2 km² respectively was excluded from calculations of the mean and standard deviation, as well as from further discussion regarding home range analysis.

Minimum convex polygons (MCPs) were computed for each individual using the R package *adehabitatHR* (Calenge 2006). A home range computed with this method contains a user-defined percentage of locations from the original data (in this study, 100% locations were used) that makes up the smallest convex polygon (Worton 1995, Noonan *et al.* 2019). The MCP approach is criticised as it is based on the assumption that location data are independent and identically distributed (Noonan *et al.* 2019). However, this assumption of independence is violated if location data are collected at short time intervals, as is often the case with modern telemetry studies. These studies frequently use tracking devices that collect location data at higher sampling frequencies and thereby result in highly autocorrelated data sets (Kays *et al.* 2015). Furthermore, the MCP method is sensitive to outliers, dependent on the sample size (increases with increasing sample size), incorporates areas that individuals may not visit due to its incorrect biological assumption of a convex home range shape (Worton 1995). The MCP method was utilised solely for the purpose of comparison with other ungulate home range literature, as the MCP is the most common home range estimator used in ecological studies (Harris *et al.* 1990, Laver and Kelly 2008).

2.5 Modelling of barrier effects on animal distribution

In this paper, barriers are defined as farm fences, as well as district and main roads. The effects of linear barriers on animal distribution and movement was termed the “barrier effect”. The term is well-known in the field of road ecology, and refers to the reduced movement of wildlife across roads as a result of unsuccessful crossings due to wildlife-vehicle collisions, or the avoidance of roads due to changed or deterring conditions (noise, pollution, traffic, or degraded habitat) (van der Ree *et al.* 2015). As the presence or absence of fences was not known for the majority of roads, no comparisons of the barrier effect of roads enclosed by fences with the barrier effects of roads lacking nearby fences could be made. Hence, the observed effects on animal distribution could not be attributed to the presence of roads specifically or the presence of fences. However, as the motivation of the study was to determine which

barriers affected animal movements (and not to determine the reason for the observed effect), this was deemed irrelevant.

Three distinct geographic regions of data were identified and labelled as “North”, “Mid” and “South”. The data set was split by species and rasterised using a 500 m x 500 m grid covering the three regions. The number of tag locations and distance to the nearest barrier were recorded in each grid cell. Modelling as per the below methodology was carried out using the MRSea Package in R (Scott-Hayward *et al.* 2017).

The modelling methodology is based on the premise that the distribution of each animal, for each species, is driven by a complex mix of environmental factors alongside some possible inhibition by one or more of the fences or roads between farms (barriers). For this reason, the analysis was focused on quantifying the effects of any fences, using models which explicitly partition any barrier effects from any underlying environmental factors which might be driving their distribution spatially.

The barrier effects were estimated by fitting a model with terms for both environmental and barrier-related effects. The geo-referenced predictions of this model were subsequently compared with geo-referenced predictions based on the scenario where no barrier-related effects are explicitly present. In this alternative reality, the distribution patterns are solely driven by a complex mix of environmental factors alone, which were captured flexibly using a spatially adaptive two-dimensional smoother. The modelling results are effectively ‘data-driven’ and the approach used does not impose or induce any kind of barrier-related effects. Indeed, if no barrier-related effects exist in the data, then the model will reflect this by evidencing no statistically significant differences in the geo-referenced predictions with and without any barrier-related effects. This approach also permits the magnitude of any barrier-related effects to be quantified and accompanied by confidence intervals which are adjusted for the longitudinal nature of the data. This provides some context to the extent of any barrier-related effects and if they pose a serious block to movement.

For each species, across each of the regions with data present, a Poisson-based count model was fitted with two terms: a one-dimensional smooth function (B-spline) based on the distance to the nearest barrier and a two dimensional smooth term using the Complex Region Spatial Smoother (CReSS) to permit a spatially adaptive surface. The response, y , was number of tag locations per cell and the

covariates were distance to nearest barrier and coordinate space (Easting and Northing). The error structure for the model was quasipoisson, which assumes a more flexible mean-variance relationship compared with a strict Poisson model. The function

$$y_i = \beta_0 + \sum_{j=1}^J \beta_j B(\text{mindistToBarrier})_i + \sum_{k=J+1}^K \beta_k C(x.\text{position}, y.\text{position})_i$$

was used, where B is a spline basis function and C is a gaussian radial basis.

Geo-referenced predictions were created based on a 500m x 500m grid for inspection and diagnostics for each model were carried out to ensure the fitted models are credible. For each species, a simpler model was fitted, which only includes barrier-related effects. Based on this simpler model, geo-referenced predictions were created each time for comparison with the predictions based on the full model. Based on a parametric bootstrap resampling exercise for each model, the difference between the predictions was calculated under each model and a 95% confidence interval was built for the difference in the distribution maps with and without the barrier. This enabled the identification of barrier areas which do not conform to the univariate barrier relationship.

2.6 Hotspot analysis

Location data were combined for each species and further analysis was carried out in QGIS. A 1,000 x 1,000 m grid was placed over each species' data set and the count points in polygon tool in the processing toolbox was used to calculate the number of location points in each 1,000 x 1,000 m polygon. A hotspot analysis was carried out (one for each species) with the hotspot analysis plugin in QGIS using the Local Getis-Ord G_i^* statistic, the gridded animal locations with the count column, a default fixed distance band to ensure at least one neighbour. A queen's case contiguity matrix was used, so that anything with an edge or corner touching is considered a neighbour (Getis and Aldstadt 2004).

The hotspot analysis plugin is useful for exploratory data analysis and the detection of spatial autocorrelation (Ord and Getis 1995, Oxoli *et al.* 2018). The Getis-Ord G_i^* method detects clusters of statistically significant low values (coldspots) and high values (hotspots) using the average of the calculated G_i^* test statistics for the entire dataset. It is a test for spatial randomness: if the neighbourhood is significantly different from the study area, it means that the observed pattern is not

random and the feature is marked as a coldspot or hotspot (depending on high or low value), and if it is not significantly different, the observed pattern is random. Satellite maps showing topographical information, as well as fences and roads were superimposed to identify any possible association of these with location hotspots.

Chapter 3: Results

3.1 Home range analysis

Collared animals ranged in NamibRand Nature Reserve, as well as in the Namib-Naukluft National Park to the west and the north, and privately owned farmland of the Rant, Naukluft and Tsaris mountains to the east of the GSNL. A comparison of estimated home ranges of collared individuals showed that there was great variability in home range sizes between species, as well as between individuals in each species (Table 2 – 4, Figure 2 and 3). Gemsbok and particularly Hartmann's zebra home range sizes were more variable compared to springbok home range sizes (Figure 2 and 3).

In general, springbok ($n = 11$) had the smallest mean estimated home range, which was $139.8 \text{ km}^2 (\pm 96.1)$ with a mean core area of $43.0 \text{ km}^2 (\pm 29.4)$ (Table 4, Figure 2 and 3). This was followed by Hartmann's zebra ($n = 15$) with a mean estimated home range size of $236.4 \text{ km}^2 (\pm 240.5)$ and mean core area of $74.3 \text{ km}^2 (\pm 79.8)$ (Table 2, Figure 2 and 3). Gemsbok ($n = 13$) had the largest mean estimated home range size with $282.5 \text{ km}^2 (\pm 289.7)$, which was almost double the size of springbok home ranges, and a mean core area of $86.4 \text{ km}^2 (\pm 81.8)$ (Table 3, Figure 2 and 3). The MCP sizes followed the same trend (Table 2 – 4): Gemsbok had the largest MCP size of $766.1 \text{ km}^2 (\pm 837.8)$, followed by Hartmann's zebra with $579.8 \text{ km}^2 (\pm 508.9)$, and springbok with $406.2 \text{ km}^2 (\pm 298.9)$.

Home ranges of collared individuals ranged (from smallest to largest) between 15.0 km^2 of a male springbok (SAT133) and $1,120.5 \text{ km}^2$ of a male gemsbok (SAT1770). Gemsbok SAT1770 and Hartmann's zebra SAT1092 had home ranges that were larger than all the other individuals ($1,120.5 \text{ km}^2$ and 925.5 km^2 respectively) (Table 2 and 3, Figure 2 and 3). Springbok SAT133 and st2010-2803 (Table 4), gemsbok SAT1101 and SAT1106 (Table 3), and Hartmann's zebra SAT1094, SAT1099 and SAT1100 (Table 2) had the smallest home ranges. These were, in ascending order: 15.0 km^2 (SAT133), 33.0 km^2 (SAT1106), 42.5 km^2 (st2010-2803), 46.0 km^2 (SAT1099), 62.8 km^2 (SAT1100) and 65.0 km^2 (SAT1101).

Table 2: Home range and core area sizes along with 95% confidence intervals and the minimum convex polygon (MCP) home range of fifteen collared Hartmann's zebra (all areas are given in km²). N = number of predicted locations. Green highlighted = largest modeled home range / orange highlighted = smallest modeled home range.

Hartmann's Zebra ID (Sex: M/F)	Location	Tracking duration (days)	N	Estimated Home Range	Lower 95% HR	Upper 95% HR	Core Area	Lower 95% CA	Upper 95% CA	100% MCP
Mean (±SD)				236.4 (±240.5)			74.3 (±79.8)			579.8 (±508.9)
SAT1092 (F)	GSNL (Central Namib – north of Kuiseb)	585	8160	925.5	867.8	985.8	315.8	288.0	347.3	1701.5
SAT1093 (F)	GSNL (Central Namib – north of Kuiseb)	650	7679	476.8	452.2	510.8	149.0	141.0	161.3	1249.7
SAT1094 (M)	NNP (Naukluft area)	730	1230	63.8	57.5	72.8	17.5	16.3	20.5	134.4
SAT1095 (M)	NNP (Naukluft area)	466	4430	133.0	122.3	218.1	50.5	48.0	68.0	457.5
SAT1096 (M)	NRNR (Nubib mountains) / farmland	485	1871	74.5	68.3	88.0	26.0	24.8	28.5	171.4
SAT1097 (M)	GSNL (Central Namib – north of Kuiseb)	649	10917	521.0	469.7	590.8	154.3	143.0	175.5	1421.0
SAT1098 (M)	GSNL (Central Namib – north of Kuiseb) / Farmland	670	4493	326.5	297.0	361.8	84.5	78.5	95.3	879.4
SAT1099 (F)	NNP (Naukluft area)	380	1065	46.0	43.3	51.0	16.3	15.5	17.8	81.3
SAT1100 (F)	NRNR (Nubib mountains) / farmland	388	1136	62.8	58.8	71.0	20.3	18.5	22.8	107.7
SAT1771 (M)	Farmland (Solitaire / Remhoogte)	698	3980	135.0	123.3	160.3	50.0	45.3	57.5	513.3
SAT1772 (M)	Farmland (Solitaire / Remhoogte)	702	2773	162.5	139.0	196.5	29.3	27.3	37.0	381.8
SAT1773 (M)	GSNL (Neuhof) / Farmland (Tsaris mountains)	149	2674	249.8	227.8	269.5	82.0	71.8	94.0	362.6
SAT1774 (F)	GSNL (Shangri-La) / Farmland (Tsaris mountains)	732	2885	126.8	84.2	190.8	40.0	21.5	73.3	378.1

Hartmann's Zebra ID (Sex: M/F)	Location	Tracking duration (days)	N	Estimated Home Range	Lower 95% HR	Upper 95% HR	Core Area	Lower 95% CA	Upper 95% CA	100% MCP
SAT1775 (M)	GSNL (Neuras)/ Farmland (Tsaris mountains)	580	3997	127.0	117.5	168.0	46.3	44.0	54.0	642.8
SAT1776 (M)	GSNL (Neuras)/ Farmland (Tsaris mountains)	588	1683	115.3	107.5	125.0	32.5	30.3	36.0	213.7

Table 3: Home range and core area sizes along with 95% confidence intervals and the minimum convex polygon (MCP) home range of thirteen collared gemsbok (all areas are given in km²). N = number of predicted locations. Green highlighted = largest modeled home range / orange highlighted = smallest modeled home range.

Gemsbok ID (Sex: M/F)	Location	Tracking duration (days)	N	Estimated Home Range	Lower 95% HR	Upper 95% HR	Estimated Core Area	Lower 95% CA	Upper 95% CA	100% MCP
Mean (±SD)				282.5 (±289.7)			86.4 (±81.8)			766.1 (±837.8)
SAT1101 (F)	NNP North (Naukluft area)	690	1142	65.0	61.3	72.3	23.3	22.3	25.5	132.1
SAT1102 (F)	NNP North (Naukluft area) / GSNL (Weltevrede)	488	2849	185.0	175.0	199.3	68.5	64.8	73.3	354.0
SAT1103 (F)	GSNL (Namib Desert Lodge and surrounds)	489	1974	108.0	100.8	117.8	40.5	37.5	44.3	194.9
SAT1104 (F)	GSNL (Sesriem) / NNP North (Namib area)	669	1894	144.0	131.0	161.8	42.8	39.8	47.0	326.4
SAT1105 (F)	NNP North (Namib area)	464	2595	156.0	147.8	172.0	61.5	57.0	67.0	267.9
SAT1106 (F)	NNP North (Naukluft area)	488	653	33.0	31.5	36.5	12.5	12.0	13.8	57.3
SAT1107_1769 (F)	GSNL (NRNR and surrounds) / NNP South / Farmland	1416	14097	556.5	501.5	640.8	154.8	145.3	169.5	2636.6
SAT1108 (F)	NRNR & NNP South	517	4329	203.8	183.5	246.3	64.3	60.8	71.5	563.9
SAT1109 (F)	NRNR & NNP South	466	6980	375.3	344.8	413.8	120.0	112.8	132.8	998.9
SAT1765 (F)	Farmland (Farm Abbabis)	911	2212	119.8	113.3	126.8	40.0	37.8	42.3	266.4
SAT1766 (F)	GSNL / NNP North (Namib area)	739	4070	264.0	246.0	291.8	74.5	69.8	82.3	626.6

Gemsbok ID (Sex: M/F)	Location	Tracking duration (days)	N	Estimated Home Range	Lower 95% HR	Upper 95% HR	Estimated Core Area	Lower 95% CA	Upper 95% CA	100% MCP
SAT1768 (F)	NRNR / NNP South	912	8044	341.5	311.0	388.3	94.8	89.3	106.5	1169.1
SAT1770 (F)	NRNR, NNP South, Farmland	857	11031	1120.5	1048.0	1206.0	325.8	307.8	349.5	2364.7

Table 4: Home range and core area sizes along with 95% confidence intervals and the minimum convex polygon (MCP) home range of eleven collared springbok (all areas are given in km²). N = number of predicted locations. Green highlighted = largest modeled home range / orange highlighted = smallest modeled home range.

Springbok ID (Sex: M/F)	Location	Tracking duration (days)	N	Estimated Home Range	Lower 95% HR	Upper 95% HR	Estimated Core Area	Lower 95% CA	Upper 95% CA	100% MCP
Mean (±SD)				139.8 (±96.1)			43.0 (±29.4)			406.2 (±298.9)
SAT131 (M)	GSNL North (Solitaire and surrounds)	230	5193	305.5	268.0	356.1	91.5	80.3	113.5	720.0
SAT132.2 (M)	NRNR / farmland	125	1613	75.3	66.5	86.3	23.5	20.8	28.5	133.0
SAT132 (M)	NRNR	73	1271	45.8	39.3	86.1	16.3	14.3	39.0	141.1
SAT133 (M)	NRNR	142	483	15.0	13.8	18.0	5.3	5.0	6.5	27.6
SAT134 (M)	GSNL (NRNR and surrounds) / farmland	380	4924	203.3	182.5	231.8	56.5	50.8	66.3	596.3
SAT135 (M)	Farmland (bordering NRNR)	211	1900	73.3	68.0	99.0	27.8	25.2	37.0	189.4
st2010-2797 (M)	NRNR / NNP	339	4480	196.5	176.0	231.8	64.5	58.7	74.5	702.6
st2010-2798 (M)	NRNR / NNP	147	5729	258.8	228.0	314.0	83.8	75.0	102.5	829.9
st2010-2799 (F)	NRNR	178	2589	160.3	145.3	179.0	51.3	47.5	58.3	324.8
st2010-2801 (M)	GSNL (Namib Desert Lodge and surrounds) / NNP	646	5090	162.3	116.5	236.8	44.0	25.0	92.5	674.8
st2010-2803 (M)	GSNL North (Solitaire and surrounds)	638	1674	42.5	38.0	54.0	9.0	8.5	16.0	128.3

3.1.1 Hartmann's mountain zebra

Hartmann's zebra in the Central Namib (SAT1092, SAT1093, SAT1097 and SAT1098) had larger home ranges than those individuals ranging in other parts of the GSNL and neighbouring farms.

The largest home ranges were (in ascending order) 925.5 km² (SAT1092 – Figure 4 a), 326.5 km² (SAT1098 – Figure 4 g), 476.8 km² (SAT1093 – Figure 4 b), and 521.0 km² (SAT1097 – Figure 4 f). SAT1092's home range (the largest 925.5 km²) was almost double the size of the next largest home range (belonging to SAT1097). The zebra was able to move relatively without obstruction within the central NNP, north of the Kuiseb. Its northward movement was only limited by the district road (D1982) and the farm fences bordering the east of the NNP.

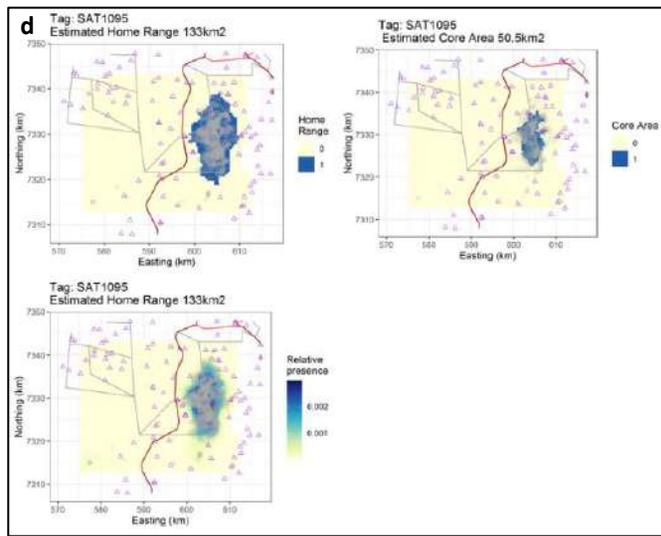
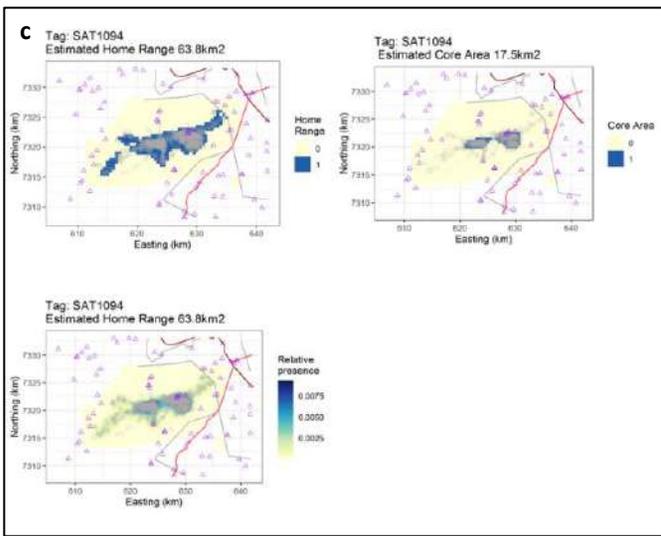
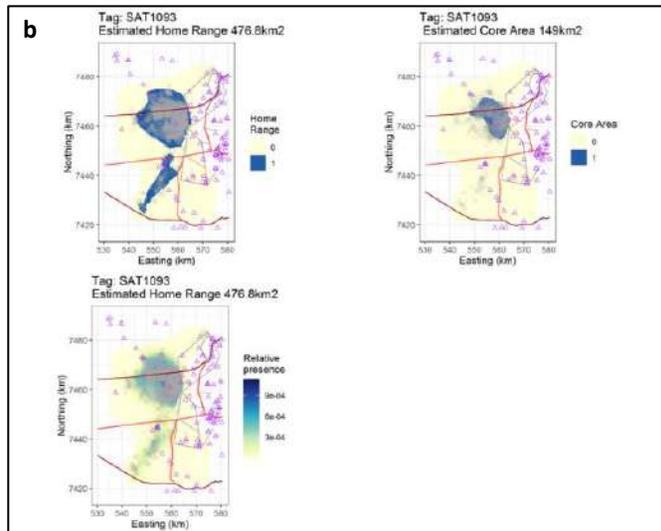
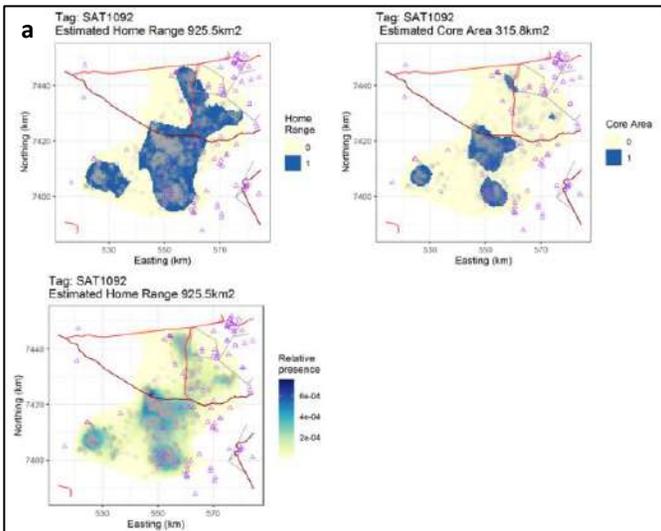
SAT1093, SAT1097, and SAT1098 were all affected by the eastern national park fence (Figure 4 b, Figure 4 f and Figure 4 g), and none of them were able to venture past the solid eastern boundary fence of the national park. Eventually, SAT1098 did find a place to access the eastern farmlands when it moved further north and crossed the fence a few kilometres from the Swakop river. SAT1097 (Figure 4 f) was affected to some extent by the C28 and C14 main roads. Apart from this, all three individuals were able to move without any limitations within the national park (reflected by their larger home range sizes). All of the zebra in the central Namib showed a distinct north-south movement, which was especially evident in SAT1093 and SAT1098 (which had two areas of higher relative presence – one in the north and one in the south), and SAT1097 (which had two areas of higher relative presence – one in the north-west and one in the south-east).

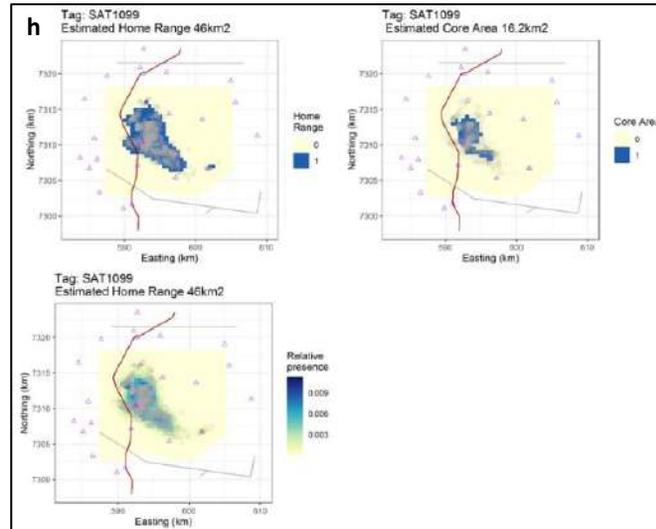
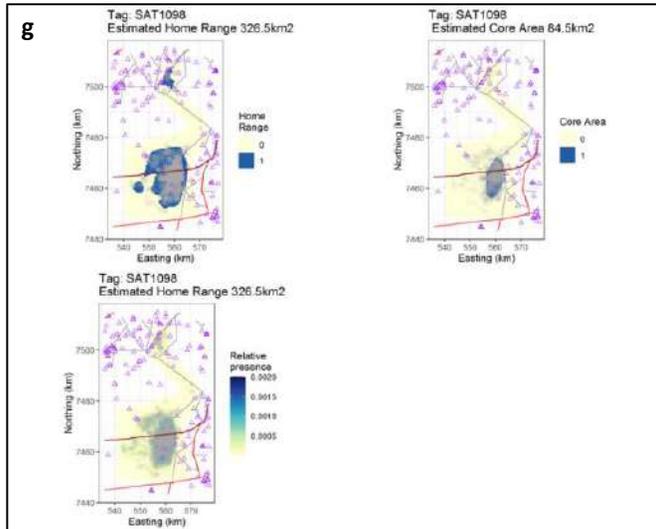
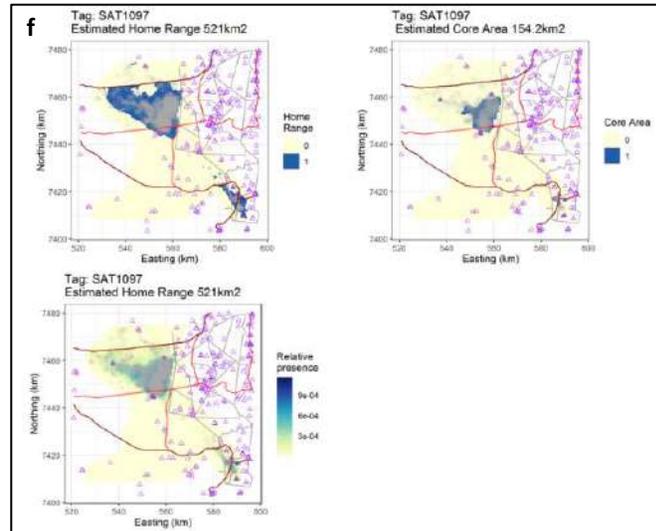
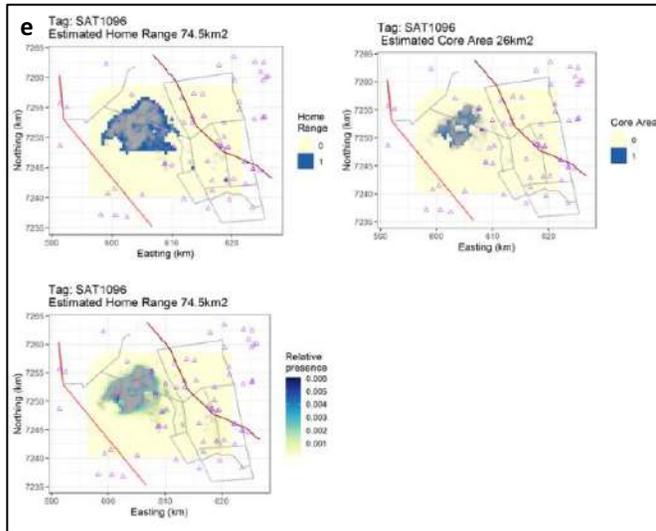
Hartmann's zebra ranging in other areas, including the Naukluft mountains, Nubib mountains and in various other areas of the GSNL and adjoining farmland, had smaller home ranges. SAT1771 to SAT1776 (except SAT1773) had comparable home range sizes (between 115.3 km² and 162.5 km²). These zebra ranged between the eastern boundary of the GSNL and the neighbouring farmlands as follows: between Solitaire and Remhoogte (SAT1771 – 135.0 km² ; SAT1772 – 162.5 km²); between Neuhof (SAT 1773 – 249.8 km²) and Shangri-La (SAT1774 – 126.8 km²) and the neighbouring farmland to the east in the Tsaris mountains; and Neuras and the adjoining farmland (SAT1775 – 127.0 km² ; SAT1776 – 115.3 km²). SAT1771 was limited by the C14 main road on the western side of its distribution, as well as the D1261 district road in the south (Figure 4 j). SAT1772 was affected by the C14 main road, although less visibly so (Figure 4 k). SAT1773 did not seem to be affected by roads or fences (Figure 4 l). SAT1774 was not able to move further west, as the C19 main road constituted a considerable barrier (Figure 4 m).

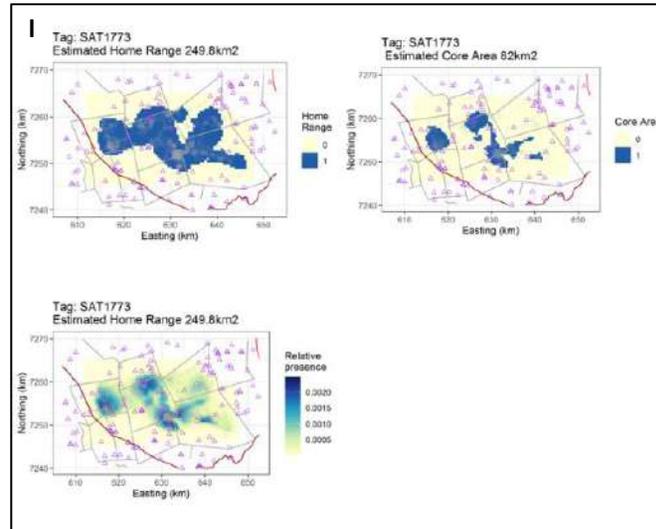
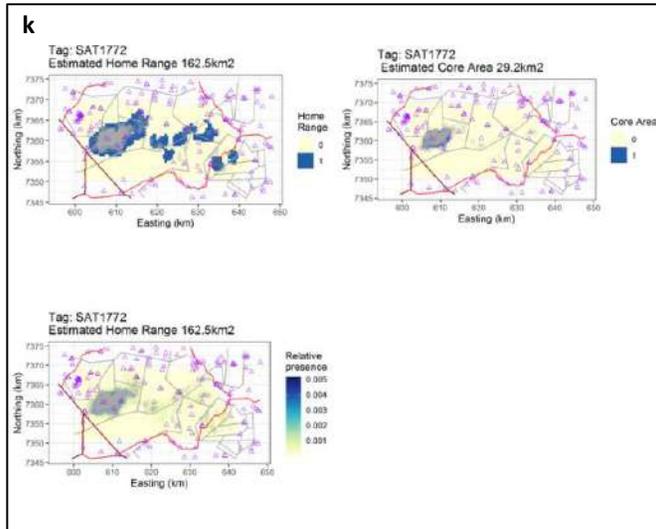
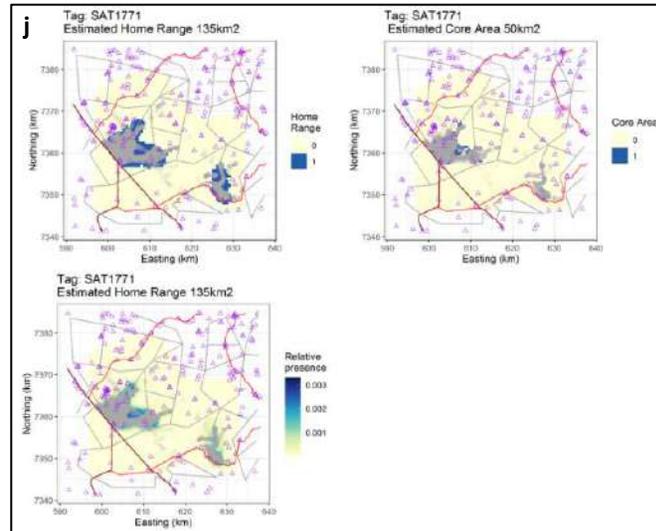
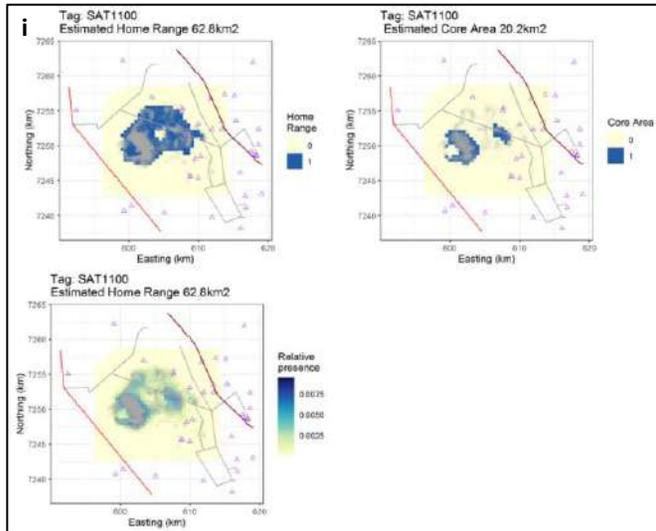
SAT1775's movement was limited by farm fences to its east and west (Figure 4 n), while SAT1776 (Figure 4 o) was restricted by district roads to its east, south and west (D0854, D0850 and D0855 respectively).

Individuals ranging in the Naukluft and Nubib mountains (bordering NamibRand) generally had the smallest home ranges. Home ranges of SAT1100 in the Nubib mountains (62.8 km² – Figure 4 i), SAT1094 in the Naukluft mountains (63.8 km² – Figure 4 c), and SAT1096 in the Nubib mountains (74.5 km² – Figure 4 e) were comparable, while that of SAT1099 in the Naukluft mountains was the smallest of all collared zebra individuals (46.0 km² – Figure 4 h). No movement limitation was visible for SAT1096 and SAT1100. SAT1094's movements were affected by the boundary fence of the national park. SAT1099's movement was limited by the C19 main road, although it was able to cross the road.

Hartmann's zebra was the only species for which sufficient males (n = 10) and females (n = 5) had been collared, which makes a comparison between sexes possible. However, no difference between sexes are apparent, as the female home range sizes were variable. Some females had large home ranges (SAT1092 and SAT1093 with 925.5 km² and 476.8 km² respectively) while others had small home ranges (SAT1099 and SAT1100 with 46.0 km² and 62.8 km² respectively). SAT1774's home range was somewhere in between (126.8 km²), but it was also one of the zebra for which a distinct east-west movement was discernible, with two separate core areas: one on the property Shangri-La, and the other deep in the Tsaris mountains (on the Friedland/ Theronsberg properties). SAT1771, 1772 and 1773 also revealed a distinct east-west movement pattern.







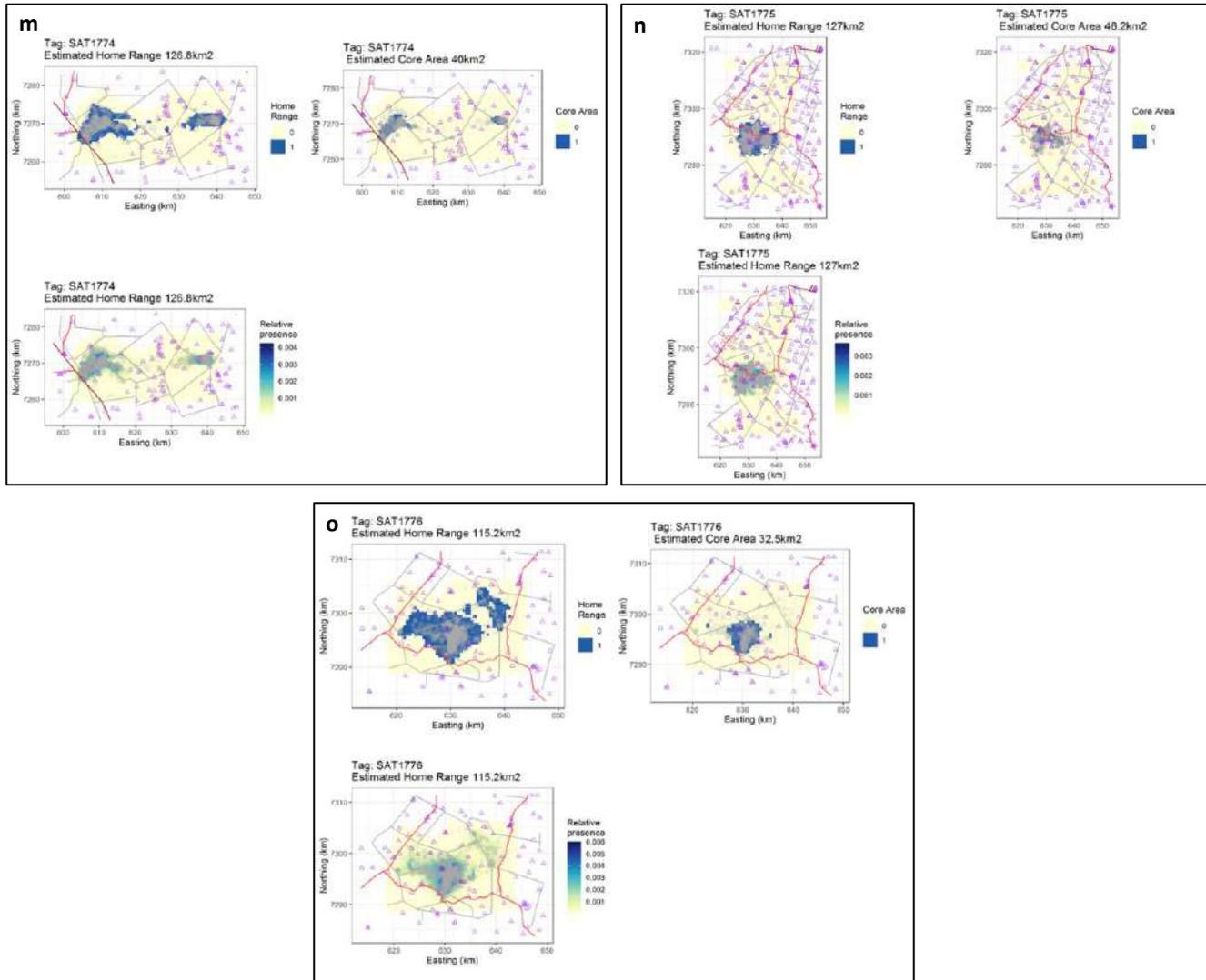


Figure 4: a - o: Estimated home ranges of Hartmann's zebra (km²). Purple triangles = water points (artificial and natural); red lines = district roads; purple lines = main roads.

3.1.2 Gemsbok

In general, gemsbok in the northern GSNL (SAT1101, SAT1102, SAT1103, SAT1104, SAT1105, SAT1106 and SAT1765) had comparatively smaller home ranges than gemsbok in the south (SAT1107_1769, SAT1108, SAT1109, SAT1768, SAT1770). Only SAT1766 (Figure 5 k) was an exception to this. It ranged in the dune fields between the national park and neighbouring farms in the GSNL north and had a comparatively large home range of 264.0 km². The supposedly solid national park boundary fence did not seem to be a hindrance to its movement.

SAT1106 (Figure 5 f) and SAT1101 (Figure 5 a), both of which ranged in the Naukluft area of the NNP, had the smallest home ranges with 33.0 km² and 65.0 km² respectively. Both did not seem to be affected much by the boundary fences of the NNP, in which they ranged, although the C24 district road did limit the northwards movement of SAT1106 to some extent.

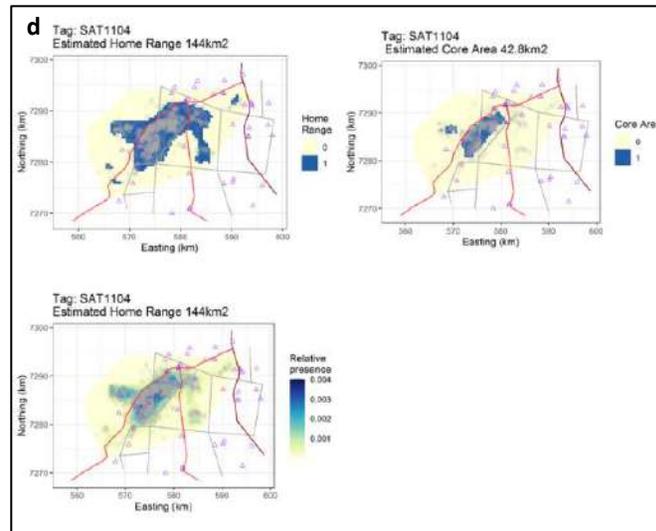
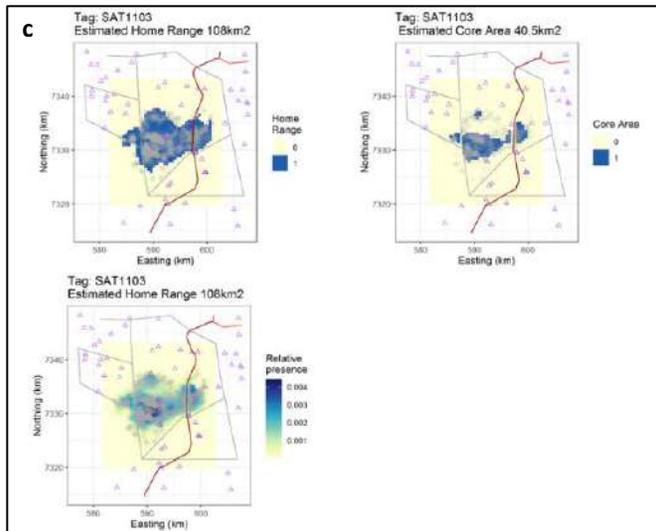
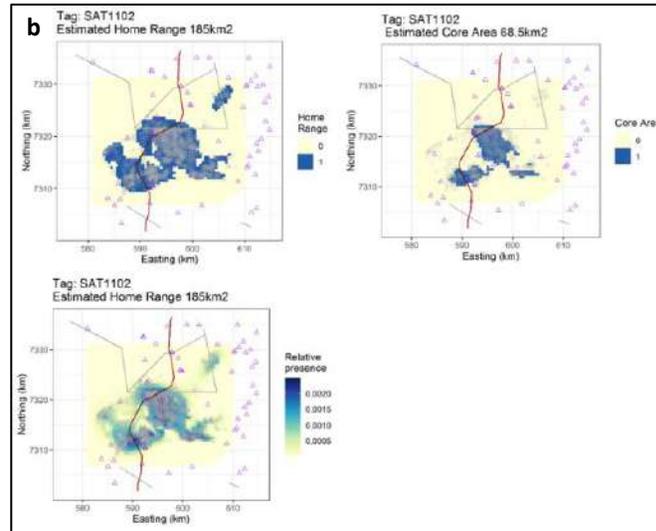
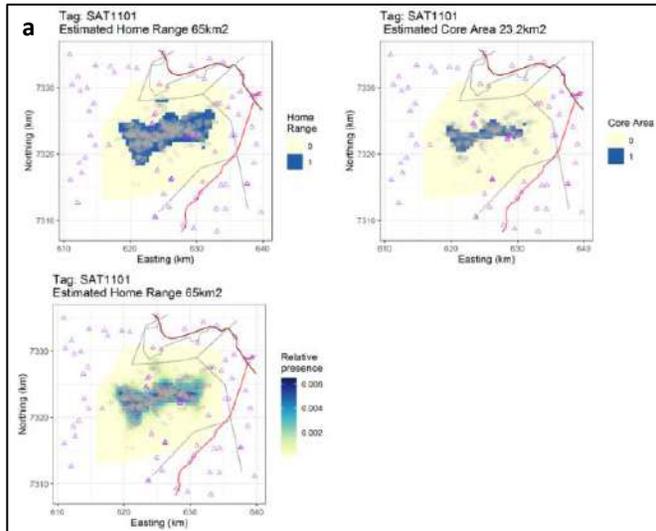
SAT1103 (Figure 5 c), SAT1765 (Figure 5 j), SAT1104 (Figure 5 d), SAT1105 (Figure 5 e), and SAT1102 (Figure 5 b) had comparable home ranges (108.0 km², 119.8 km², 144.0 km², 156.0 km², and 185.0 km² respectively). SAT1102 and SAT1103 were both affected by the Weltevrede boundary fence, with the former ranging south and the latter ranging north of the said fence. SAT1104 (144.0 km² – Figure 5 d) was located around Sesriem, with its core area wedged between the C27 and D0872 district roads. The main road (C19) affected its north-eastward movement to some extent. SAT1765 (home range of 119.8 km²) was clearly affected by the Abbabis boundary fence, as well as the C14 main road and the D1261 district road (Figure 5 j) as it moved consistently along these solid barriers.

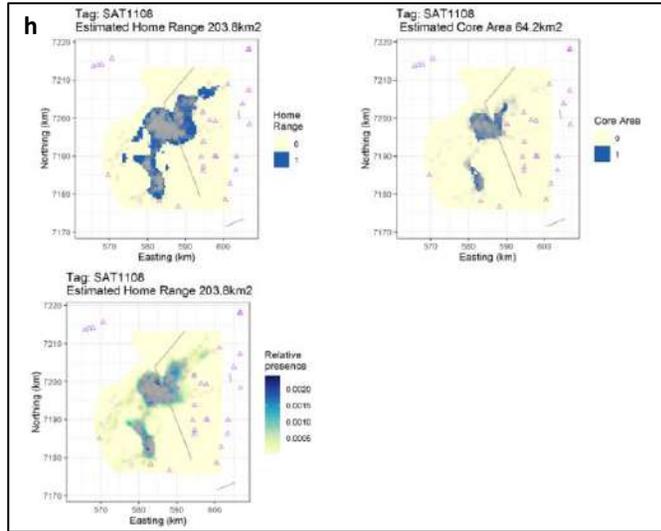
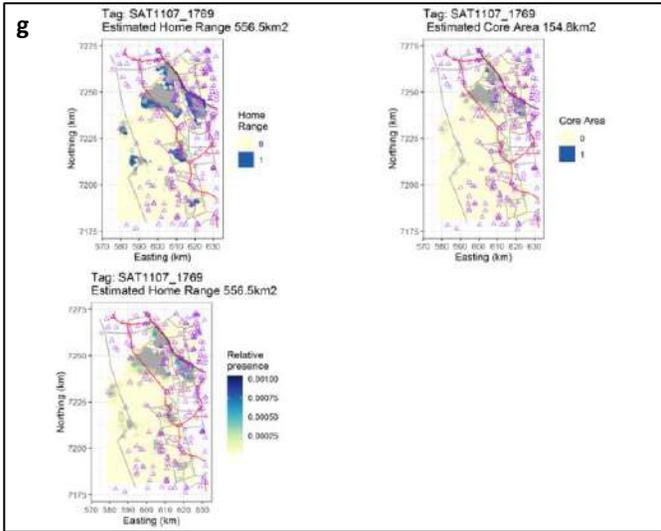
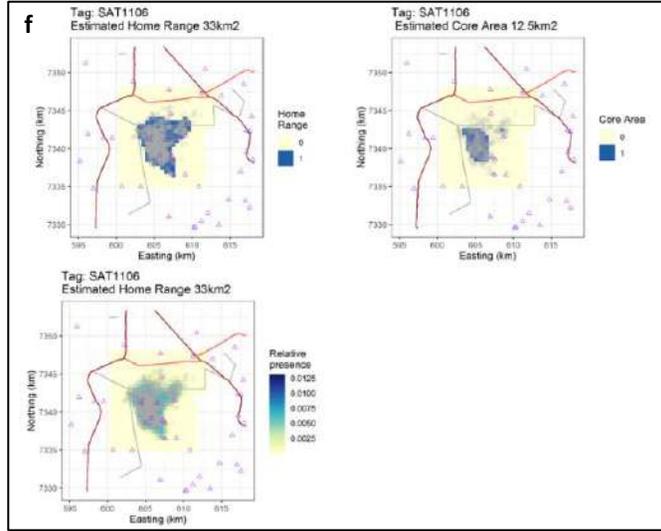
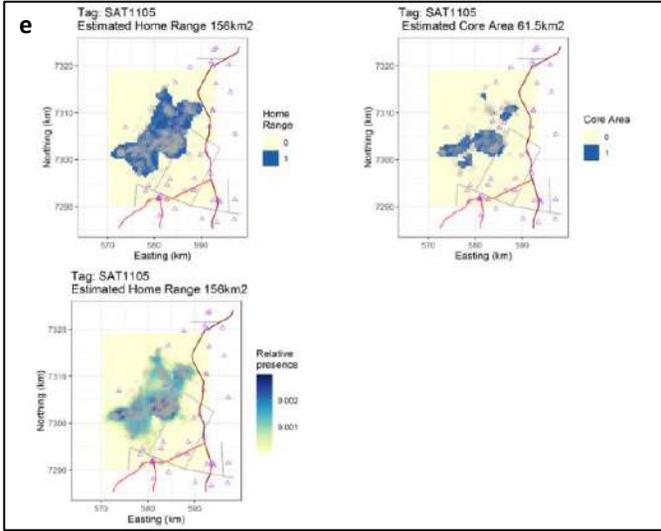
The largest home range of a gemsbok individual was 1,120.5 km² (SAT1770 – Figure 5 m). It ranged freely between the south of the NamibRand reserve and the NNP. Only its eastward movement was restricted by the solid fences of farms neighbouring the reserve, as well as in the area where two road sections (part of the C27) meet at an angle.

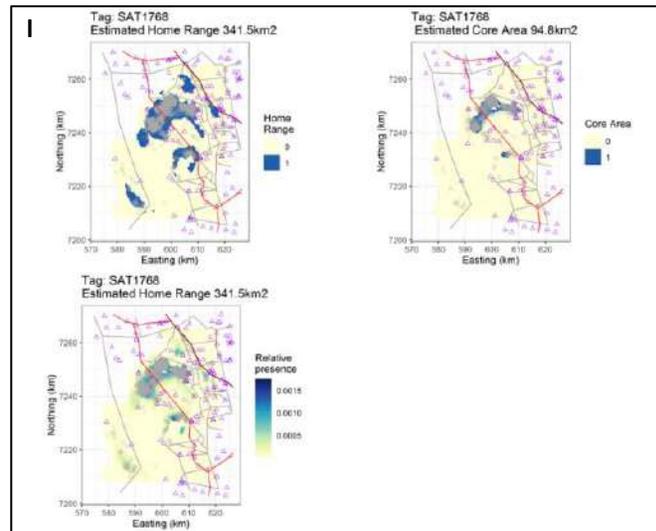
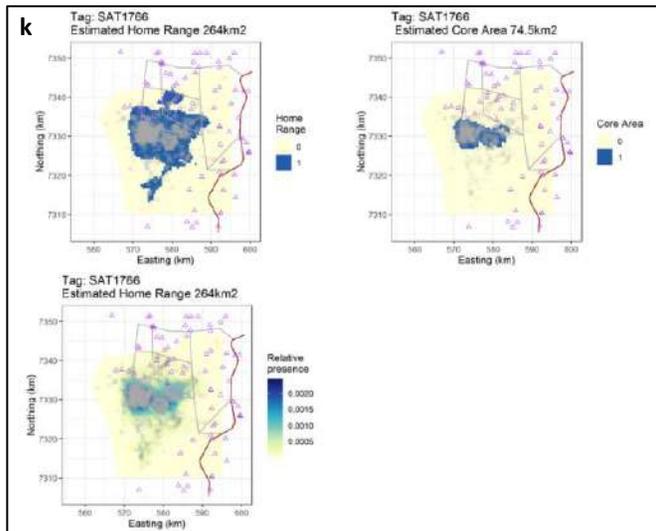
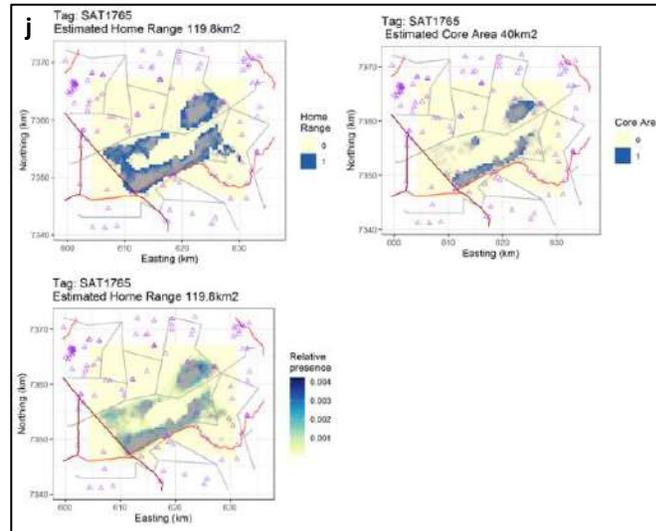
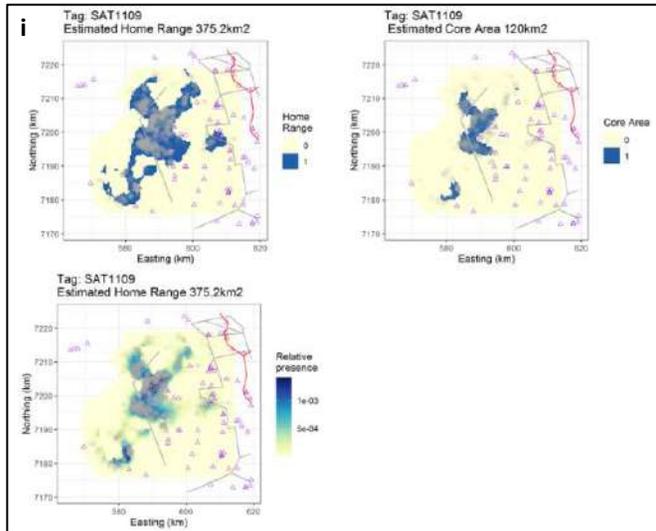
SAT1107_1769 had the second largest home range (556.5 km² – Figure 5 g). The gemsbok moved freely on NamibRand, into the national park and across the Nubib mountains to farmland further east. SAT1768 (341.5 km² – Figure 5 l) was also able to move freely between NamibRand and the national park. However, both individuals' movements were stopped by the C19 main road corridor fence towards the north-east of their distribution, as they moved consistently along the west of the C19. Some

movement limitation was caused by farm fences to the east and south of gemsbok SAT1107_1769's distribution.

Both SAT1108 (Figure 5 h) and SAT1109 (Figure 5 i) were unaffected by fences and moved freely between NamibRand and the Chowagas mountains in the national park. This freedom of movement was reflected by their comparatively large home ranges of 203.8 km² (SAT1108) and 375.3 km² (SAT1109).







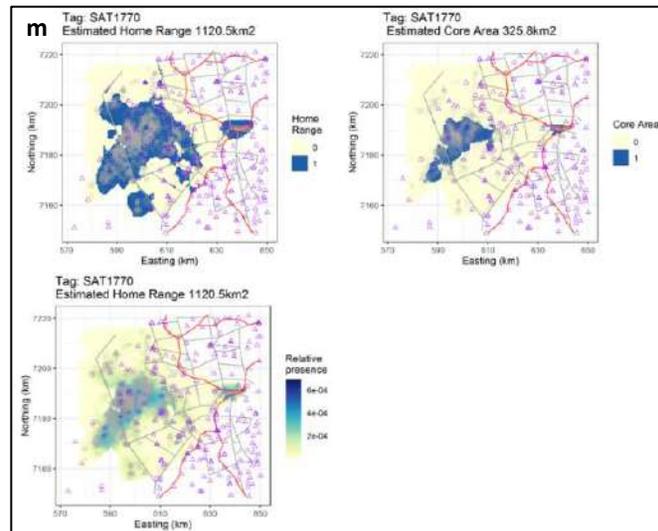


Figure 5: a - m: Estimated home ranges of gemsbok (km²). Purple triangles = water points (artificial and natural); red lines = district roads; purple lines = main roads.

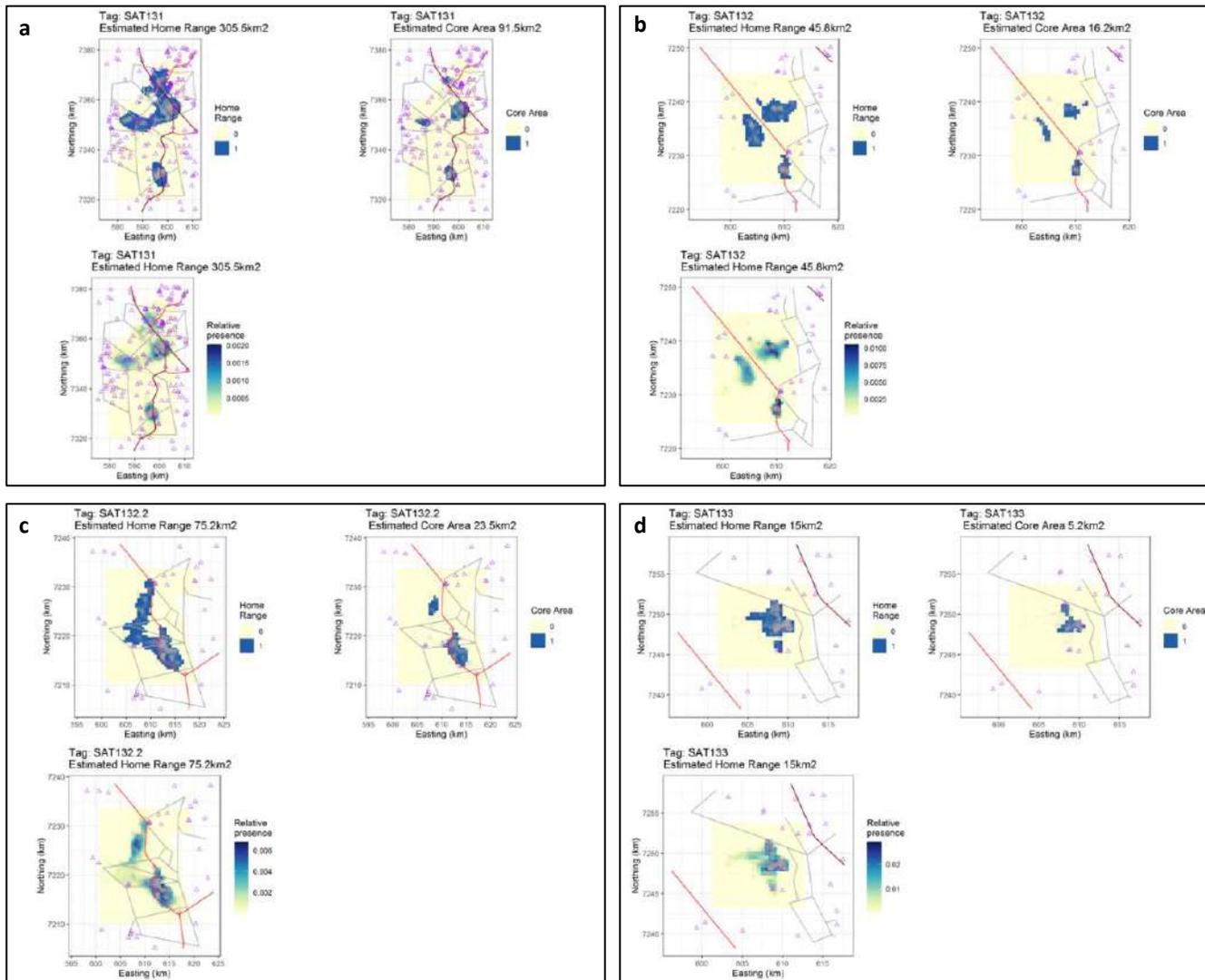
3.1.3 Springbok

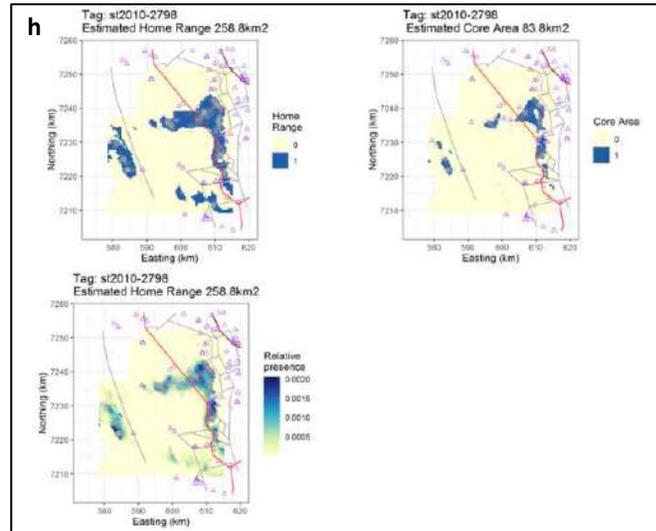
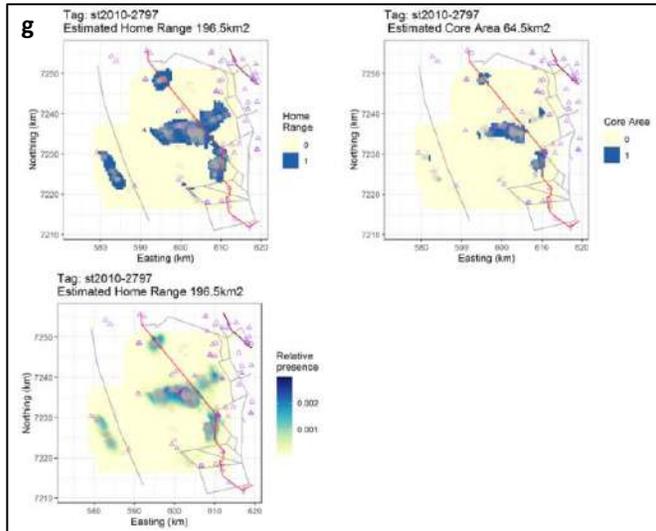
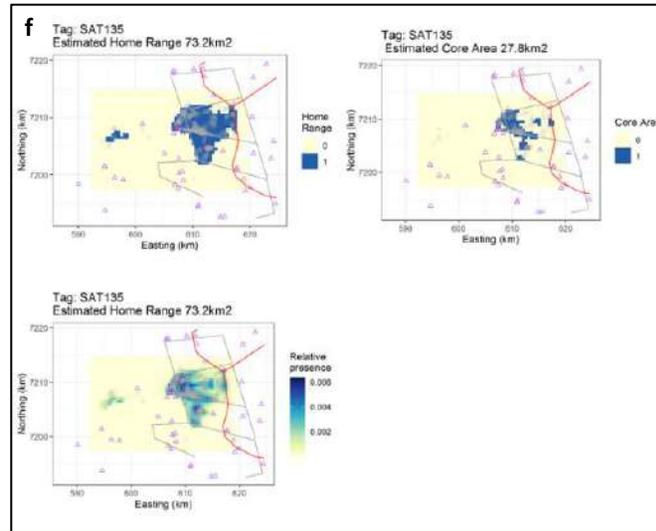
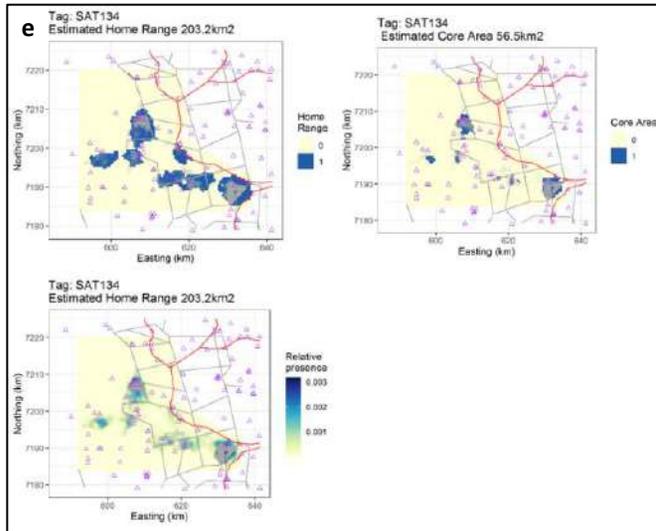
The largest springbok home range (305.5 km²) was that of SAT131 in the northern GSNL area (around Solitaire), where a large section of the fences between land units has been taken down or has been made more permeable (Figure 6 a). St2010-2798 was able to move freely between NamibRand and the national park, and had the second largest home range (258.8 km² – Figure 6 h). SAT134 had a large home range as well (203.3 km²) and was able to move freely through the perforated fences and sections where fences have been removed between NamibRand and some neighbouring farms (e.g. farm Excelsior). It was only affected by solid farm fences along parts of its home range further south-east (Kameelhof), as well as the C27 district road (Figure 6 e).

St2010-2799 (the only female springbok) and st2010-2797, both of which ranged on NamibRand, had comparatively large home ranges of 160.3 km² (Figure 6 i) and 196.5 km² (Figure 6 g) respectively. As did st2010-2801 (162.3 km²– Figure 6 k), which moved around freely on the Namib Desert Lodge property and its neighbouring properties, and extended its range into the national park.

SAT132 (Figure 6 b), SAT133 (Figure 6 d), and st2010-2803 (Figure 6 l) were more or less sedentary around NamibRand (the former two) and Solitaire (the latter), even though fences in these areas had either been made more permeable or have been taken down completely. A farm fence (between Solitaire and Abbabis) did pose an obstruction to st2010-2803, although the springbok was able to move across a permeable section of the fence. SAT133 had the smallest home range (15.0 km²) and remained in the same area (along the foot slopes of the Nubib mountains) throughout its tracking period.

Part of SAT132.2's range was on farmland adjoining NamibRand and its home range was relatively small (75.3 km² – Figure 6 c). Its movement was visibly obstructed by the C27 district road. SAT135's movement was completely restricted to one farm (Wêreldend) and even further limited by the C27 main road to its east (Figure 6 f). This movement restriction was reflected by its small home range of 73.3 km².





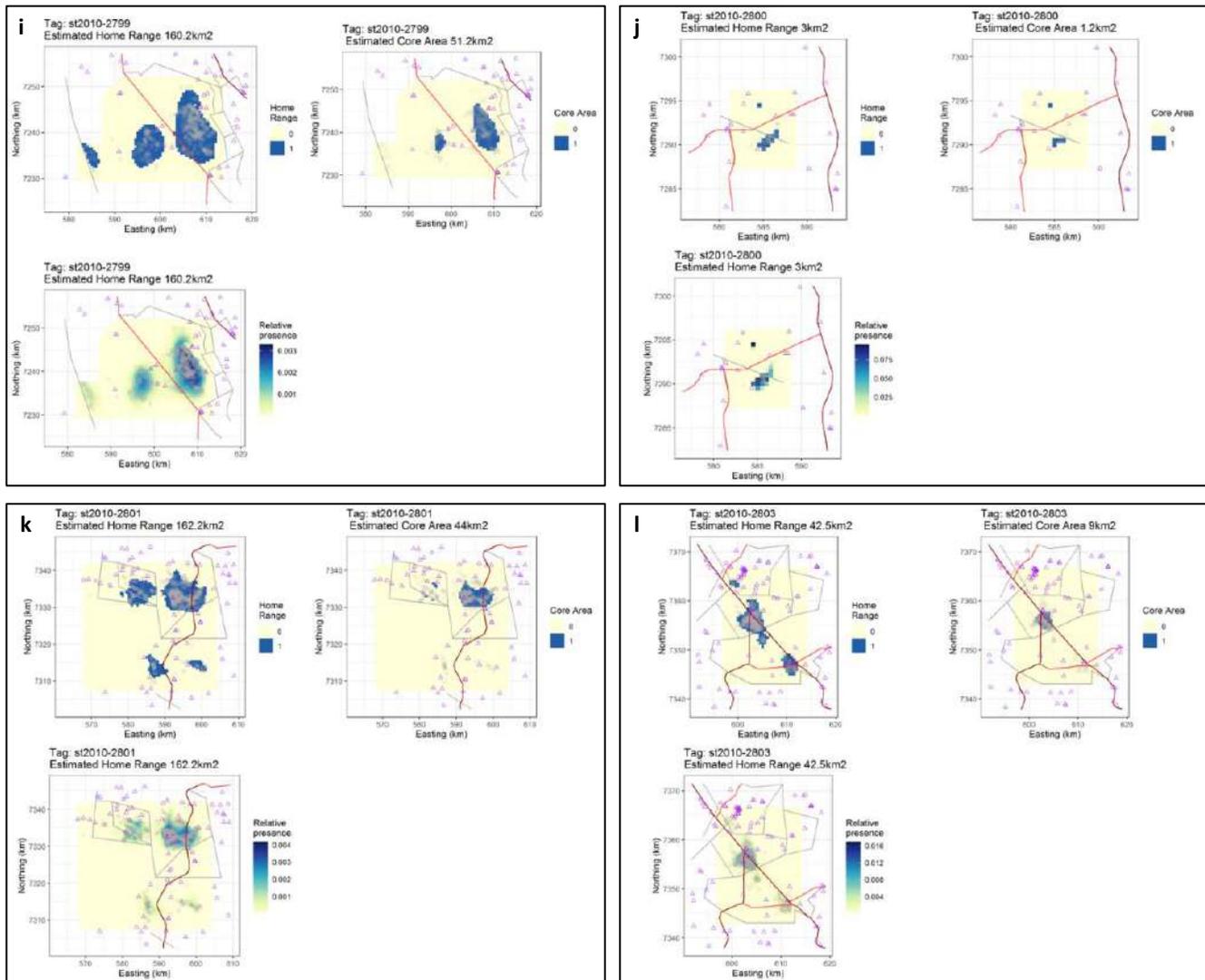


Figure 6: a - l: Estimated home ranges of springbok (km²). Purple triangles = water points (artificial and natural); red lines = district roads; purple lines = main roads.

3.2 The impact of barriers on animal distribution

Data for Hartmann's zebra were available for all three regions, north (Figure 7 a), mid (Figure 8 a) and south (Figure 9 a), while springbok and gemsbok data were only available in the mid (Figure 8 a) and south regions (Figure 9 a).

The mid region of land units is located at a distance of approximately 15 km from barriers in the north (Figure 7 b), and 5 to 10 km in the mid (Figure 8 b) and south regions (Figure 9 b). The mid and south regions of the study area contain frequent barrier encounters, mostly due to cattle and sheep farm inner and outer fences and district roads.

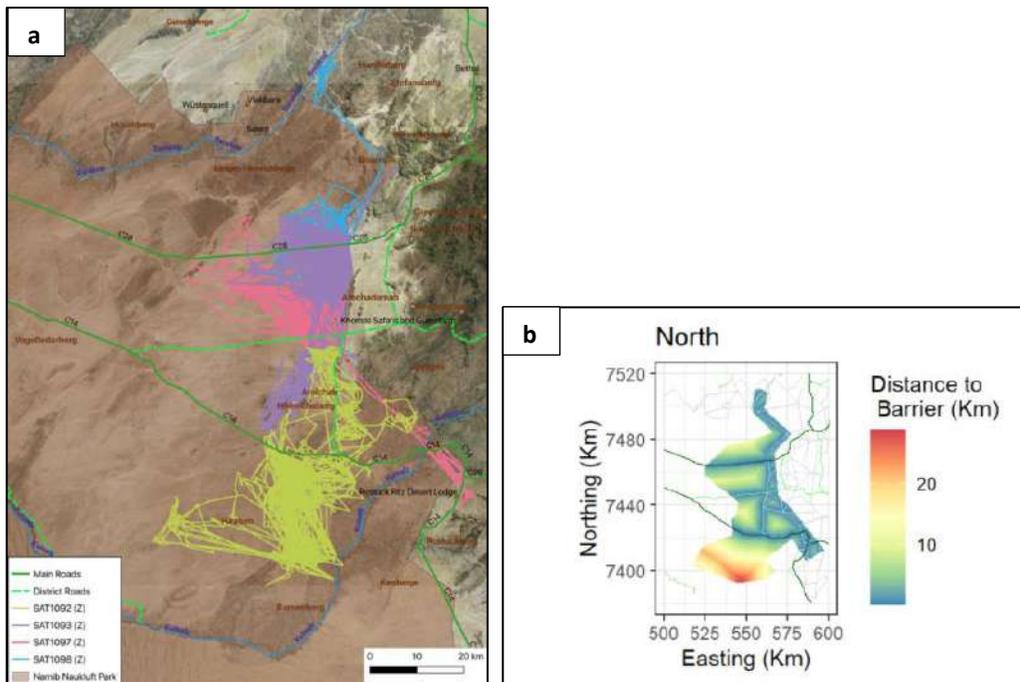


Figure 7: a) The distances to the nearest barriers for the north region of the study area. b) a scale map of the north region with geographical features for orientation.

3.2.1 Hartmann's mountain zebra

There was a general trend of more Hartmann's zebra telemetry locations being close to any barrier (road or fence), with fewer points far from barriers (Figure 10 a). The largest proportion of estimated tag locations was within 1 km of the nearest barrier with another peak at 2 km (Figure 10 b).

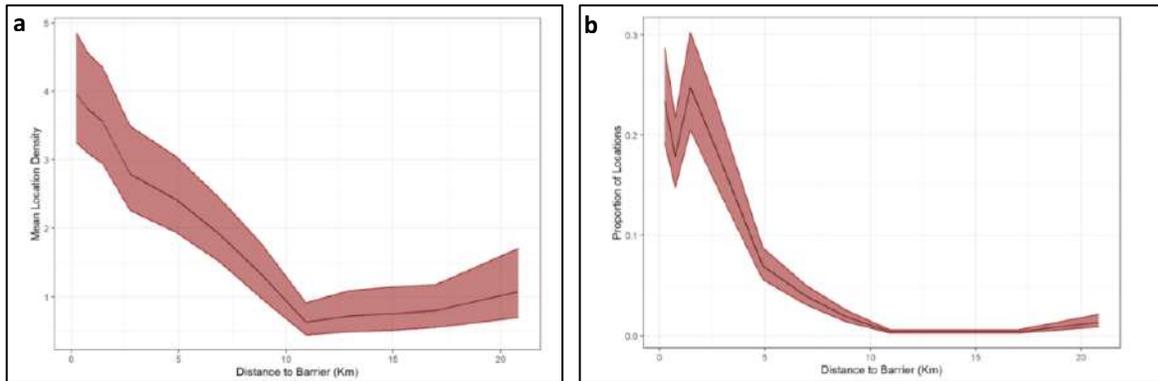


Figure 10: a) Relationship between distance to nearest barrier and the density of Hartmann's zebra locations, with upper and lower confidence intervals (universal barrier relationship). b) Proportion of estimated Hartmann's zebra locations that lie a certain distance from the nearest barrier, with upper and lower confidence intervals.

3.2.2 Gemsbok

Gemsbok showed a general trend of being located at a distance of approximately 3 to 5 km from any barrier (Figure 11 a and b).

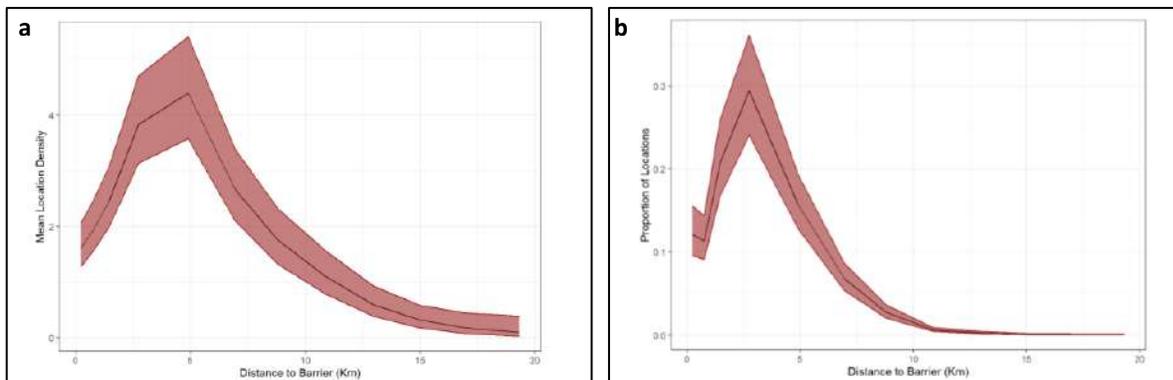


Figure 11: a) Relationship between distance to nearest barrier and the density of gemsbok locations, with upper and lower confidence intervals (universal barrier relationship). b) Proportion of estimated gemsbok locations that lie a certain distance from the nearest barrier, with upper and lower confidence intervals.

3.2.3 Springbok

There is a general trend that springbok movements were close (less than 1 km) to barriers and approximately 3 to 5 km from barriers (Figure 12 a). The largest proportion of estimated springbok locations were located less than 1 km and approximately 3 km from the nearest barrier (Figure 12 b).

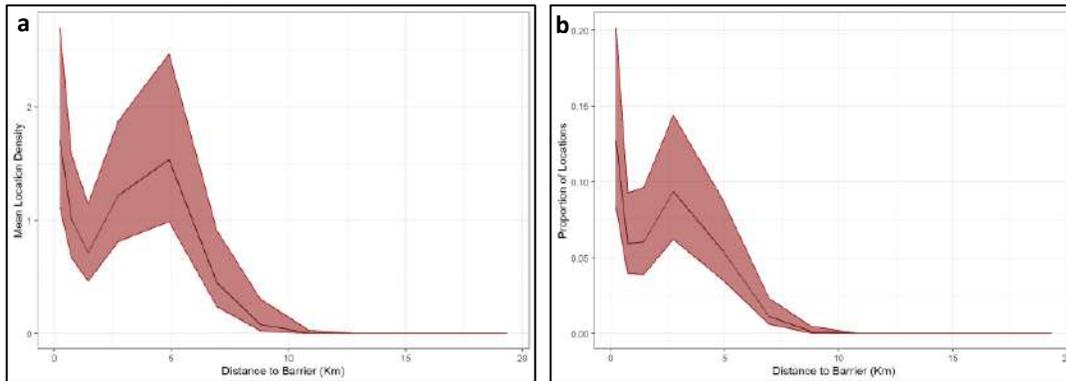


Figure 12: a) Relationship between distance to nearest barrier and the density of springbok locations, with upper and lower confidence intervals (universal barrier relationship). b) Proportion of estimated springbok locations that lie a certain distance from the nearest barrier, with upper and lower confidence intervals.

3.3 The barrier effect on ungulate movements

The above trends (Figure 10 – 12) were not consistent for all barriers and in some areas, more ungulate locations than expected were near a barrier, as will be elaborated on below.

3.3.1 Hartmann's mountain zebra

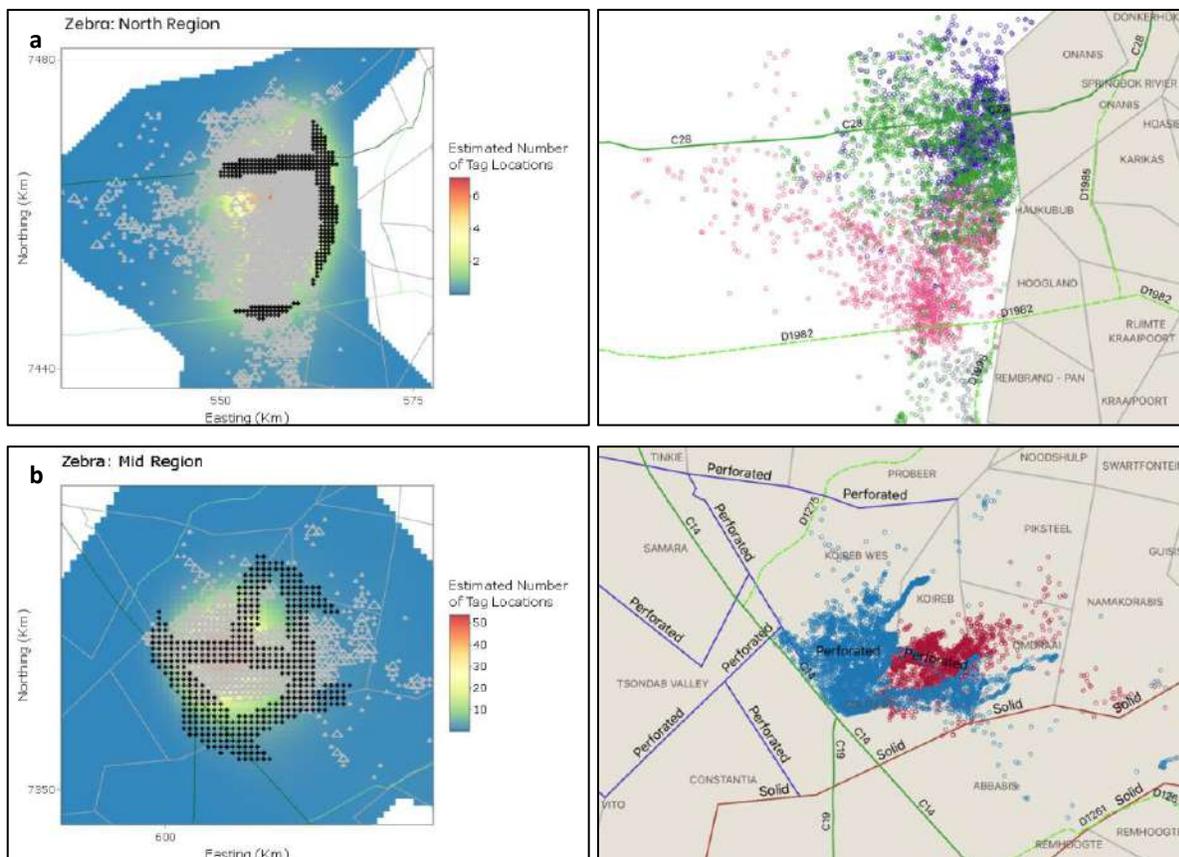
There was a significantly high proportion of Hartmann's zebra locations close to the NNP north fence (Figure 13 a). The movements of SAT1092, SAT1093, SAT1097 and SAT1098 onto farmland to the east were clearly impacted by this fence. The main road (C28) and district road D1982 did not result in an increased density of movement in their vicinity.

The C14 main road also caused a significant increase in Hartmann's zebra locations (Figure 13 b). Though identified as increasing the number of Hartmann's zebra telemetry locations significantly, the perforated farm fences between Solitaire and Koireb/Koireb Wes, and between Solitaire and Omdraai did not prevent Hartmann's zebra movement to the north and east respectively.

Though identified as increasing the number of Hartmann’s zebra telemetry locations significantly (Figure 13 c), the solid NNP/Weltevrede fence and the well-maintained (with some gaps) northern Weltevrede boundary fence did not block the movement of Hartmann’s zebra SAT1095.

The D0855 district road had a slightly disproportionately high distribution of Hartmann’s zebra movement points (Figure 13 d). However, the Neuras / Neuras Nord fences, which are supposedly solid, did not affect the movement of SAT1775 and SAT1776, as both were able to move across these, nor did the D0850 cause movement limitations.

There was a significantly high number of Hartmann’s zebra (SAT1774 and SAT1773) telemetry locations along the C19 main road (Figure 13 e). The C27 did not affect their movement, nor did the perforated fence between NamibRand and Voorspoed.



3.3.2 Gemsbok

A significantly higher number of gemsbok location points were present at the boundary fence of Farm Abbabis, as well as along the C14 main road and C24 district roads (Figure 14 a). It is evident that while gemsbok SAT1769 was able to move across the fence from Abbabis to Namakorabis and Remhoogte, the fence between Solitaire and Abbabis as well as the C14 and C24 seem to be resulting in a movement blockage.

The northern boundary fence of livestock farm Weltevrede, which is well-maintained, caused gemsbok to be up against the fence (Figure 14 b). SAT1103 was not able to move across this fence towards the south and remained on the northern side of the fence for the entire study period, while SAT1102 remained on the south side of that fence. The fence between Escourt and the neighbouring Namib Desert Lodge (Namibruhe) property caused movement limitations, as SAT1766 was only able to cross at some points along the fence towards the east, while SAT1103 movement towards the west was also limited. The Namib-Naukluft Park fence along the southern border of Weltevrede blocked gemsbok movement to some degree.

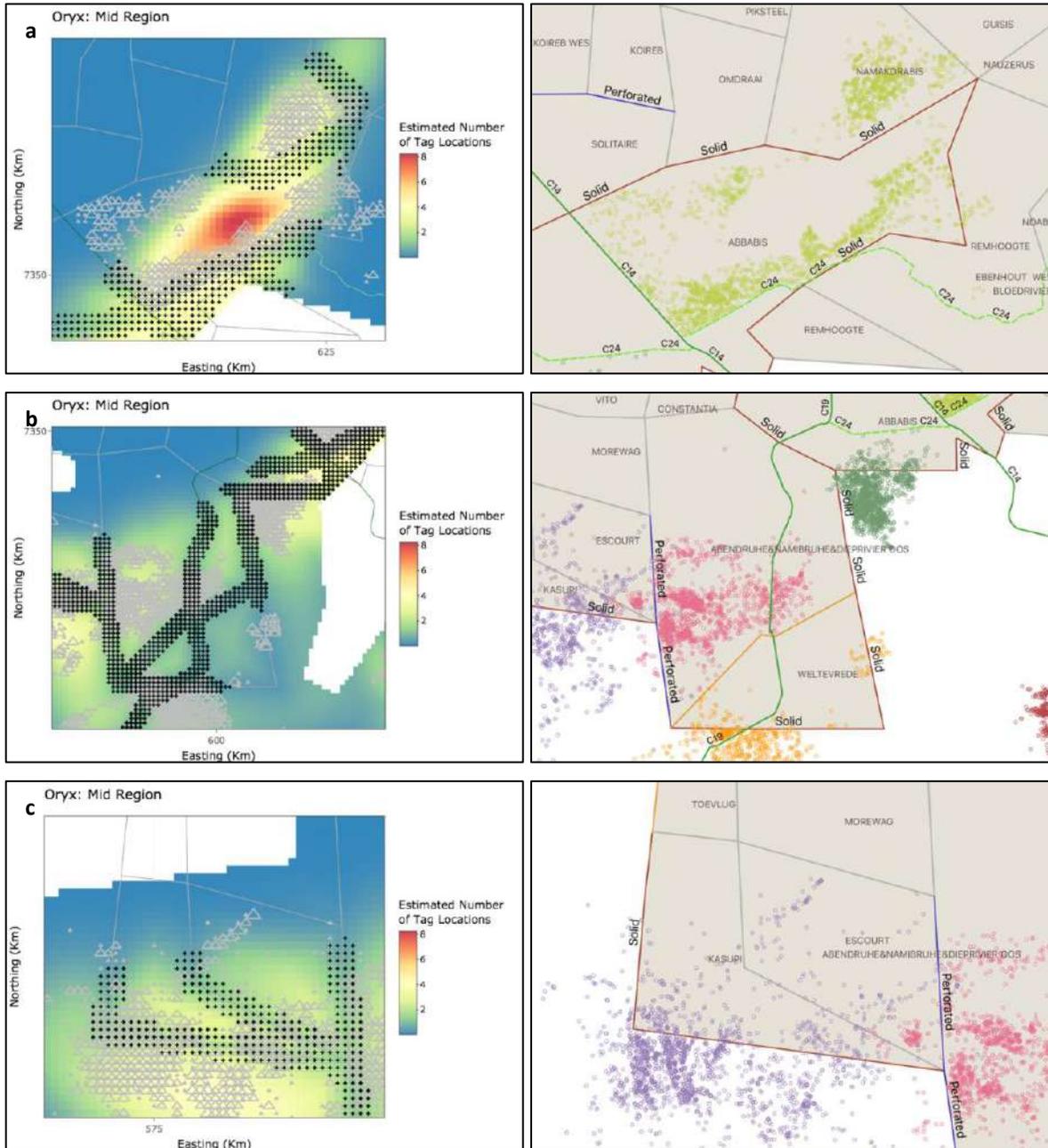
The C19 road (Figure 14 b) and the Namib-Naukluft Park fence along farm Kasupi (Figure 14 c) did in fact not block the movement of gemsbok, as SAT1766 and SAT1102 were able to cross these barriers frequently (Figure 14 b and c).

The Namib-Naukluft Park fence bordering farms Blasskranz and Bullspoot was indicated as a potential barrier (Figure 14 d). Although the gemsbok SAT1101 was able to cross NNP fence to farms Blasskranz and Bullspoot, not enough telemetry locations exist close to the fence in order for there to be a significant effect.

A significant number of gemsbok locations were found along the perforated fences between Oorwinning, Sesriem and the NNP, as well as along the road that leads to Sossusvlei (indicated as “no route” on the map) (Figure 14 e). These did allow gemsbok SAT1104 movement and hence were not a major barrier.

The C19 caused a significant increase in the number of gemsbok locations than would be present without this barrier (Figure 14 f). The same applied to the Hammerstein game farm fence. Upon

inspection of the location data, gemsbok SAT1107_1769 and SAT1768 were persistently along the C19 corridor road fence, and SAT1107_1769 was not able to move eastwards across the Hammerstein and southwards across the Witkam boundary fences. None of the other barriers, which were marked as possible blockages were found to be a problem. The fence between NamibRand and Voorspoed allowed gemsbok movement across, while the C27 district road (that crosses NamibRand) does not have a fence along it, and the road did not seem to offer any resistance to movement.



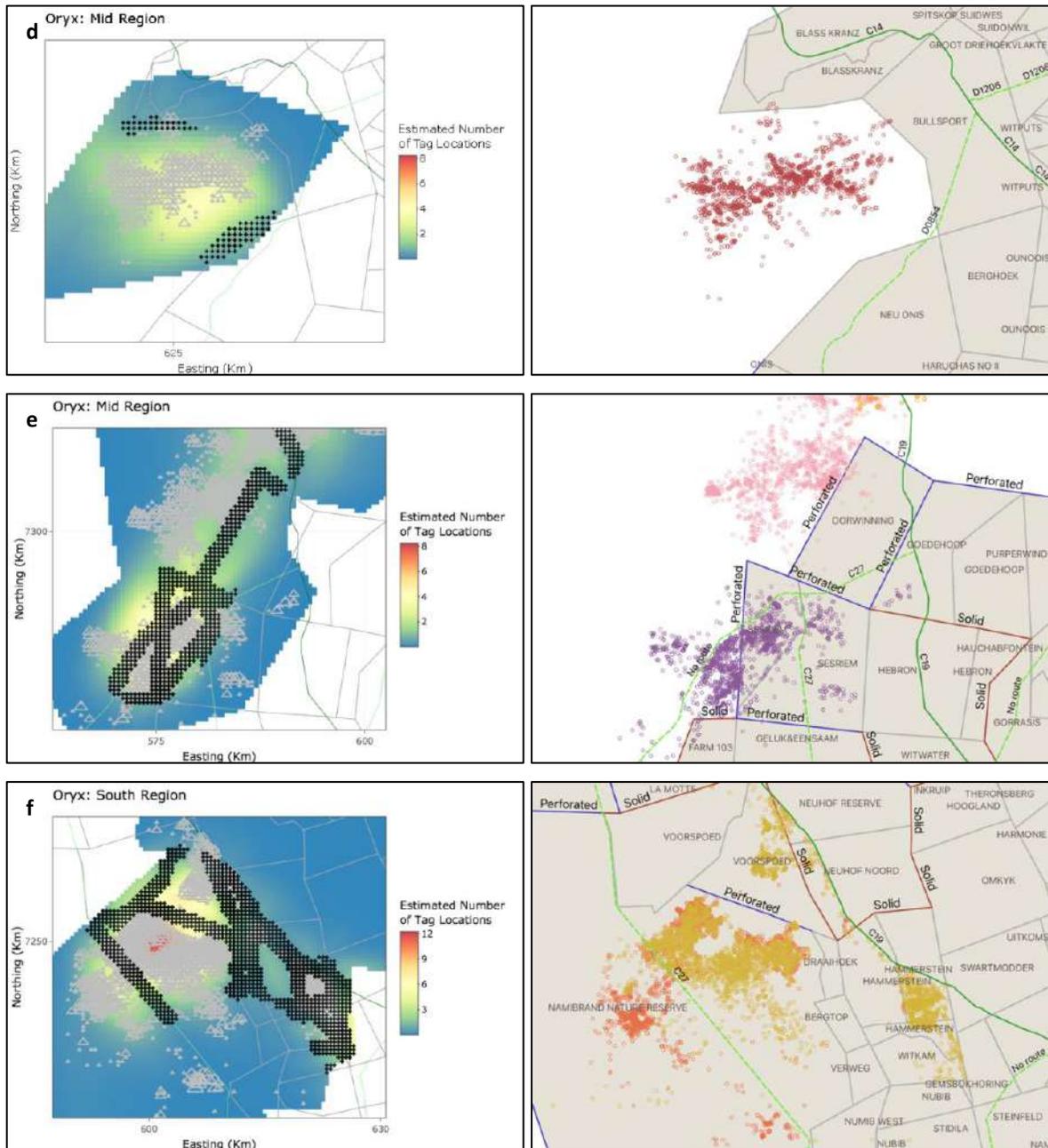


Figure 14: a - f: Estimated number of gemsbok telemetry locations per cell. The '+' symbols on the plots indicate where there are significantly more telemetry locations within 1 km of the barrier than would be expected under the universal barrier relationship. The grey triangles represent the observed number of telemetry locations per cell on the log scale. The larger the triangles the more telemetry locations. Grey lines: farm boundary condition unknown, red lines: solid farm boundaries, orange lines: well-maintained fences with some gaps, blue lines: perforated farm boundary fences, dark green lines: main roads, lime green lines: district roads.

3.3.3 Springbok

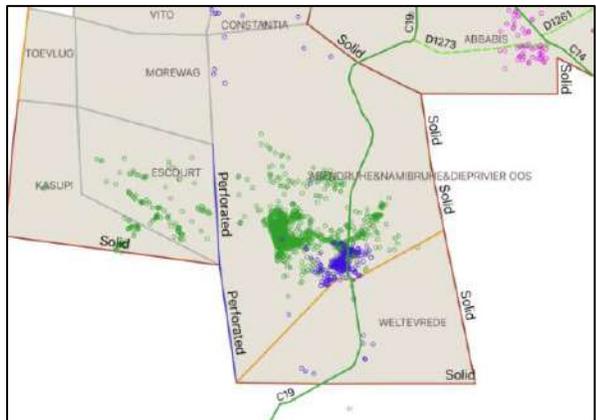
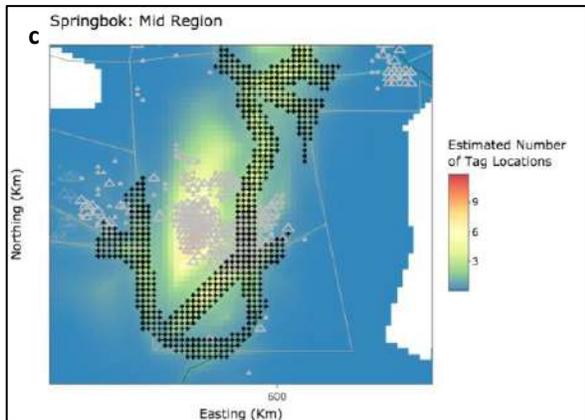
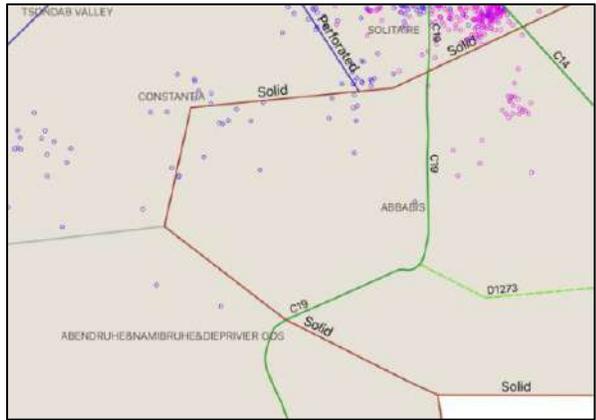
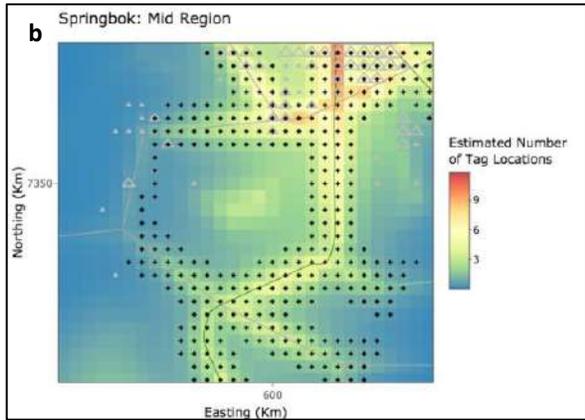
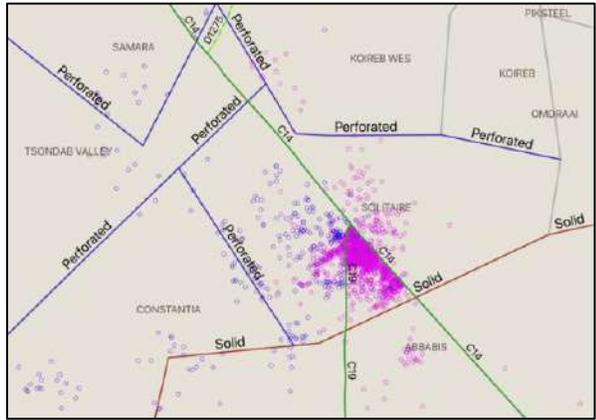
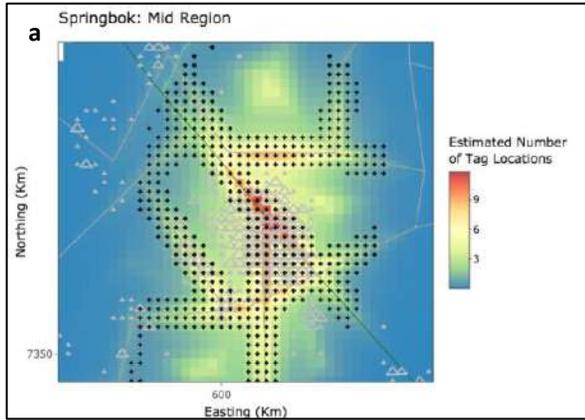
There was a significantly higher number of springbok location points within 1 km of the C14 and C19 main roads (Figure 15 a). Some blockage was caused by the C14 road (although springbok were able to cross at some points along the road). There was also a significant number of springbok locations along the Abbabis farm boundary fence (Figure 15 a and b). The actual springbok data show that the fence, which is supposed to be solid (well-maintained), did allow the movement of springbok across it, albeit much reduced.

The north and south Weltevrede farm boundary fence seemingly impeded the movement of springbok significantly (Figure 15 c). This fence, though it has some gaps which allow the passage of animals, is mostly well-maintained. Although the fence between the Namib Desert Lodge and neighbouring properties to the west was marked as a possible hindrance, there was no disproportional location point distribution. in their vicinity.

The C19 was marked as a potential obstruction across the entire mid region (Figures 15 a – c). Upon further inspection of the actual springbok data, the C19 road may pose an obstruction to springbok movement in the north part (Figure 15 a and b).

In the southern region of the study area, the boundary fences to the east of NamibRand were found to significantly increase springbok locations (Figure 15 d).

The boundary fence of Wereldend livestock farm, as well as the C27, were identified as problem barriers (Figure 15 e), as springbok locations were abundant against the farm/road fence and none of the springbok were able to cross onto the other side (neither from Weltevrede onto NamibRand or vice versa, nor across the C27). A significant number of estimated springbok locations were located along the solid farm fence between Dina and Kameelhof, as well as the C27 road (Figure 15 f).



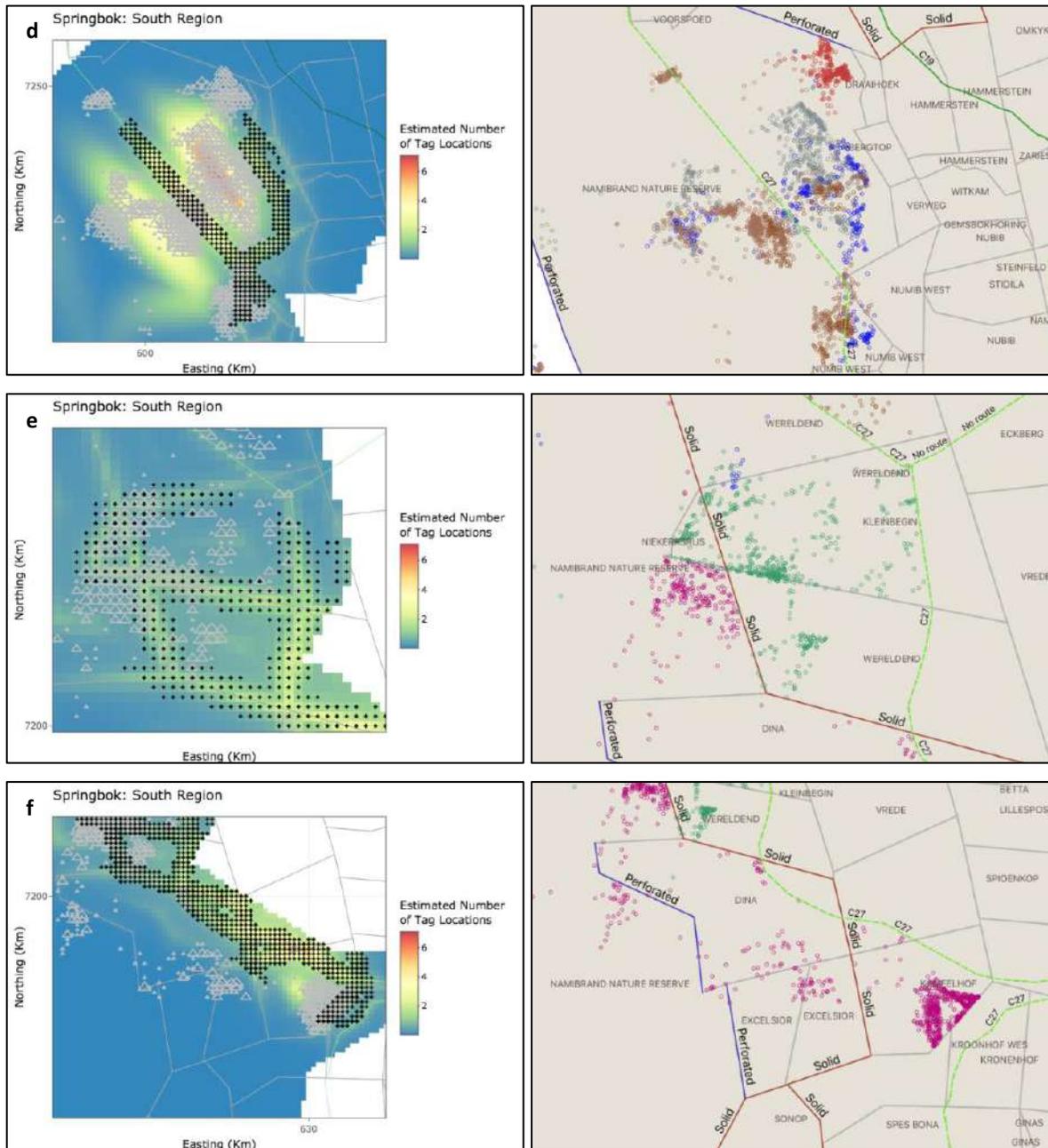


Figure 15: a - f: Estimated number of springbok telemetry locations per cell. The '+' symbols on the plots indicate where there are significantly more telemetry locations within 1 km of the barrier than would be expected under the universal barrier relationship. The grey triangles represent the observed number of telemetry locations per cell on the log scale. The larger the triangles the more telemetry locations. Grey lines: farm boundary condition unknown, red lines: solid farm boundaries, orange lines: well-maintained fences with some gaps, blue lines: perforated farm boundary fences, dark green lines: main roads, lime green lines: district roads.

3.4 Hotspot analysis related to topography

No coldspots were identified in any of the species' data sets, indicating no specific areas of avoidance. In general for all species, statistically significant hotspots of animal locations occurred at the base of mountains and hills, and also along certain roads and fencelines. These will be discussed in detail, for each species, in the section below.

3.4.1 Hartmann's mountain zebra

Hartmann's zebra hotspots in the Central Namib occurred along the eastern border of the NNP, between the Langer Heinrich Mountains and the D1982 district road, as well as along the C14 main road, and in the Central plains around Hirabeb (Figure 16 a). Zebra had hotspots of occurrence around Solitaire, in the ecotone of the Rant mountains, along the D1261 district road, in the Naukluft mountains (NNP), and along the C19 main road (Figure 16 b). More hotspots were found around Neuras (Naukluft mountains), in the Tsaris and Nubib mountains (Figure 16 c).

3.4.2 Gemsbok

Highly significant hotspots ($P > 0.99$) occurred on the northern edge of the NNP along the mountain outcrops, which SAT1106 preferred, and along a section of the Rant mountains on Farm Abbabis, which was inhabited by SAT1765 (Figure 17 a).

Hotspots of gemsbok occurrence (SAT1766 and SAT1103) were identified around Namib Desert Lodge and in the neighbouring dune fields; in the Naukluft mountains on the eastern side of the NNP, where SAT1101 was located; on the outskirts of the Naukluft mountains which were preferred by SAT1102 and SAT1105; and on the Sesriem property where SAT1104 moved around and penetrated into the adjacent dunes (Figure 17 b).

Furthermore, highly significant hotspots occurred at the base of the Nubib mountains on the Kwessigat/Draaihoek side of NamibRand which was frequented by Gemsbok SAT1100 and SAT1107_1769, as well as on the eastern side of the Nubib mountains, on the Voorspoed and Hammerstein properties, which were traversed by gemsbok SAT1107_1769 (Figure 17 c). Other hotspot areas included Losberg, the Chowagas mountains and Satanskop, where gemsbok SAT1108, SAT1109, SAT1107_1769 and SAT1770 roamed.

3.4.3 Springbok

Highly significant hotspots occurred in the Solitaire area, where SAT131 and st2010-2803 ranged (Figure 18 a). The former mostly concentrated its activities on the eastern side of the C19 road and the latter more on the road's western side. One springbok, st2010-2800, moved into the dune fields adjacent to the Namib Desert Lodge, but its main area of preference (highly significant hotspot) was on the Namib Desert Lodge property.

Springbok SAT132, SAT132.2, SAT133, st2010-2797, st2010-2798, and st2010-2799 roamed on the northern section of NamibRand, and their areas of preference tended to be along the western side of the Nubib mountains, at the base of the Losberg mountain and Bushman Hill, as well as the area around Keerweder (Figure 18 b).

A highly significant hotspot was located at the fence separating Die Duine (NaDeet) from Niekerksrus, and another further southeast, in an area where two district roads join each other at an angle (Figure 18 c).

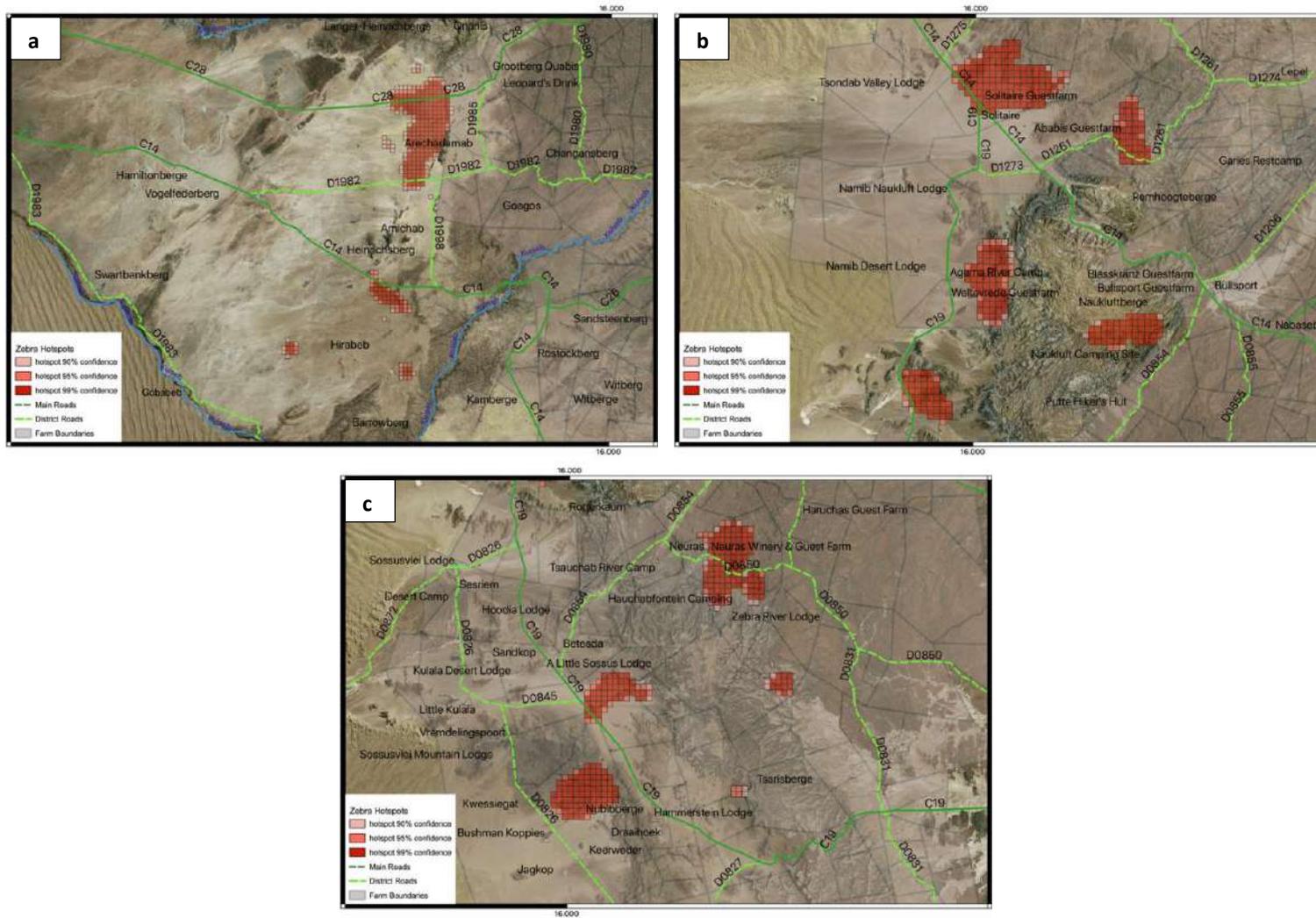


Figure 16: a - c: Hartmann's mountain zebra hotspots.

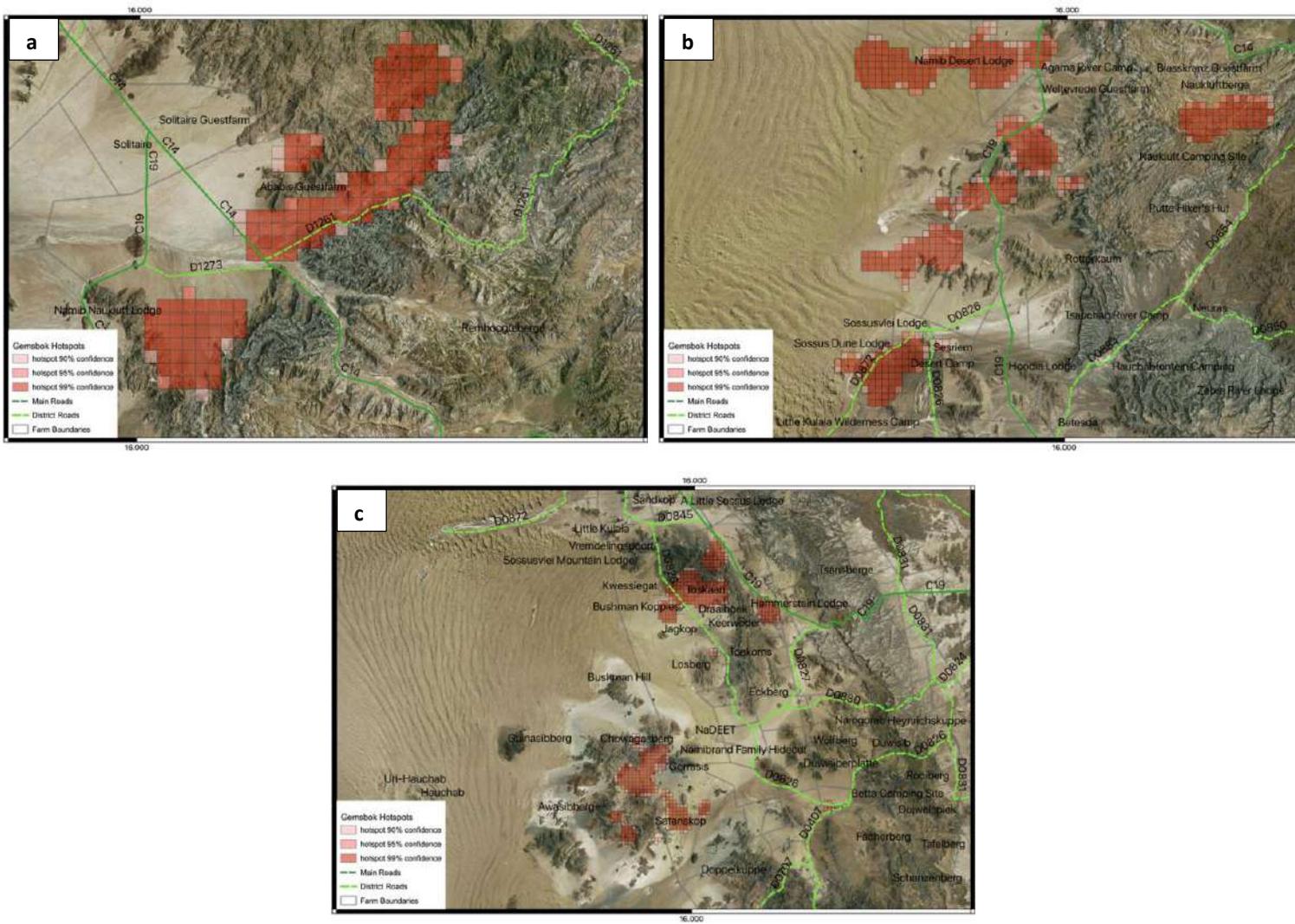


Figure 17: a - c: Gemsbok hotspots.

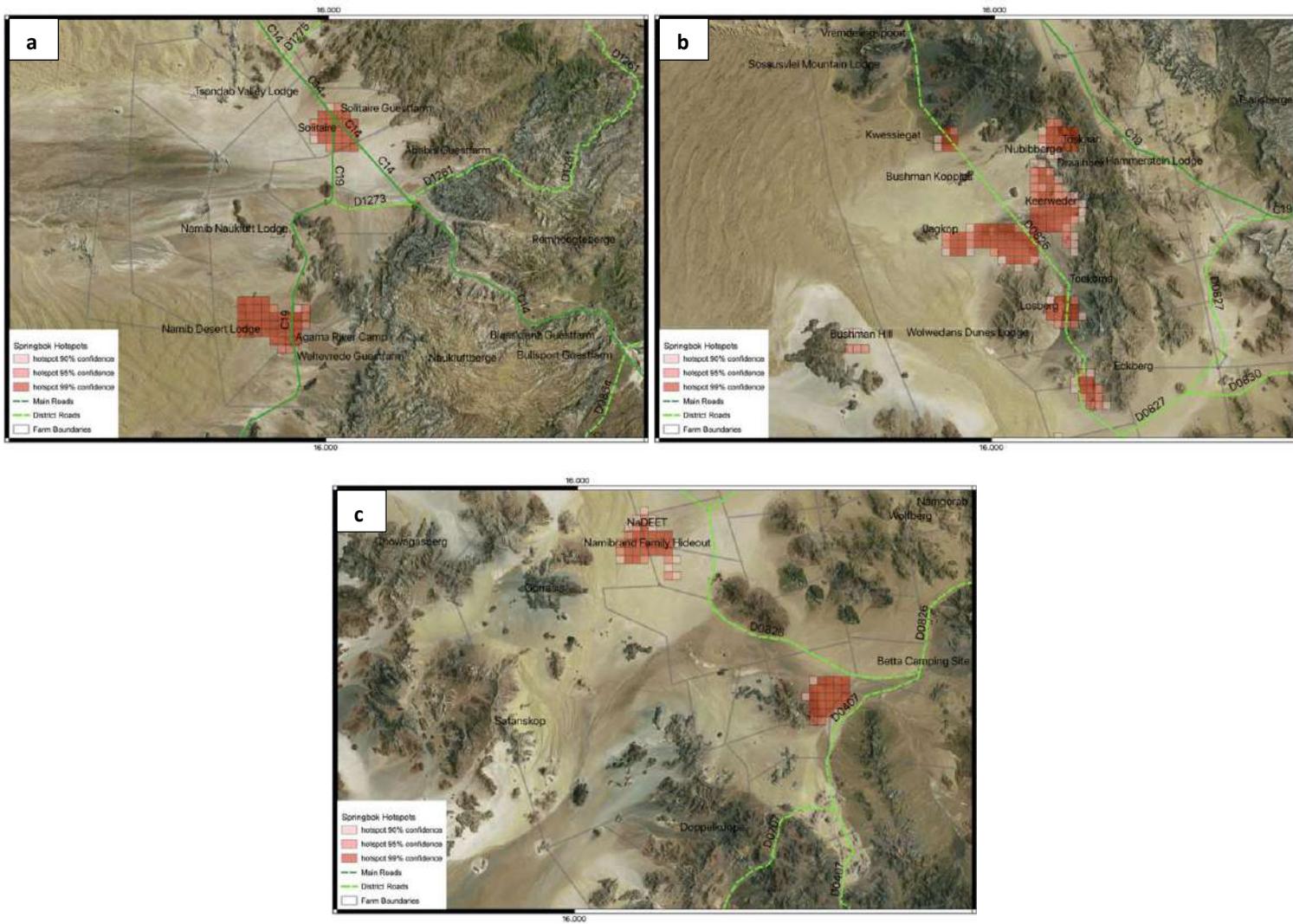


Figure 18: a - c: Springbok hotspots.

Chapter 4: Discussion

It is clear that fences affect the home range size and shape, and movement of all three species in the study area. The effect is however varied in intensity between species and per geographic location. Springbok and gemsbok were found to be most affected with several areas where fences significantly affected their movement, while Hartmann's zebra were least affected and moved rather freely through most fences. Water (McKee *et al.* 2015), food availability (Brown and Orians 1970, Tufto *et al.* 1996) and social organisation (Burt 1943) also affect home range size and shape considerably.

4.1 Home range sizes

The larger home ranges of gemsbok and Hartmann's zebra compared to springbok is explained by the relationship of energy demands and body weight (McNab 1963). Species with larger body sizes (i.e. body weight) have higher energy expenditure and must therefore consume more food and in this arid environment move further distances to meet their energy demands than species with smaller body size.

4.1.1 Hartmann's mountain zebra

Hartmann's zebra in the GSNL ranged over exceptionally large areas, compared to those in the Daan Viljoen Game Reserve and the Etosha National Park (Joubert 1972b) where previous studies on the species were conducted. The larger home range sizes in the GSNL are likely due to the aridity of the area. Animals in these environments have to move over larger areas in order to satisfy their energy demands. They also exceeded the range sizes given by Bothma and du Toit (2010) for unrestricted areas which was 200 km². The home ranges sizes (based on the 95% KDE) of six Hartmann's mountain zebra monitored between 2011 and 2013 in a 14,227 km² study area in the Kunene region of Namibia averaged 681 km² and 256 km² in the rainy and dry season respectively (Muntifering *et al.* 2019). The largest was approximately 950 km², which is comparable to that of SAT1092 (925.5 km²) in the central Namib, north of the Kuiseb.

The home ranges were comparable to the 100% MCP ranges of Przewalski's horses *Equus ferus przewalskii* in a large protected area in the arid Mongolian Gobi (which ranged from 152 – 826 km² with a mean of 471 km²). The MCP sizes of Hartmann's zebra in the GSNL were larger than those of Burchell's zebra *Equus burchelli antiquorum* in the Kruger National Park, which varied between 49 km² to 566 km²

(with a mean of 164 km²) (Smuts 1975), but much smaller than those of plains zebra (*Equus quagga*) in the Serengeti which were estimated to be at least 1,000 km² (Klingel 1969).

Hartmann's zebra are said to be migratory (Gosling *et al.* 2019) and to have separate dry and wet season ranges, some as far apart as 120 km (Joubert 1972b). Individuals in the Kunene region displayed differing degrees of overlap between dry and wet season ranges, with some having less pronounced (i.e. highly overlapping) seasonal home ranges (Muntifering *et al.* 2019). This trend of different movement patterns displayed by different individuals is representative of the GSNL: my study individuals in the Naukluft and Nubib mountains generally had smaller and more concentrated home ranges, indicating that they were more sedentary, while those in the central Namib and on farmland to the east of the GSNL generally displayed a distinctive north-south and east-west movement pattern respectively.

Home range sizes and space use of equids are strongly influenced by resource availability and the distribution of water sources (Schoenecker *et al.* 2016). The observed north-south and east-west movements may be seasonal in nature as with other Hartmann's zebra discussed above, or it may have been in response to patchy rainfall, as is the case with plains zebra in the Laikipia district of Kenya (Georgiadis *et al.* 2003). In fact, primary productivity is highly correlated with precipitation in arid regions (Noy-Meir 1973). Muntifering *et al.* (2019) found that Hartmann's zebra selected for areas of high primary productivity and hence high-quality grazing. The north-south movement of individuals in the central Namib, may have been between areas where grass cover appears with some regularity (which is mostly between Gobabeb and Ganab) mainly after summer rainfall (Seely 1978b), the permanent water sources that occur in this area (Kok and Grobbelaar 1985) and the Kuiseb river in the dry season when water is still available for a while in small pools in the canyon section or due to animal excavations after the Kuiseb river flowed (Kok and Nel 1996). Likewise, the east-west movement of Hartmann's zebra was probably in response to the tracking of improved food resources along the rainfall gradient towards the east.

It is conceivable that the individuals with smaller and more concentrated home ranges selected areas close to permanent water sources, as was the case with Hartmann's zebra in the Kunene region which did not venture more than 4 km from water sources (Muntifering *et al.* 2019). Contrary to findings by Joubert (1972b), the collared individuals in this study did not follow seasonal patterns of movement, as

each individual maintained a stable home range in different parts of the Naukluft mountains (north, east and west) over the entire 1.5 to 2 years that the three individuals were tracked.

4.1.2 Gemsbok

Female gemsbok in the Central Kalahari Game Reserve (CKGR), which were tracked by satellite over 9 months, had home ranges between 152.7 km² to 1,154.6 km², with a mean home range of 604.7±332.0 km² (estimated using the MCP method) (Tromp 2015). The mean MCP of gemsbok in the CKGR and GSNL are comparable, with individual gemsbok MCPs in the GSNL showing even greater variability. In another, much older, study carried out in the CKGR, a female's home range was 52 km² (Williamson and Williamson 1988, as cited in Skinner and Chimimba 2005), and hence comparable to the smaller home range size of gemsbok SAT1106 in the Naukluft area of the GSNL.

The gemsbok in the GSNL had considerably smaller mean home ranges than those in the Kgalagadi Transfrontier Park, which were studied by Knight (1991). In the Kalahari Gemsbok National Park, radio-collared female MCP home ranges over the entire study period were between 430 km² and 1,941 km² (\bar{x} = 1,103±629 km², n=6), while they were between 2,529 km² and 10,224 km² (6,516±3,867 km², n=3) in the Gemsbok National Park (Knight 1991).

The larger home ranges of gemsbok individuals ranging further south, around NamibRand and the surrounding areas, suggests a greater freedom of movement than those in the northern GSNL. This was made especially clear by SAT1770's extremely large home range, as well as that of SAT1107_1769, both of which ranged on the unfenced NamibRand and surrounds. There was a visible pattern that gemsbok on NamibRand moved at the bases of various hills, mountain outcrops and the Nubib mountains. This is consistent with findings from Kilian (1995) that gemsbok distribution is influenced by the vegetation on sandstone substrates mainly occurring along large granite outcrops or mountains. Female gemsbok in the Palmwag concession of the Kunene region (north-west Namibia) responded to resource fluctuations by exploiting a combination of habitats (open areas, riverbeds and hillsides) differing in vegetation cover, plant productivity and topography (Lehmann *et al.* 2020). Furthermore, spatial configuration of the underlying landscape is an important determinant of home range size, as it determines the actual distance an animal has to move to fulfil essential requirements for survival (Bevanda *et al.* 2015). Due to the lack of fences, gemsbok on NamibRand were able to increase their range to exploit possibly better resource availability after localised rain showers, to move between the various mountains and hills that

were located at different distances from each other, and to include in their home ranges the different habitat types (sand and gravel plains, vegetated dune belts, dry river beds, and mountain ranges) on NamibRand.

Conversely, two gemsbok in the Naukluft area of the NNP had comparatively small home ranges, which could not be sufficiently explained by the presence of fences. These differences again can be described by differences in resources and food availability in response to rainfall in the GSNL, which is highly variable both spatially and temporally (Noy-Meir 1973, Seely 1978b, Seely and Pallett 2012).

Female gemsbok in the Palmwag concession of the Kunene region (north-west Namibia) responded to resource fluctuations by exploiting a combination of habitats (open areas, riverbeds and hillsides) (Lehmann *et al.* 2020). While core areas remained stable with variations in NDVI values, the total home ranges increased with decreasing NDVI values, which shows the inverse relationship between food availability and home range size. Gemsbok in the Naukluft mountains had the smallest home ranges, which is expected in an area that lies in a higher rainfall area (between 100 – 150 mm annual rainfall isopleth).

4.1.3 Springbok

Springbok home range and core area sizes were much larger compared to those reported in most of the literature. Most studies report about the territory sizes of springbok males (Mason 1976, David 1978, Jackson *et al.* 1993). Less is known about the home range sizes of females and of non-territorial males (Mechkour *et al.* 2008), especially in large and open areas such as NamibRand. The home ranges of springbok family herds (consisting of adult ewes, subadult female and male and female juveniles) are between 3.00 – 8.00 km² in size (Furstenburg 2016b) while those of territorial males ranged anywhere between 0.01 – 0.70 km² depending on the location in question (Apps 2012). Specifically, territory sizes were between 0.27 to 0.70 km² in the former 31 km² Jack Scott Nature Reserve in the Transvaal, South Africa (Mason 1976), and 0.10 – 0.40 km² in the 27.86 km² Bontebok National Park, Swellendam, South Africa (David 1978).

A study conducted in a small (0.18 km²) reserve in southern France using scan sampling to sample springbok locations reported home range sizes (derived from the 95% MCP method) of 0.15±0.004 km² for thirteen adult females, as well as 0.1 km² and 0.06 km² for two adult male springbok (Mechkour *et al.*

2008). The same study reported a mean core area (estimated using the 50% fixed kernel estimation method) of $0.04 \pm 0.005 \text{ km}^2$ for the females, and 0.03 km^2 and 0.02 km^2 for the two males. Territory sizes in the $52,145 \text{ km}^2$ Central Kalahari Game Reserve (CKGR) in Botswana (Selebatso *et al.* 2018) were still only $0.17 - 0.30 \text{ km}^2$ (Williamson 1985, as cited in Mechkour *et al.* 2008). However, comparisons should be made with caution as different studies use different location sampling and home range estimation methods. The studies mentioned above mostly used springbok sightings in the field and home range estimation was often carried out by linking the outer points of observation. Most of the above studies were also conducted in small reserves or national parks.

There is a paucity of modern home range studies using satellite telemetry and contemporary home range estimation methods for springbok. Furthermore, little is known about the home range sizes of springbok in large natural areas, such as the $1,722 \text{ km}^2$ NamibRand Nature Reserve. In general it is said that springbok are highly mobile and move long distances to reach the green vegetation that emerges after localised rain events (Coetzee 1969, Bothma and du Toit 2010, Furstenburg 2016b). Furstenburg (2016b) reports that, though nomadic populations are rare, so-called “trek-springbok” or “trekbokke” with a herd size of 400 to 1,200 individuals were recorded in the Western Cape (South Africa) and moved around in an enormous area. In a study of springbok in the south of the Kgalagadi Transfrontier Park, females and non-territorial males moved over large areas in response to environmental conditions (Jackson *et al.* 1993), though it was not investigated how large these areas were. Springbok centered their activities on the Nossob riverbed during favourable food conditions and dispersed into the dunes when food resources became limited.

Dougherty *et al.* (2017) investigated the home range sizes of springbok (four female and two male), based on GPS locations and using the Time Local Convex Hull (T-LoCoH) home range estimation method, in Namibia’s Etosha National Park in relation to anthrax. The mean home range sizes were 203.88 km^2 (SE = 59.7 km^2), 251.2 km^2 (SE = 72.5 km^2 ; $p = 0.04$), and 265.4 km^2 (SE = 76.2 km^2 ; $p = 0.03$) depending on different parameter selection (parameter selection based on the algorithm, using the low value of the range based on the guidelines, and using the high value of the range based on the guidelines respectively). These were comparable to some of the male springbok home ranges in this study.

In this study, more than half of the springbok individuals had home ranges larger than 160 km^2 , and one individual had an exceptionally large home range of 305.5 km^2 . It was notable that these springbok

individuals were able to move around relatively freely, with no obstruction or only partial obstruction by fences (refer to the next section on fences). Conversely, one male individual (SAT135) which was confined within the boundaries of one farm, had a much smaller home range (73.3 km²).

Yet, a male springbok (SAT133) which ranged in the northern section of the NamibRand private reserve, had the smallest home range of 15.0 km². The fact that this area is open and that there were no barriers that significantly affected its movement, may point towards possible territoriality of this individual. The springbok SAT133 was only tracked for 142 days (between August and January, which fall into the summer season), while springbok st2010-2798 which was tracked for 147 days and also ranged in the NamibRand area, had a much larger home range of 258.8 km² (the second largest of any springbok in the study). Although male territorial behaviour starts during the rut in late summer and autumn (Jackson *et al.* 1993) and lasts until food is depleted by the end of the dry season (Skinner 2013), territorial behaviour in springbok has been observed during summer, although this is less common (Bigalke 1972). It is interesting to note that both st2010-2803 and SAT132 were relatively sedentary and preferred to stay in close proximity to human settlements (one on Keerweder, the other on Solitaire). This suggests the presence of favourable resources, or access to more female springbok in these areas. Indeed, Ritter and Bednekoff (1995) found that the provision of artificial water resulted in the concentration of female movements close to the waterhole and affected male territoriality.

Several studies show that greater food availability reduces an animal's home range size, and vice versa (Brown and Orians 1970, Tufto *et al.* 1996, Jerina and Leslie 2012). The reason for this phenomenon is that greater food availability (corresponding to the rainy season) results in animals having to forage over smaller areas to find food (McLoughlin and Ferguson 2000). This could be another reason for the differences in individual home range sizes observed in the GSNL.

For comparison purposes, Mhorr gazelle (*Nanger dama mhorri*), extinct in the wild since 1968 and comparable to the springbok in both height and weight (Castelló 2016), were re-introduced into the 3,075 km² Safia Nature Reserve in southern Morocco, had an average home range of 119.9±27.5 km² and core area of 20.0±4.2 km² (Abáigar *et al.* 2020). Grant's gazelle were found to have a large annual home range of 290 km², while Thomson's gazelle had a seasonal home range of 42 – 65 km² (wet season) and 142 km² (dry season) (Martin 2000).

However, home ranges of springbok were considerably less than Mongolian gazelles (a medium-sized gazelle). Olson *et al.* (2010) found that eleven adult female Mongolian gazelle had annual range sizes of between 14,661 – 32,298 km² (determined by the MCP method), while Imai *et al.* (2017) found that annual range sizes of twenty Mongolian gazelles varied between 900 to 37,000 km² (determined by the 95% fixed kernel home range method of Worton (1989)). Mongolian gazelles are considered either nomadic (Olson *et al.* 2010, Nandintsetseg *et al.* 2019), migratory (Miura *et al.* 2004), or even display a wide variety of different movement patterns from residency to seasonal migration (Imai *et al.* 2017).

The mean home range size of female mountain gazelles (*Gazella gazella gazella*) on Mount Carmel, in Ramat HaNadiv, Israel, in an area of 4.5 km² surrounded by agricultural fields and human settlements, was found to be 0.17±0.005 km² (using 90% MCP method) (Geffen *et al.* 1999).

4.2 The barrier effect of roads and fences

Farmland in the east of the study area (particularly in the mid and southern areas) causes large-scale fragmentation of the landscape through fences and roads. The main ecological consequences of roads and fences in the GSNL were related to barrier avoidance or blockage to movement, which influenced the distribution patterns of ungulate species, and the physical effect of barriers, which prevented movement of individuals across these barriers. The presence of barriers also affected ungulate home range sizes, as those individuals ranging in more open systems (less barriers) had larger home ranges and vice versa.

4.2.1 Home ranges as related to barriers

In general, ungulate home range sizes were smaller in areas where there were physical barriers, including either roads (fenced and unfenced) or fences around land units. The effect of roads and fences on decreasing home range sizes has been found in tortoises (Peadar *et al.* 2017) and ungulates (Gulsby *et al.* 2011). The decrease in home range size could be due to multiple factors, including road avoidance behaviour, the inability to cross roads due to the physical barrier of fenced corridors, or the increased availability of food resources along roads that reduces the need of animals to move large distances to find forage (Lightfoot and Whitford 1991, Gonser *et al.* 2009, Keken *et al.* 2019).

Fences and roadside fences are problematic for ungulate species, particularly in arid ecosystems, where they need to be highly mobile to access important food and water resources, and even more so in the face of climate change (Mbaiwa and Mbaiwa 2006, Durant *et al.* 2015, Bennett 2017). In the GSNL, gemsbok and springbok movements were found to be more characteristic of movements performed by nomadic desert-dwelling ungulates that inhabit arid areas (Jonzén *et al.* 2011). As these are not spatially/temporally predictable and a lack of seasonality exists (Nandintsetseg *et al.* 2019), the highly unpredictable food availability coupled with the low food abundance in these environments does necessitate a high mobility of desert-dwelling ungulates in order to satisfy their food requirements. This high mobility of ungulates in the GSNL was reflected in their generally large home ranges. In those areas such as NamibRand, where the ungulate species were free to roam without major obstructions caused by roads and fences, home ranges were generally larger and location points were less concentrated. Those individuals that ranged in areas with higher fence and road densities had considerably smaller home ranges, which is likely to have had a restrictive impact on their ability to move to areas with greater food abundance and quality after localised rainfall.

Fences and roads are more likely to negatively impact Hartmann's zebra's ability to move in response to their food and water requirements, as they display migratory movement patterns (Gosling *et al.* 2019). However, some individuals in this study that roamed on farmlands east to the GSNL had elongated home ranges, that were east-west. This indicates that their movement is not as affected by farm fences as much as gemsbok and springbok are. Hartmann's zebra are known to move across fences, either by using permanent fence gaps or by crossing breaks created by rivers or other animals (Gosling *et al.* 2019). Also, fences may not be as well maintained in mountainous areas due to their inaccessibility, and hence movement across these permeable barriers was possible. It is notable that Hartmann's zebra home ranges were still much larger in areas without fences (such as the Central Namib area) than those with fences, indicating a degree of movement limitation caused by fences.

The availability of more forage along roads (which is discussed further down) may have had an impact on decreasing home ranges of animals, especially for Hartmann's zebra and springbok which were found to prefer areas close to barriers (within 1 km).

4.2.2 Ungulate distribution in relation to barriers

Springbok and Hartmann's zebra were at most stages close to road and fence barriers. Gemsbok seemed to be barrier averse, and were generally not found close to any barriers. Springbok location densities and proportions were greatest less than 1 km, as well as between 3 to 5 km from barriers. Gemsbok location densities and proportions were greatest approximately 3 to 5 km from any barrier. Hartmann's zebra location densities were generally close to barriers, which declined with distance from the barrier, with the largest proportion of locations located within 1 km of the nearest barrier with another peak at 2 km.

Contrary to expectations, springbok were associated with areas closer to barriers. Similar observations were made for Kenyan wildebeest (Stabach *et al.* 2016) and gemsbok introduced to the San Andes mountains, New Mexico (Hoenes and Bender 2010). Several explanations for the proximity of springbok to barriers could be possible. Springbok may have been attracted to roadsides due to increased forage availability. The availability of greater vegetation growth along roads may be due to the effect of greater rainwater runoff (Frenkel 1977, Lee *et al.* 2015), which is often a driving factor for plant growth adjacent to roads in arid ecosystems which are limited by water (Noy-Meir 1973, Westoby 1979) and in turn affect animal distributions (Noy-Meir 1973, Smith and Morton 1990). Furthermore, some individuals may have chosen to forage close to roads in order to escape competition, or were forced to forage in these areas due to the presence of territorial springbok individuals in more favoured/preferred habitat. It was also observed that springbok preferred to remain close to human settlements (such as Keerweder and Solitaire), possibly due to the presence of permanent water sources, thereby automatically being in closer proximity to roads and fences (Hoenes and Bender 2010, Stabach *et al.* 2016). The most likely explanation for the observed spatial pattern was the above in combination with barrier effects to springbok movements. It was clear that springbok movements were significantly affected by barriers in the GSNL due to the consistent aggregation of locations closer to barriers. The same observations of fence aggregation were made for African savannah elephants in the wet season (Loarie *et al.* 2009).

The Hartmann's zebra distribution model indicated a high association with areas close to barriers. This was contrary to observed frequencies of Burchell's zebra, which were found to peak at 1.4 – 3 km from the highway (Newmark *et al.* 1996), but was in line with findings for Hartmann's zebra ranging in the north-west of Namibia (Muntifering *et al.* 2019). Apart from higher availability of vegetation along roads which could have shaped the associated density patterns, Hartmann's zebra's preference for being close

to barriers may have resulted from the high density of fences and roads in the areas where they occurred. The most obvious restriction of their movements was caused by main roads especially, as well as district roads. Road fences are better maintained than fences between farms in mountainous areas, due to their high accessibility and the hazard of wildlife vehicle collisions. When looking at the presence of roads in relation to the landscape characteristics of the GSNL, it is notable that roads often closely follow the outlines of mountain outcrops and meander between mountain ranges. This may interfere with Hartmann's zebra's movements between mountains and plains, and may bisect their available habitat, causing an accumulation of locations along roads. Although zebra movements were not generally restricted by farm fences, as was shown by the east-west movement and high mobility of some collared individuals, they still had to find areas where fence crossings were possible, leading to an accumulation of locations along some fence segments.

No studies quantifying the effects of barriers on the density distribution of springbok, naturally occurring gemsbok and Hartmann's zebra could be found in literature. Only a few studies quantify the distance of ungulates to barriers (e.g. for roads, this is referred to the road effect zone) (Bennett 2017), with most studies having been carried out on other animal taxa including birds, birds of prey and reptiles in relation to roads, i.e. the road effect zone (Silva *et al.* 2012, Clarke *et al.* 2013, Nafus *et al.* 2013) or in relation to road-related behaviour such as crossing frequency (Grosman *et al.* 2011, Gulsby *et al.* 2011) or movement rates (Sawyer *et al.* 2013).

Gemsbok and springbok movements seemed to peak in density around 3 – 5 km from barriers, which was similar to other ungulate species, in terms of disturbance avoidance. Roe deer and red deer, as well as reindeer all showed a disturbance-averse behaviour, with the former two most frequently occurring between 1.5 to more than 3 km away from human disturbances (human settlements, logging sites and cropland) (Jiang *et al.* 2008), while reindeer avoided areas close to roads within 0 – 1 km (Beyer *et al.* 2016) or areas within 5 km from roads and powerlines combined (Nellemann *et al.* 2001). Several species show an avoidance behaviour towards fences, including endangered Przewalski's gazelle *Procapra przewalskii* (Zhang *et al.* 2014), which were influenced by fence density, type (barbed wire) and height; and elephant *Loxodonta africana* (Vanak *et al.* 2010).

Such avoidance behaviour of fences can result in edge effects which are exacerbated if the area (e.g. farms) the animals are restricted to have a high edge-to-area ratio, and a complex shape as opposed to

compact shapes (refer to Ewers and Didham (2006) for a review on species responses to habitat fragmentation). For example, one springbok (SAT135) was confined completely to a small farm section east to NamibRand and gemsbok SAT1765, which was confined to farm Abbabis, was also restricted by the mountains which is not their preferred habitat. Hence the actual area that was available for foraging and home ranging behaviour was much reduced. Similar observations were made in the Pilanesberg National Park (570 km²), where the edge effect on elephant movements of the impermeable boundary fence extended up to 3.8 km inward (Vanak *et al.* 2010).

Although edge effects are more pronounced in tropical ecosystems (van der Ree *et al.* 2015), it is a useful concept to bring into this discussion. According to classical edge effect theory, animal abundance should increase monotonically with distance from the edge (the edge being defined as the location of human disturbance) and therefore should be highest at the furthest distance from the edge (Fortin *et al.* 2013). However, several studies show that abundance increases up to a certain distance from the edge and then decreases again. For example, Fortin *et al.* (2013) reported that forest-dwelling caribou abundance was highest in proximity (4.5 km) to cutovers and roads and decreased in an oscillatory manner. They attributed this non-monotonic response to three behaviours, including that animals move away from a site once it is disturbed, but at limited distances (most likely due to energy costs); that those animals that are already farther away do not relocate; and that the relocated animals remain away and adjust their movements to the disturbance. Studies that report an increase in abundance with distance from a disturbance (Nellemann *et al.* 2001, 2003) often do not incorporate sampling distances large enough into their study design to reflect the actual extent of edge effects (Ewers and Didham 2008).

Nevertheless, species-specific comparisons and interpretation of these varying distances to barriers should be made with caution. Most gemsbok individuals occurred in areas with less fencing (e.g. NamibRand, NNP) (see Figure 8 and 9 for comparison) and therefore their distance to barriers was automatically larger (and may have not been directly as a result of barrier avoidance). Collared Hartmann's zebra occurred mostly on farms to the east of the GSNL – their presence at barriers may have been a result of the higher density of fences and roads in this area, and generally more fragmented habitat (Figure 8 and 9). Furthermore, due to the marked east-west movement of some individuals, the probability of encountering fences was higher. For springbok individuals, most of which occurred on NamibRand, a combination of preferences for being close to roads in combination with aggregation at

barriers such as fences around NamibRand and on adjacent farmland due to movement limitations is a good explanation, as they could have avoided these barriers had they wanted to (due to higher freedom of movement on NamibRand).

It is also important to keep in mind that various areas of the GSNL are affected differently in terms of road traffic volumes and speed (e.g. Solitaire/Sesriem vs. NamibRand). For example, there is a speed limit of 40 km/h on NamibRand, while the national speed limit of 120 km/h applies to the main road between Solitaire and Sesriem. Parts of the GSNL are undeveloped and set aside for biodiversity conservation and low impact usage, such as several sensitive ecosystems in the NNP (including the Bushman Hills, Chowagasberge, Awasibberge, and parts of the Naukluft mountains) (Ministry of Environment and Tourism 2013a). Other parts, such as Sossusvlei, are very popular tourist attractions and therefore experience high intensity tourism. According to a survey carried out in 2012/2013, Sossusvlei and the Namib-Naukluft Park are among the 10 most visited places for holiday tourists, with 45% and 24% of tourists visiting these destinations respectively (Ministry of Environment and Tourism 2013b). The early morning traffic towards Sesriem gate into Sossusvlei reaches high volumes and dust is a nuisance and source of air pollution (although part of the road is currently being upgraded) (Southern African Institute for Environmental Assessment 2014). High traffic intensity and increased human activity exacerbate the avoidance of roads by wildlife (Beyer *et al.* 2013), which has been evidenced by several studies (Dyer *et al.* 2002).

4.2.3 Movement restrictions in relation to barriers

One of the main causes of road-related movement limitations for ungulates in the GSNL are associated with physical hindrances (as most roads are delineated by fences on both sides). In general, the main roads C14 and C19 that run from the coast to Maltahöhe and from Solitaire to Maltahöhe respectively were the most significant barriers to the movements of all three species. District roads, including the C24 that runs from Rehoboth and meets the C14 around Remhoogte, the C27 that runs from NamibRand further south to Helmeringhausen, and the D0872 to Sossusvlei also constituted significant barriers. The D0855 leading past Neuras towards the C14 also significantly affected zebra movements. However, the identification of movement restrictions was based on only 40 sampled animals in an area as large as the GSNL— more problematic barriers might be identified with additional animal tracking data.

This study showed that the national park fence in the north region of the study area (central Namib) was relatively impenetrable to Hartmann's zebra movements, especially the portion between the C28 to the north and the D1982 to the south. On the other hand, it did not totally obstruct ungulate movements in the mid (Naukluft area) and south (along NamibRand) where permeability permitted fence crossings. Farm (livestock) fences affected wildlife movements to varying degrees. While Hartmann's zebra were able to cross some fences, springbok and gemsbok were not as successful, their movements sometimes being completely restricted within farms or along fences until they found a fence gap to cross. Hartmann's zebra in the Kunene region similarly moved alongside the veterinary fence to find locations at which to cross (Muntifering *et al.* 2019).

Other studies have also found that the severity of fences varies. The majority of mammal species frequently crossed in and out of the boundary fences in the Lake Nakuru National Park (Kenya) (Wilkinson *et al.* 2021). Not even fence maintenance effectively prevented or slowed down fence crossings, as these resumed after 24 hours. Animal crossings are often further facilitated by fence breaking species (Schumann *et al.* 2006, Ferguson *et al.* 2012). Studies have also shown that animals display a strong fidelity to the same crossing sites (Dupuis-Desormeaux *et al.* 2018, Wilkinson *et al.* 2021). This shows that fencing is often ineffective in keeping in even the target species that they are designed for, and fence maintenance does not make fences more effective in some cases. Yet other studies showed that fencing was an effective tool in curbing wildlife movements outside parks and in mitigating human-wildlife conflicts (Kassilly *et al.* 2008, Loarie *et al.* 2009). Permeability of fences that cause the observed differences in the GSNL are possibly linked to several extrinsic and intrinsic factors, including fence design, type and alignment (Gadd 2012, Dean *et al.* 2018, Jakes *et al.* 2018), the landscape features, hydrology and resources that drive the movements both temporally and spatially (e.g. access to water and food) (Ferguson *et al.* 2012, Wilkinson *et al.* 2021), and species-specific predictors of crossing (body size, agility and fence behaviour) (Karhu and Anderson 2006, Pirie *et al.* 2017). Fence condition plays an important role (Pirie *et al.* 2017), as holes in the fence can benefit even species such as springbok (personal observation), which otherwise have little chance to cross fencelines, as well as holes underneath fences dug by species such as porcupine, armadillo or armadillo (Cunningham 2019), which permit springbok and gemsbok to crawl underneath.

Another important finding is that even when individuals succeeded in crossing fence segments, it often took a great amount of time for them to find weak spots, indicated by their persistent movement along

farm and road segments. This movement barrier was particularly evident in a gemsbok (SAT1107_1769), which was tracked for the longest time (1,416 days). It moved along approximately 38 km of road fence and 21 km of farm fence in order to move eastwards (approximately 16 months of its tracking period), yet it never succeeded in crossing these barriers. It is highly likely that its crossing attempts lasted for a longer time, but this could not be verified as there was an 8-month gap in its tracking period. Such persistence was also observed in Mongolian gazelle *Procapra gutturosa* which moved persistently along a fenceline for 59 days for a median distance of 11 km (ranging from a few hundred meters to 80 km) (Nandintsetseg *et al.* 2019). Yet even those individuals that were tracked for a shorter time or those that crossed successfully showed persistent movements along barriers. These fence interactions amount to high energy expenditures by wildlife in order to negotiate fences (McInturff *et al.* 2020, Xu *et al.* 2021).

The findings support those of other studies that human infrastructure plays a substantial role in shaping animal distribution, and that species-specific differences in responses to edge effects exist (Johnson *et al.* 2005, Jiang *et al.* 2008, Fahrig and Rytwinski 2009, Duffett *et al.* 2020). For ungulates, these responses are driven by predation risk (e.g. browsing/grazing less intensively at high risk sites) due to predator's preferential use of linear features (for example, wild dogs and cheetah use roads when hunting) (Frair *et al.* 2005, Bothma and du Toit 2010), the perception of ungulates that human disturbance equates predation risk (Gavin and Komers 2006, Bonnot *et al.* 2013), improved forage (Frenkel 1977, Rea 2003, Gonser *et al.* 2009, Keken *et al.* 2019), and behavioural traits related to morphology (body mass), foraging habits and social aggregation (Duffett *et al.* 2020), as well as gender and life history stage (Beauchesne *et al.* 2013).

Ungulates frequently surf the wave of improved greenness (i.e. "the green wave"), signified by higher NDVI values, to exploit higher quality forage (Mueller *et al.* 2008, Merkle *et al.* 2016, Aikens *et al.* 2017, Middleton *et al.* 2018). The barrier effect of linear infrastructure can lead to the interruption of these movement responses, by reducing high quality forage habitat available to ungulates, with effects felt most severely in the dry season or in resource-poor patches (Nellemann *et al.* 2001, Boone and Hobbs 2004, Jones *et al.* 2019). The consequences of these movement limitations are felt most severely in droughts. In the 1980 – 1982 drought, hundreds of Hartmann's zebra carcasses were counted along the veterinary fence in north-western Namibia (Gosling *et al.* 2019), while a decline in gemsbok numbers in dry periods in the GSNL were attributed to the NNP fence (Global Environment Facility n.d.).

Avoidance effects of roads (e.g. gemsbok) can prevent access to areas with higher vegetation abundance (Zhang *et al.* 2014), while barrier attraction (such as observed with springbok and Hartmann's zebra) can result in increased vehicle collisions and fence entanglements.

The consequences of movement limitations are likely to worsen due to the effects of climate change in southern Africa, which will experience increases in surface temperatures (James and Washington 2013, Engelbrecht *et al.* 2015) and intensified droughts (IPCC 2012), with the region projected to become generally drier (James and Washington 2013). These factors may also increase human-wildlife conflict in the GSNL, in terms of fence damage, grazing (e.g. Hartmann's zebra and livestock) and the pressure of increasing tourism on water levels which will be in direct competition with wildlife water needs.

4.3 Hotspots of occurrence

Identified hotspots of Hartmann's zebra movements confirmed the above findings of movement restrictions caused by linear barriers. In particular. The results showed the importance of topographical features, such as the bases of mountains, mountain outcrops and hills for ungulates in the GSNL. Similar findings have been made of gemsbok in the southern Namib by Kilian (1995), who observed that they aggregated on sandslope substrates along mountains and granite outcrops. In the Haiber region (around the Bushman Hills, Chowagas- and Awasib mountains), these topographical features support dicotyledonous vegetation and sufficient browse along drainage lines from the mountains.

The topographical features of granite outcrops and mountains have an impact on the distribution of rainfall and runoff (Günster 1995). Primary production, while dependent on rainfall, is influenced by topography, which results in greater water run-on in certain areas (such as at the edge of mountains) (Patten and Ellis 1995). Seely (1978b) found that areas close to inselbergs had a higher grass standing crop after the rainy season. Topography also constitutes an increased cost of locomotion (Powell and Mitchell 1998), meaning that animals such as gemsbok and springbok may choose not to enter mountain ranges or to cross topographical features, thereby moving around these for foraging.

Chapter 5: Conclusion

Hartmann's zebra had larger home ranges compared to individuals of the same species tracked in other parts of Namibia. Gemsbok had the largest home range during the study period, followed by Hartmann's zebra and springbok. It seems that gemsbok and springbok were most affected by fences. Hartmann's zebra were most adept at moving across barriers than the other species – moving into the adjacent commercial farming area. There are distinct barriers which impede the movement of the study animals (see summary of barrier impacts in Figure 19 below). These are the main roads C14 and C19, several district roads (C24, C27, D0855), parts of the Namib-Naukluft fence (especially in the north region of the study area in the central Namib), as well as farm (livestock) fences, including those to the east of NamibRand). Barriers were found to impact ungulate movements considerably in some areas, and had differential effects on ungulate distribution – some species found further away from fences (gemsbok), while others (Hartmann's zebra and springbok) were found close to fences. The findings should provide an incentive for further research on the impact of linear barriers on wildlife in Namibia, especially in the more arid parts of the country. In light of the negative effects of these barriers on wildlife in combination with projected trends in climate change and the increasing habitat fragmentation caused by anthropogenic activities, mitigation measures should be prioritised by landowners in the GSNL.

Chapter 6: Management implications & future research opportunities

The vulnerabilities of the three ungulate species to habitat fragmentation by roads and fences is likely to differ, based on their different traits and interaction with barriers. Henle *et al.* (2004) found six traits that are good predictors of species vulnerability to habitat fragmentation, all of which can interact and increase vulnerability, namely population size and variability (fluctuations), competitiveness, disturbance sensitivity, ecological specialisation, rarity and biogeographic location. The study of barrier effects in the GSNL suggests that gemsbok could be more affected by barriers due to their apparent barrier avoidance and the restriction of their movement due to roads and fences. Gemsbok and springbok are classified as fence-crawlers and non-jumpers respectively (Bothma and du Toit 2010). They both crawl underneath fences, and either jump over fences (gemsbok) or jump through holes in fences if there are weak spots (personal observation). This indicates the important role that barrier permeability plays in combination with barrier behaviour for mitigation strategies in areas where complete fence removal is not an option. Though Hartmann's zebra did not seem to be as affected by fences as they were relatively mobile, populations of Hartmann's zebra are more sensitive to fragmentation due to their small population size and rarity. Based on the above factors, increasing freedom of movement and limiting habitat fragmentation in the GSNL is of utmost importance for all three ungulate species.

A map of significant and possible barriers to ungulate movements details where such mitigation options could be applied (Figure 19). It is acknowledged that inferences from modelling efforts should be made with caution as these depend on factors such as the limited sample size for an area as large as the GSNL and the accuracy of model predictions made on such a large scale. Nevertheless, this map is a first step in identifying possible problem fences and roads on a coarse scale. Much more follow-up research is needed to refine our understanding of local barrier effects and behavioural responses of ungulates in order to provide a complete picture.

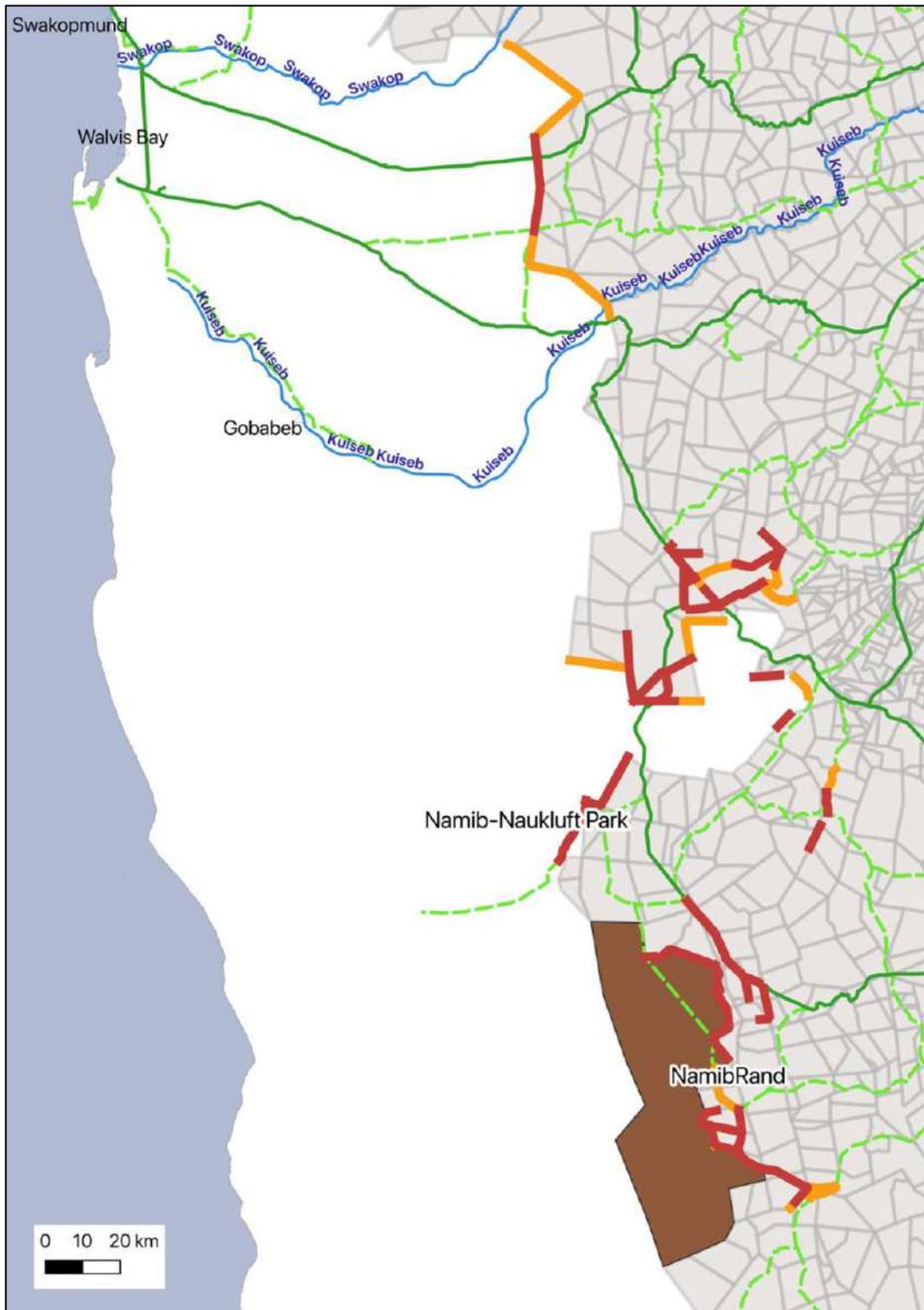


Figure 19: The identified barriers to ungulate movements in the GSNL. Orange = possible barriers. Red = significant barriers.

A few mitigation options exist, though it should be kept in mind that some mitigation measures are not as effective as others and not all impacts can be mitigated. Barrier permeability plays an important role in mitigating barrier effects (Xu *et al.* 2021), and can be employed to reduce the barrier effect of the identified fence segments. Furthermore, fence modifications or the construction of wildlife-friendly fences is a strategy employed by more and more wildlife and land managers (Paige 2012, Landguth *et al.* 2020). Recommendations are country-specific to the type of fence design used (in this case the US), and should be modified to suit the types of fences that are employed in the GSNL (and the target species they intend to keep in). They include the replacement of barbed wire with smooth wire, raising the bottom-most wire (or clipping it to the wires above with a carabineer/clip) to enable wildlife to crawl underneath fences without getting caught, lowering the top wire to enable wildlife to jump over successfully, and making the top wire more visible by using PVC-pipes. This will also aid kudu, which are fence jumpers (Bothma and du Toit 2010), to safely navigate fences. Because nomadic species do not follow specific movement corridors as migratory species do (Nandintsetseg *et al.* 2019), crossing options (roads) should be as frequent as possible and fence modifications/permeability should be employed at high risk sites (near water sources, areas with high density of ungulates, where ungulate mortalities frequently occur and where ungulates frequently try to cross linear barriers) (Harrington and Conover 2006).

It should also be kept in mind that if fences are purposely not maintained in order to facilitate wildlife movements, that these can become death traps (e.g. due to broken or loose wires) (Gadd 2012). Therefore, active fence removal of damaged fences and the removal of broken wires in the vicinity of fences is highly recommended. Where fence segments are removed to allow passage of wildlife but livestock movement restriction is desired simultaneously, horizontal grills could be used, as proposed by Gross *et al.* (1983). These type of grills should also be used as fence-end treatments if fence segments along roads are removed or made more permeable, in order to prevent ungulates from entering road corridors.

Although mitigation options can be costly (Huijser *et al.* 2009), fence damage requires substantial maintenance costs from landowners (time and materials spent to fix fences) (Harrington and Conover 2006) and more importantly, ethical factors regarding animal welfare and the “protection of nature for nature’s sake” (McCauley 2006), should be taken into consideration in a profit-driven world.

Wildlife-vehicle collisions have a strong temporal and spatial pattern, related to climatic variables (D'Amico *et al.* 2016, Carvalho *et al.* 2017), animal biology (seasonal breeding and dispersal, daily foraging), hunting activities (Hell *et al.* 2005, Diaz-Varela *et al.* 2011, Haigh 2012, Morelle *et al.* 2013), road density and traffic volumes (Morelle *et al.* 2013, Rhodes *et al.* 2014), and vehicle speed (Seiler 2005). Although road density is not expected to be an issue in the GSNL, other spatial and temporal factors should be investigated to come up with predictive models to identify hotspots of accidents. Wildlife crossing structures in combination with fences are most effective in reducing mortalities (by 83%) (Rytwinski *et al.* 2016) while enhancing connectivity. However, they are costly (Huijser *et al.* 2009), especially if not included in the road construction planning phase (Morelle *et al.* 2013). Other measures such as sign posts and lowering speed limits (Morelle *et al.* 2013) could be implemented in these key areas to reduce collisions, and hence enhance wildlife and human safety.

The effectiveness of wildlife warning reflectors, which are sometimes used to deter wildlife from crossing when a vehicle passes, is refuted by several studies (Rytwinski *et al.* 2016, Brieger *et al.* 2017, Bente *et al.* 2018) and hence not advisable. Another study demonstrated the effectiveness of Roadside Animal Detection Systems (RADS) that use electronic sensors to warn drivers when animals are close to roads, especially in the peak tourist season when tourists have been shown to drive faster (Grace *et al.* 2017). These have been found to reduce mortalities by 57% (Rytwinski *et al.* 2016) and hence are comparable to the effectiveness of road-side fencing. These are more likely to work for large animals, similar in size to deer, and not small- to medium-size animals (Huijser *et al.* 2015).

Fences along roads are often cited as a mitigation measure for wildlife-vehicle collisions (Rytwinski *et al.* 2016, Spanowicz *et al.* 2020). For example, one study found that fencing, by preventing wildlife crossings, reduces wildlife mortalities up to 80% (Clevenger *et al.* 2001), while another found this figure to be lower at 54% (Rytwinski *et al.* 2016). However, fencing increases the barrier effect of roads, as has been observed in the GSNL, and has adverse effects on wildlife species that need to access vital resources on both sides of the road, and ultimately may affect population persistence (Jaeger and Fahrig 2004).

Mitigation measures, such as fences, should not exacerbate the road avoidance behaviour of wildlife, or even stop wildlife from crossing roads altogether if this is not absolutely necessary for human and animal safety. An individual-based simulation model of population persistence carried out by Jaeger and

Fahrig (2004) showed that if wildlife mortalities caused by vehicle collisions were below a lower threshold value, then fences were always detrimental, whereas if wildlife mortalities were above an upper threshold value, then fences were always of benefit. In other words, for low traffic mortality, fences negatively affect population persistence. If traffic volumes are low but fences along roads have been put up to mitigate collisions, then these fences do not serve their original purpose. This principle could be used as a guideline for the GSNL to determine along which roads fences could either be completely removed (with cattle grids along both sides to prevent wildlife from moving into the road corridors) or made more wildlife-friendly if poaching and property safety is a concern. It should be kept in mind that if parts of fences will be removed, then there should be other mitigation measures or so-called “fence-end treatments” in place (Huijser *et al.* 2016), in the form of signs to reduce speed in combination with cattle grids on either side. This is because fence ends increase mortalities (Clevenger *et al.* 2001, Plante *et al.* 2019) and enable animals to wander inside the road corridor to forage on vegetation (Huijser *et al.* 2016).

In order to identify these places, data on traffic volumes along roads that significantly impact movements, such as those identified in this study, should be collected, and the threshold values could be determined based on the data. Furthermore, data on wildlife-vehicle collisions could be supplemented by using the invaluable citizen science tool to identify problematic areas or “hotspots” of wildlife-vehicle collisions (Olson *et al.* 2014, Périquet *et al.* 2018, Valerio *et al.* 2021). The infrastructure for this type of data collection is already in place for the GSNL (the user-friendly Epicollect app) and should be used on a larger scale. By finding spatial aggregations or “hotspots”, certain roads can be prioritized for mitigation measures, thereby allowing for the efficient use of financial and other resources (Spanowicz *et al.* 2020).

The notion that the mitigation of animal mortalities due to collisions is of higher priority than reduced connectivity, as is mentioned in some papers (Spanowicz *et al.* 2020) lacks an appreciation of differences in human and vehicular density between localities. Here it is argued that mitigating traffic mortalities is more important than mitigating the barrier effects of wildlife movements in areas where there is a high density of vehicles or of animals. In most parts of the GSNL, excepting those of high use such as the Sesriem road, it is expected that barrier effects are more important to mitigate than wildlife-vehicle collisions, as a result of the generally low density of wildlife and vehicles and also because of the greater importance of movement in this arid habitat.

Future studies could quantify the threshold level at which traffic volume and other road-related disturbances affects wildlife behavioural responses. These threshold levels are an indicator of when minor alterations in management can have disproportionately large effects on wildlife populations (Beyer *et al.* 2013) and can be used to implement mitigation measures. The behaviour of ungulates at fences should be researched in more depth, as it can give important insights into the negative impacts of fences. There are many R packages available with which one can research movement patterns of animals, but a particularly interesting one is a new package called *Barrier Behaviour Analysis (BaBA)* (Xu *et al.* 2021). It is a spatio-temporally explicit tool to identify individual-level behaviours in response to linear barriers, and can be used to identify problem fences and to determine fence permeability for different species. This could be a next step for the GSNL in identifying problematic fence segments at the individual and species level.

References

- Abáigar, T., Martínez, C., Amaouch, Z., Alifal, M., Lemdimigh, A., El Makki, S., El Mokhtar, M., Samlali, M.L., Fernández de Larrinoa, P., and Rodríguez-Caballero Almería, E., 2020. Habitat requirements of the Mhorr gazelle: What does this species need to survive in the wild? *Global Ecology and Conservation*, 24, e01389.
- Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinnell, S.P.H., Fralick, G.L., and Monteith, K.L., 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters*, 20 (6), 741–750.
- Apio, A., Plath, M., and Wronski, T., 2015. Recovery of ungulate populations in post-civil war Akagera National Park, Rwanda. *Journal of East African Natural History*, 104 (1–2), 127–141.
- Apps, P., 2012. *Smither's mammals of Southern Africa: a field guide*. 4th ed. Cape Town, South Africa: Struik Nature.
- Barnes, J.I. and de Jager, J.L.V., 1996. Economic and financial incentives for wildlife use on private land in Namibia and the implications for policy. *South African Journal of Wildlife Research*, 26 (2), 37–46.
- Bartlam-Brooks, H.L.A., Beck, P.S.A., Bohrer, G., and Harris, S., 2013. In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, 118 (4), 1427–1437.
- Bartlam-Brooks, H.L.A., Bonyongo, M.C., and Harris, S., 2011. Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra *Equus burchelli* migration in Botswana. *Oryx*, 45 (2), 210–216.
- Beale, C.M., van Rensberg, S., Bond, W.J., Coughenour, M., Fynn, R., Gaylard, A., Grant, R., Harris, B., Jones, T., Mduma, S., Owen-Smith, N., and Sinclair, A.R.E., 2013. Ten lessons for the conservation of African savannah ecosystems. *Biological Conservation*, 167, 224–232.
- Beauchesne, D., Jaeger, J.A.G., and St-Laurent, M.-H., 2013. Disentangling woodland caribou movements in response to clearcuts and roads across temporal scales. *PLoS ONE*, 8 (11), e77514.
- van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M., and Mysterud, A., 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology*, 80 (4), 771–785.
- Belote, R.T., Dietz, M.S., Jenkins, C.N., McKinley, P.S., Irwin, G.H., Fullman, T.J., Leppi, J.C., and Aplet, G.H., 2017. Wild, connected, and diverse: Building a more resilient system of protected areas. *Ecological Applications*, 27 (4), 1050–1056.
- 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.
- Bennitt, E., Bonyongo, M.C., and Harris, S., 2016. Effects of divergent migratory strategies on access to resources for Cape buffalo (*Syncerus caffer caffer*). *Journal of Mammalogy*, 97 (6), 1682–1698.
- Benten, A., Hothorn, T., Vor, T., and Ammer, C., 2018. Wildlife warning reflectors do not mitigate wildlife-vehicle collisions on roads. *Accident Analysis & Prevention*, 120, 64–73.
- Berger, J., 2004. The last mile: How to sustain long-distance migration in mammals. *Conservation Biology*, 18 (2), 320–331.
- Bevanda, M., Fronhofer, E.A., Heurich, M., Müller, J., and Reineking, B., 2015. Landscape configuration is a major determinant of home range size variation. *Ecosphere*, 6 (10), 1–12.
- Beyer, H.L., Gurarie, E., Börger, L., Panzacchi, M., Basille, M., Herfindal, I., van Moorter, B., Lele, S.R., and Matthiopoulos, J., 2016. 'You shall not pass!': Quantifying barrier permeability and proximity avoidance by animals. *Journal of Animal Ecology*, 85 (1), 43–53.

- Beyer, H.L., Ung, R., Murray, D.L., and Fortin, M.-J., 2013. Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. *Journal of Applied Ecology*, 50 (2), 286–294.
- Bigalke, R.C., 1972. Observations on the behaviour and feeding habits of the springbok, *Antidorcas marsupialis*. *Zoologica Africana*, 7 (1), 333–359.
- Bigalke, R.G., 1970. Observations on springbok populations. *Zoologica Africana*, 5 (1), 59–70.
- Bissonette, J.A. and Rosa, S., 2012. An evaluation of a mitigation strategy for deer-vehicle collisions. *Wildlife Biology*, 18 (4), 414–423.
- Bojarska, K., Kwiatkowska, M., Skórka, P., Gula, R., Theuerkauf, J., and Okarma, H., 2017. Anthropogenic environmental traps: Where do wolves kill their prey in a commercial forest? *Forest Ecology and Management*, 397, 117–125.
- Bolger, D.T., Newmark, W.D., Morrison, T.A., and Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, 11 (1), 63–77.
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., and Hewison, A.J.M., 2013. Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, 59 (2), 185–193.
- Boone, R.B. and Hobbs, N.T., 2004. Lines around fragments: Effects of fencing on large herbivores. *African Journal of Range & Forage Science*, 21 (3), 147–158.
- Börger, L., Franconi, N., Ferretti, F., Meschi, F., Michele, G. de, Gantz, A., and Coulson, T., 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist*, 168 (4), 471–485.
- Bothma, J. du P. and du Toit, J.G., eds., 2010. *Game ranch management*. 5th ed. Pretoria, South Africa: Van Schaik Publishers.
- Boyers, M., Parrini, F., Owen-Smith, N., Erasmus, B.F.N., and Hetem, R.S., 2019. How free-ranging ungulates with differing water dependencies cope with seasonal variation in temperature and aridity. *Conservation Physiology*, 7 (1), coz064.
- Bracis, C. and Mueller, T., 2017. Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, 284 (1855), 20170449.
- Bradby, K., Fitzsimons, J.A., Del Marco, A., Driscoll, D.A., Ritchie, E.G., Lau, J., Bradshaw, C.J.A., and Hobbs, R.J., 2014. Ecological connectivity or barrier fence? Critical choices on the agricultural margins of Western Australia. *Ecological Management & Restoration*, 15 (3), 180–190.
- Bradby, K., Keesing, A., and Wardell-Johnson, G., 2016. Gondwana Link: Connecting people, landscapes, and livelihoods across southwestern Australia. *Restoration Ecology*, 24 (6), 827–835.
- Brain, C.K. and Koste, W., 1993. Rotifers of the genus *Proales* from saline springs in the Namib desert, with the description of a new species. *Hydrobiologia*, 255, 449–454.
- Brieger, F., Hagen, R., Kröschel, M., Hartig, F., Petersen, I., Ortmann, S., and Suchant, R., 2017. Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations. *European Journal of Wildlife Research*, 63 (5), 1–11.
- Brook, R.K., 2010. Incorporating farmer observations in efforts to manage bovine tuberculosis using barrier fencing at the wildlife–livestock interface. *Preventive Veterinary Medicine*, 94 (3–4), 301–305.
- Brown, J.L. and Orians, G.H., 1970. Spacing patterns in mobile animals. *Annual Review of Ecology and Systematics*, 1, 239–262.
- Bullock, K.L., Malan, G., and Pretorius, M.D., 2011. Mammal and bird road mortalities on the Upington to Twee Rivieren main road in the southern Kalahari, South Africa. *African Zoology*, 46 (1), 60–71.

- Burkholder, E.N., Jakes, A.F., Jones, P.F., Hebblewhite, M., and Bishop, C.J., 2018. To jump or not to jump: Mule deer and white-tailed deer fence crossing decisions. *Wildlife Society Bulletin*, 42 (3), 420–429.
- Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24 (3), 346–352.
- Cagnacci, F., Boitani, L., Powell, R.A., and Boyce, M.S., 2010. Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365 (1550), 2157–2162.
- Calenge, C., 2006. The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197 (3–4), 516–519.
- Caro, T., Jones, T., and Davenport, T.R.B., 2009. Realities of documenting wildlife corridors in tropical countries. *Biological Conservation*, 142 (11), 2807–2811.
- Caro, T.M., Shargel, J.A., and Stoner, C.J., 2000. Frequency of medium-sized mammal road kills in an agricultural landscape in California. *The American Midland Naturalist*, 144 (2), 362–369.
- Carvalho, C.F., Custódio, A.E.I., and Júnior, O.M., 2017. Influence of climate variables on roadkill rates of wild vertebrates in the Cerrado biome, Brazil. *Bioscience Journal*, 33 (6), 1632–1641.
- Castelló, J.R., 2016. *Bovids of the world: Antelopes, gazelles, cattle, goats, sheep, and relatives*. Princeton, NJ: Princeton University Press.
- Chardonnet, P., Soto, B., Fritz, H., Crosmary, W., Drouet-Hoguet, N., Mésochina, P., Pellerin, M., Mallon, D., Bakker, L., Boulet, H., and Lamarque, F., 2010. *Managing the conflicts between people and lion: Review and insights from the literature and field experience*. *Wildlife Management Working Paper 13*. Rome, Italy: FAO.
- Chyn, K., Lin, T.-E., Chen, Y.-K., Chen, C.-Y., and Fitzgerald, L.A., 2019. The magnitude of roadkill in Taiwan: Patterns and consequences revealed by citizen science. *Biological Conservation*, 237, 317–326.
- Clarke, R.T., Liley, D., Sharp, J.M., and Green, R.E., 2013. Building development and roads: Implications for the distribution of stone curlews across the Brecks. *PLOS ONE*, 8 (8), e72984.
- Clevenger, A.P., Chruszcz, B., and Gunson, K.E., 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*, 29 (2), 646–653.
- Coetsee, C.G., 1969. The distribution of mammals in the Namib desert and adjoining inland escarpment. *Scientific Papers of the Namib Desert Research Station*, 40, 23–36.
- Coffin, A.W., 2007. From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography*, 15 (5), 396–406.
- Collinson, W.J., Parker, D.M., Bernard, R.T.F., Reilly, B.K., and Davies-Mostert, H.T., 2015. An inventory of vertebrate roadkill in the Greater Mapungubwe Transfrontier Conservation Area, South Africa. *African Journal of Wildlife Research*, 45 (3), 301–311.
- Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., and Butler, P.J., 2004. Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology and Evolution*, 19 (6), 334–343.
- Cown, P.E. and Rhodes, D.S., 1992. Restricting the movements of brushtail possums (*Trichosurus vulpecula*) on farmland with electric fencing. *Wildlife Research*, 19 (1), 47–57.
- Cozzi, G., Broekhuis, F., McNutt, J.W., and Schmid, B., 2013. Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for interspecific relationships and connectivity. *Journal of Animal Ecology*, 82 (3), 707–715.
- Creel, S., Becker, M.S., Durant, S.M., M’Soka, J., Matandiko, W., Dickman, A.J., Christianson, D., Dröge, E., Mweetwa, T., Pettorelli, N., Rosenblatt, E., Schuette, P., Woodroffe, R., Bashir, S., Beudels-Jamar, R.C., Blake, S., Borner, M., Breitenmoser, C., Broekhuis, F., Cozzi, G., Davenport, T.R.B.,

- Deutsch, J., Dollar, L., Dolrenry, S., Douglas-Hamilton, I., Fitzherbert, E., Foley, C., Hazzah, L., Henschel, P., Hilborn, R., Hopcraft, J.G.C., Ikanda, D., Jacobson, A., Joubert, B., Joubert, D., Kelly, M.S., Lichtenfeld, L., Mace, G.M., Milanzi, J., Mitchell, N., Msuha, M., Muir, R., Nyahongo, J., Pimm, S., Purchase, G., Schenck, C., Sillero-Zubiri, C., Sinclair, A.R.E., Songorwa, A.N., Stanley-Price, M., Tehou, C.A., Trout, C., Wall, J., Wittemyer, G., and Zimmermann, A., 2013. Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, 16 (11), 1413-e3.
- Cumming, D.H.M., Osofsky, S.A., Atkinson, S.J., and Atkinson, M.W., 2015. Beyond fences: Wildlife, livestock and land use in Southern Africa. In: J. Zinsstag, E. Schelling, D. Waltner-Toews, M. Whittaker, and M. Tanner, eds. *One health: The theory and practice of integrated health approaches*. Abingdon, UK: CABI International, 243–257.
- Cunningham, P.L., 2019. Do swing gates prevent black-backed jackal (*Canis mesomelas*) from entering commercial sheep farms? *Namibian Journal of Environment*, 3, 1–7.
- Cunningham, P.L. and Wronski, T., 2011. Seasonal changes in group size and composition of Arabian sand gazelle *Gazella subgutturosa marica* Thomas, 1897 during a period of drought in central western Saudi Arabia. *Current Zoology*, 57 (1), 36–42.
- Cushman, S.A., Chase, M., and Griffin, C., 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: S.A. Cushman and F. Huettmann, eds. *Spatial complexity, informatics, and wildlife conservation*. New York: Springer, 349–367.
- D’Amico, M., Périquet, S., Román, J., and Revilla, E., 2016. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *Journal of Applied Ecology*, 53 (1), 181–190.
- David, J.H.M., 1978. Observations on territorial behaviour of springbok, *Antidorcas marsupialis*, in the Bontebok National Park, Swellendam. *Zoologica Africana*, 13 (1), 123–141.
- Davies, R.A.G., Botha, P., and Skinner, J.D., 1986. Diet selected by springbok *Antidorcas marsupialis* and merino sheep *Ovis aries* during Karoo drought. *Transactions of the Royal Society of South Africa*, 46 (2), 165–176.
- Davies, T.E., Wilson, S., Hazarika, N., Chakrabarty, J., Das, D., Hodgson, D.J., and Zimmermann, A., 2011. Effectiveness of intervention methods against crop-raiding elephants. *Conservation Letters*, 4 (5), 346–354.
- Davies-Mostert, H.T., Mills, M.G.L., and Macdonald, D.W., 2013. Hard boundaries influence African wild dogs’ diet and prey selection. *Journal of Applied Ecology*, 50 (6), 1358–1366.
- Day, J.A., 1993. The major ion chemistry of some southern African saline systems. *Hydrobiologia*, 267, 37–59.
- Day, J.A. and Seely, M.K., 1988. Physical and chemical conditions in an hypersaline spring in the Namib desert. *Hydrobiologia*, 160 (2), 141–153.
- Dean, W.R.J., Seymour, C.L., and Joseph, G.S., 2018. Linear structures in the Karoo, South Africa, and their impacts on biota. *African Journal of Range & Forage Science*, 35 (3–4), 223–232.
- Dechen Quinn, A.C., Williams, D.M., and Porter, W.F., 2012. Postcapture movement rates can inform data-censoring protocols for GPS-collared animals. *Journal of Mammalogy*, 93 (2), 456–463.
- Desy, E.A., Batzli, G.O., and Liu, J., 1990. Effects of food and predation on behaviour of prairie voles: A field experiment. *Oikos*, 58 (2), 159–168.
- Diaz-Varela, E.R., Vazquez-Gonzalez, I., Marey-Pérez, M.F., and Álvarez-López, C.J., 2011. Assessing methods of mitigating wildlife–vehicle collisions by accident characterization and spatial analysis. *Transportation Research Part D: Transport and Environment*, 16 (4), 281–287.
- Dieckmann, R.C., 1980. The ecology and breeding biology of the gemsbok (*Oryx gazella gazella*) (Linnaeus, 1785) in the Hester Malan Nature Reserve. Master’s thesis. University of Pretoria, South Africa.

- Dingle, H., 2014. *Migration: The biology of life on the move*. 2nd ed. UK: Oxford University Press.
- Dougherty, E.R., Carlson, C.J., Blackburn, J.K., and Getz, W.M., 2017. A cross-validation-based approach for delimiting reliable home range estimates. *Movement Ecology*, 5 (1), 19.
- Druce, H.C., Pretorius, K., and Slotow, R., 2008. The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation*, 141 (12), 3127–3138.
- Dube, T., Murwira, A., Caron, A., and de Garine-Wichatitsky, M., 2010. Preliminary results on the permeability of veterinary fences to buffalo (*Syncerus caffer*) and cattle in Gonarezhou National Park, Zimbabwe. In: K. Ferguson and J. Hanks, eds. *Fencing impacts : A review of the environmental, social and economic impacts of game and veterinary fencing in Africa with particular reference to the Great Limpopo and Kavango-Zambezi Transfrontier Conservation Areas*. South Africa: University of Pretoria, 229–232.
- Duffett, D., D’Amico, M., Mulero-Pázmány, M., and González-Suárez, M., 2020. Species’ traits as predictors of avoidance towards roads and traffic. *Ecological Indicators*, 115, 106402.
- Dupuis-Desormeaux, M., Kaaria, T.N., Mwololo, M., Davidson, Z., and MacDonald, S.E., 2018. A ghost fence-gap: Surprising wildlife usage of an obsolete fence crossing. *PeerJ*, 6, e5950.
- Durant, S.M., Becker, M.S., Creel, S., Bashir, S., Dickman, A.J., Beudels-Jamar, R.C., Lichtenfeld, L., Hilborn, R., Wall, J., Wittemyer, G., Badamjav, L., Blake, S., Boitani, L., Breitenmoser, C., Broekhuis, F., Christianson, D., Cozzi, G., Davenport, T.R.B., Deutsch, J., Devillers, P., Dollar, L., Dolrenry, S., Douglas-Hamilton, I., Dröge, E., Fitzherbert, E., Foley, C., Hazzah, L., Hopcraft, J.G.C., Ikanda, D., Jacobson, A., Joubert, D., Kelly, M.J., Milanzi, J., Mitchell, N., M’Soka, J., Msuha, M., Mweetwa, T., Nyahongo, J., Rosenblatt, E., Schuette, P., Sillero-Zubiri, C., Sinclair, A.R.E., Price, M.R.S., Zimmermann, A., and Petteorelli, N., 2015. Developing fencing policies for dryland ecosystems. *Journal of Applied Ecology*, 52 (3), 544–551.
- Dyer, S.J., O’Neill, J.P., Wasel, S.M., and Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology*, 80 (5), 839–845.
- van Dyk, G. and Slotow, R., 2003. The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology*, 38 (1), 79–94.
- East, R., 1999. *African Antelope Database 1998. Occasional Paper of the IUCN Species Survival Commission No. 21*. Gland, Switzerland: IUCN.
- Ebner, M., Miranda, T., and Roth-Nebelsick, A., 2011. Efficient fog harvesting by *Stipagrostis sabulicola* (Namib dune bushman grass). *Journal of Arid Environments*, 75 (6), 524–531.
- Eckardt, F.D., Soderberg, K., Coop, L.J., Muller, A.A., Vickery, K.J., Grandin, R.D., Jack, C., Kapalanga, T.S., and Henschel, J., 2013. The nature of moisture at Gobabeb, in the central Namib desert. *Journal of Arid Environments*, 93, 7–19.
- Ekernas, L.S. and Berger, J., 2016. Challenges and opportunities for conserving equid migrations. In: J.I. Ransom and P. Kaczensky, eds. *Wild equids: Ecology, management, and conservation*. Baltimore, MD: Johns Hopkins University Press, 187–195.
- Ellington, E., 2007. Disturbance effects of roads and fences on the spatial patterns of large mammal dispersal and migration in Amboseli/Tsavo ecosystem, Kenya. Honour’s thesis. Ohio State University, Columbus.
- Eloff, P.J. and van Niekerk, A., 2005. Game, fences and motor vehicle accidents: Spatial patterns in the Eastern Cape. *South African Journal of Wildlife Research*, 35 (2), 125–130.
- Engelbrecht, F., Adegoke, J., Bopape, M.-J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M., Ichoku, C., and Gatebe, C., 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*, 10 (8), 085004.

- Erb, K.P., 2004. Consumptive wildlife utilization as a land-use form in Namibia. Master's thesis. University of Stellenbosch, South Africa.
- Estevinho Santos Faustino, C., 2020. Movement ecology and conservation: the case of African vultures. Doctoral dissertation. University of St Andrews, Scotland.
- Ewers, R.M. and Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, 81 (1), 117–142.
- Ewers, R.M. and Didham, R.K., 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences*, 105 (14), 5426–5429.
- Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forster, J., and Mueller, T., 2013. Spatial memory and animal movement. *Ecology Letters*, 16 (10), 1316–1329.
- Fahrig, L. and Rytwinski, T., 2009. Effects of roads on animal abundance: An empirical review and synthesis. *Ecology and Society*, 14 (1), 1–21.
- Fennessy, J., 2009. Home range and seasonal movements of *Giraffa camelopardalis angolensis* in the northern Namib desert. *African Journal of Ecology*, 47 (3), 318–327.
- Ferguson, K., Adam, L., and Jori, F., 2012. An adaptive monitoring programme for studying impacts along the western boundary fence of Kruger National Park, South Africa. In: M.J. Somers and M.W. Hayward, eds. *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* New York, NY: Springer, 105–123.
- Ferronato, B.O., Roe, J.H., and Georges, A., 2014. Reptile bycatch in a pest-exclusion fence established for wildlife reintroductions. *Journal for Nature Conservation*, 22 (6), 577–585.
- Fitzsimons, J.A., Pulsford, I., and Wescott, G., eds., 2013. *Linking Australia's landscapes: Lessons and opportunities from large-scale conservation networks*. Collingwood, Australia: CSIRO.
- Forman, R.T.T. and Deblinger, R.D., 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation Biology*, 14 (1), 36–46.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R.L., Goldman, C.R., Heanue, K., Jones, J., Swanson, F., Turrentine, T., and Winter, T.C., 2003. *Road ecology: Science and solutions*. Washington, D.C.: Island Press.
- Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Gingras, C.T., Moorcroft, P.R., Courtois, R., and Dussault, C., 2013. Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. *The American Naturalist*, 181 (6), 827–836.
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L., and Morales, J.M., 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, 20 (3), 273–287.
- Frenkel, R.E., 1977. *Ruderal vegetation along some California roadsides*. Berkeley: University of California Press.
- Fryxell, J.M., Wilmschurst, J.F., and Sinclair, A.R.E., 2004. Predictive models of movement by Serengeti grazers. *Ecology*, 85 (9), 2429–2435.
- Fuller, A., Maloney, S.K., Mitchell, G., and Mitchell, D., 2004. The eland and the oryx revisited: Body and brain temperatures of free-living animals. In: *International Congress Series*. Amsterdam, Netherlands: Elsevier, 275–282.
- Furstenburg, D., 2016a. Gemsbok (*Oryx gazella*). In: P. Oberem and P. Oberem, eds. *The new game rancher*. Queenswood, South Africa: Briza, 153–160.
- Furstenburg, D., 2016b. Springbok (*Antidorcas marsupialis*). In: P. Oberem and P. Oberem, eds. *The new game rancher*. Queenswood, South Africa: Briza, 226–234.
- Fynn, R.W.S. and Bonyongo, M.C., 2011. Functional conservation areas and the future of Africa's wildlife. *African Journal of Ecology*, 49 (2), 175–188.

- Gadd, M.E., 2012. Barriers, the beef industry and unnatural selection: A review of the impact of veterinary fencing on mammals in Southern Africa. In: M.J. Somers and M.W. Hayward, eds. *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* New York, NY: Springer, 153–186.
- Gagnon, J.W., Theimer, T.C., Dodd, N.L., and Schweinsburg, R.E., 2007. Traffic volume alters elk distribution and highway crossings in Arizona. *The Journal of Wildlife Management*, 71 (7), 2318–2323.
- Gandiwa, E., Mashapa, C., Muboko, N., Chemura, A., Kuvaoga, P., and Mabika, C.T., 2020. Wildlife-vehicle collisions in Hurungwe Safari Area, northern Zimbabwe. *Scientific African*, 9, e00518.
- Gavin, S.D. and Komers, P.E., 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology*, 84 (12), 1775–1780.
- Geffen, H., Perevolotsky, A., Geffen, E., and Yom-Tov, Y., 1999. Use of space and social organization of female mountain gazelles (*Gazella gazella gazella*) in Ramat HaNadiv, Israel. *Journal of Zoology*, 247 (1), 113–119.
- Geisser, H. and Reyer, H.-U., 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *The Journal of Wildlife Management*, 68 (4), 939–946.
- Georgiadis, N., Hack, M., and Turpin, K., 2003. The influence of rainfall on zebra population dynamics: Implications for management. *Journal of Applied Ecology*, 40 (1), 125–136.
- Getis, A. and Aldstadt, J., 2004. Constructing the spatial weights matrix using a local statistic. *Geographical Analysis*, 36 (2), 90–104.
- Global Environment Facility, n.d. Namibia Protected Landscape Conservation Areas Initiative (NAM-PLACE) [online]. Available from: <https://www.thegef.org/project/namibia-protected-landscape-conservation-areas-initiative-nam-place> [Accessed 17 Oct 2020].
- Gonser, R.A., Jensen, R.R., and Wolf, S.E., 2009. The spatial ecology of deer-vehicle collisions. *Applied Geography*, 29 (4), 527–532.
- Gosling, L.M., Muntifering, J., Kolberg, H., Uiseb, K., and King, S.R.B., 2019. Equus zebra ssp. hartmannae, *Hartmann's mountain zebra*. Gland, Switzerland: IUCN.
- Goudie, A. and Viles, H., 2015. *Landscapes and landforms of Namibia*. Dordrecht, Netherlands: Springer.
- Grace, M.K., Smith, D.J., and Noss, R.F., 2017. Reducing the threat of wildlife-vehicle collisions during peak tourism periods using a roadside animal detection system. *Accident Analysis and Prevention*, 109, 55–61.
- Greenwald, L.I., 1967. Water economy of the desert dwelling springbok (*Antidorcas marsupialis*). Master's thesis. University of Syracuse, New York, NY.
- Grosman, P.D., Jaeger, J.A.G., Biron, P.M., Dussault, C., and Ouellet, J.-P., 2011. Trade-off between road avoidance and attraction by roadside salt pools in moose: An agent-based model to assess measures for reducing moose-vehicle collisions. *Ecological Modelling*, 222 (8), 1423–1435.
- Gross, B.D., Holechek, J.L., Hallford, D., and Pieper, R.D., 1983. Effectiveness of antelope pass structures in restriction of livestock. *Journal of Range Management*, 36 (1), 22–24.
- Gross, E.M., Lahkar, B.P., Subedi, N., Nyirenda, V.R., Lichtenfeld, L.L., and Jakoby, O., 2019. Does traditional and advanced guarding reduce crop losses due to wildlife? A comparative analysis from Africa and Asia. *Journal for Nature Conservation*, 50, 125712.
- Gulsby, W.D., Stull, D.W., Gallagher, G.R., Osborn, D.A., Warren, R.J., Miller, K.V., and Tannenbaum, L.V., 2011. Movements and home ranges of white-tailed deer in response to roadside fences. *Wildlife Society Bulletin*, 35 (3), 282–290.
- Günster, A., 1995. Grass cover distribution in the central Namib - A rapid method to assess regional and local rainfall patterns of arid regions? *Journal of Arid Environments*, 29 (1), 107–114.

- Haigh, A.J., 2012. Annual patterns of mammalian mortality on Irish roads. *Hystrix, the Italian Journal of Mammalogy*, 23 (2), 58–66.
- Hamilton, W.J., Buskirk, R., and Buskirk, W.H., 1977. Intersexual dominance and differential mortality of gemsbok *Oryx gazella* at Namib desert waterholes. *Madoqua*, 10 (1), 5–19.
- Hardin, G., 1968. The tragedy of the commons. *Science*, 162 (3859), 1243–1248.
- Harper-Simmonds, L., Mendelsohn, J., Roux, J.-P., Pallet, J., Brown, C., Middleton, A., and Kruse, J., n.d. *Development of an inventory of ecosystem services in Namibia*. Namibia: Ministry of Environment and Tourism.
- Harrington, J.L. and Conover, M.R., 2006. Characteristics of ungulate behavior and mortality associated with wire fences. *Wildlife Society Bulletin*, 34 (5), 1295–1305.
- Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P.G.M., and Berger, J., 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, 7 (1), 55–76.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., and Wray, S., 1990. Home range analysis using radio-tracking data – A review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20 (2–3), 97–123.
- Hayward, M.W., Adendorff, J., O'Brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L.C., Bean, P., Fogarty, A., Howarth, D., Slater, R., and Kerley, G.I.H., 2007. Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape province. *The Open Conservation Biology Journal*, 1 (1), 1–11.
- Hayward, M.W. and Kerley, G.I.H., 2009. Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation*, 142 (1), 1–13.
- Hell, P., Plavý, R., Slamečka, J., and Gašparík, J., 2005. Losses of mammals (Mammalia) and birds (Aves) on roads in the Slovak part of the Danube basin. *European Journal of Wildlife Research*, 51 (1), 35–40.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C., and Settele, J., 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, 13 (1), 207–251.
- Henschel, J.R., Burke, A., and Seely, M., 2005. Temporal and spatial variability of grass productivity in the central Namib desert. *African Study Monographs*, 30, 43–56.
- Hilty, J.A., Lidicker Jr., W.Z., and Merenlender, A.M., eds., 2006. *Corridor ecology: The science and practice of linking landscapes for biodiversity conservation*. Washington, D.C: Island Press.
- Hoenes, B.D. and Bender, L.C., 2010. Relative habitat-and browse-use of native desert mule deer and exotic oryx in the greater San Andres Mountains, New Mexico. *Human-Wildlife Interactions*, 4 (1), 12–24.
- Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, 78 (4), 443–457.
- Hofmann, R.R., Knight, M.H., and Skinner, J.D., 1995. On structural characteristics and morphophysiological adaptation of the springbok (*Antidorcas marsupialis*) digestive system. *Transactions of the Royal Society of South Africa*, 50 (2), 125–142.
- Hofmann, R.R. and Stewart, D.R.M., 1972. Grazer or browser: A classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia*, 36 (2), 226–240.
- Hofmeyr, M.D. and Louw, G.N., 1987. Thermoregulation pelage conductance and renal function in the desert-adapted springbok, *Antidorcas marsupialis*. *Journal of Arid Environments*, 13 (2), 137–151.
- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., and Spiegel, O., 2008. Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences*, 105 (49), 19060–19065.

- Huijser, M.P., Duffield, J.W., Clevenger, A.P., Ament, R.J., and McGowen, P.T., 2009. Cost–benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: A decision support tool. *Ecology and Society*, 14 (2).
- Huijser, M.P., Fairbank, E.R., Camel-Means, W., Graham, J., Watson, V., Basting, P., and Becker, D., 2016. Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife–vehicle collisions and providing safe crossing opportunities for large mammals. *Biological Conservation*, 197, 61–68.
- Huijser, M.P., Mosler-Berger, C., Olsson, M., and Strein, M., 2015. Wildlife warning signs and animal detection systems aimed at reducing wildlife-vehicle collisions. In: R. van der Ree, D.J. Smith, and C. Grilo, eds. *Handbook of road ecology*. Chichester, UK: Wiley-Blackwell, 198–212.
- Humavindu, M.N. and Barnes, J.I., 2003. Trophy hunting in the Namibian economy: An assessment. *South African Journal of Wildlife Research*, 33 (2), 65–70.
- Huygens, O.C. and Hayashi, H., 1999. Using electric fences to reduce Asiatic black bear depredation in Nagano prefecture, central Japan. *Wildlife Society Bulletin*, 27 (4), 959–964.
- Imai, S., Ito, T.Y., Kinugasa, T., Shinoda, M., Tsunekawa, A., and Lhagvasuren, B., 2017. Effects of spatiotemporal heterogeneity of forage availability on annual range size of Mongolian gazelles. *Journal of Zoology*, 301 (2), 133–140.
- IPCC, 2012. Summary for policymakers. In: C.B. Field, V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M. Tignor, and P.M. Midgley, eds. *Managing the risks of extreme events and disasters to advance climate change adaptation. Special report of the Intergovernmental Panel on Climate Change*. UK: Cambridge University Press, 3–21.
- Ito, T.Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar, B., and Chimeddorj, B., 2013. Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. *PLoS ONE*, 8 (2), e56995.
- IUCN SSC Antelope Specialist Group, 2016. *Antidorcas marsupialis* [online]. *The IUCN Red List of Threatened Species*. Available from: <https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T1676A50181753.en> [Accessed 6 Dec 2020].
- IUCN SSC Antelope Specialist Group, 2020. *Oryx gazella* [online]. *The IUCN Red List of Threatened Species*. Available from: <https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T15573A166485425.en> [Accessed 6 Dec 2020].
- Jackson, N.D. and Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biological Conservation*, 144 (12), 3143–3148.
- Jackson, T.P., Skinner, J.D., and Richardson, P.R.K., 1993. Some costs of maintaining a perennial territory in the springbok, *Antidorcas marsupialis*. *African Journal of Ecology*, 31 (3), 242–254.
- Jacobson, P.J. and Jacobson, K.M., 2013. Hydrologic controls of physical and ecological processes in Namib desert ephemeral rivers: Implications for conservation and management. *Journal of Arid Environments*, 93, 80–93.
- Jacobson, P.J., Jacobson, K.M., and Seely, M.K., 1995. *Ephemeral rivers and their catchments: Sustaining people and development in western Namibia*. Windhoek: Desert Research Foundation of Namibia.
- Jaeger, J.A. and Fahrig, L., 2004. Effects of road fencing on population persistence. *Conservation Biology*, 18 (6), 1651–1657.
- Jakes, A.F., Jones, P.F., Paige, L.C., Seidler, R.G., and Huijser, M.P., 2018. A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. *Biological Conservation*, 227, 310–318.

- James, R. and Washington, R., 2013. Changes in African temperature and precipitation associated with degrees of global warming. *Climatic Change*, 117 (4), 859–872.
- Jerina, K. and Leslie, D.M., 2012. Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. *Journal of Mammalogy*, 93 (4), 1139–1148.
- Jiang, G., Zhang, M., and Ma, J., 2008. Habitat use and separation between red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* in relation to human disturbance in the Wandashan mountains, northeastern China. *Wildlife Biology*, 14 (1), 92–100.
- Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., and Mulders, R., 2005. Cumulative effects of human developments on Arctic wildlife. *Wildlife Monographs*, 160 (1), 1–36.
- Jones, P.F., Jakes, A.F., MacDonald, A.M., Hanlon, J.A., Eacker, D.R., Martin, B.H., and Hebblewhite, M., 2020. Evaluating responses by sympatric ungulates to fence modifications across the northern Great Plains. *Wildlife Society Bulletin*, 44 (1), 130–141.
- Jones, P.F., Jakes, A.F., Telander, A.C., Sawyer, H., Martin, B.H., and Hebblewhite, M., 2019. Fences reduce habitat for a partially migratory ungulate in the northern sagebrush steppe. *Ecosphere*, 10 (7), 1–25.
- Jonzén, N., Knudsen, E., Holt, R.D., and Sæther, B.-E., 2011. Uncertainty and predictability: The niches of migrants and nomads. In: E.J. Milner-Gulland, J.M. Fryxell, and A.R.E. Sinclair, eds. *Animal migration: A synthesis*. New York, NY: Oxford University Press, 91–109.
- Joubert, E., 1972a. Activity patterns shown by Hartmann zebra *Equus zebra hartmannae* in South West Africa with reference to climatic factors. *Madoqua*, 1 (5), 33–52.
- Joubert, E., 1972b. The social organisation and associated behaviour in the Hartmann zebra *Equus zebra hartmannae*. *Madoqua*, 1 (6), 17–56.
- Joubert, E., 1973. Habitat preference, distribution and status of the Hartmann Zebra *Equus zebra hartmannae* in South West Africa. *Madoqua*, 1973 (Series 1 Issue 7), 5–15.
- Joubert, E., 1974. Composition and limiting factors of a Khomas Hochland population of Hartmann zebra *equus zebra hartmannae*. *Madoqua*, 1974 (Series 1 Issue 8), 49–53.
- Joubert, E., Brand, P.A.J., and Visagie, G.P., 1983. An appraisal of the utilisation of game on private land in South West Africa. *Madoqua*, 13 (3), 197–219.
- Kambourova-Ivanova, N., Koshev, Y., Popgeorgiev, G., Ragyov, D., Pavlova, M., Mollov, I., and Nedialkov, N., 2012. Effect of traffic on mortality of amphibians, reptiles, birds and mammals on two types of roads between Pazardzhik and Plovdiv region (Bulgaria) – Preliminary results. *Acta Zoologica Bulgarica*, 64 (1), 57–67.
- Karhu, R.R. and Anderson, S.H., 2006. The effect of high-tensile electric fence designs on big-game and livestock movements. *Wildlife Society Bulletin*, 34 (2), 293–299.
- Kassilly, F.N., Tsingalia, H.M., and Gossow, H., 2008. Mitigating human-wildlife conflicts through wildlife fencing: A Kenyan case study. *Wildlife Biology in Practice*, 4 (1), 30–38.
- Kays, R., Crofoot, M.C., Jetz, W., and Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. *Science*, 348 (6240), aaa2478.
- Keken, Z., Sedoník, J., Kušta, T., Andrášik, R., and Bíl, M., 2019. Roadside vegetation influences clustering of ungulate vehicle collisions. *Transportation Research Part D: Transport and Environment*, 73, 381–390.
- Kerley, G.I.H., Behrens, K.G., Carruthers, J., Diemont, M., du Plessis, J., Minnie, L., Richardson, P.R.K., Somers, M.J., Tambling, C.J., Turpie, J., van Niekerk, H.N., and Balfour, D., 2017. Livestock predation in South Africa: The need for and value of a scientific assessment. *South African Journal of Science*, 113 (3–4), 1–3.
- Kilian, J.W., 1995. *The ecology of gemsbok (Oryx gazella gazella) in the southern Namib*. Windhoek: Ministry of Environment and Tourism, Internal report.

- Kioko, J., Kiffner, C., Jenkins, N., and Collinson, W.J., 2015. Wildlife roadkill patterns on a major highway in northern Tanzania. *African Zoology*, 50 (1), 17–22.
- Klingel, H., 1969. The social organisation and population ecology of the plains zebra (*Equus quagga*). *Zoologica Africana*, 4 (2), 249–263.
- Knight, M., 2013. *Oryx gazella* Gemsbok (Southern Oryx). In: J. Kingdon and M. Hoffmann, eds. *Mammals of Africa. Volume 6: Pigs, hippopotamuses, chevrotain, giraffes, deer and bovids*. London, UK: Bloomsbury, 572–576.
- Knight, M.H., 1991. Ecology of the gemsbok *Oryx gazella gazella* (Linnaeus) and blue wildebeest *Connochaetes taurinus* (Burchell) in the southern Kalahari. Doctoral dissertation. University of Pretoria, South Africa.
- Kok, O.B. and Grobbelaar, J.U., 1985. Notes on the availability and chemical composition of water from the gravel plains of the Namib-Naukluft Park. *Journal of the Limnological Society of Southern Africa*, 11 (2), 66–70.
- Kok, O.B. and Nel, J.A.J., 1996. The Kuiseb river as a linear oasis in the Namib desert. *African Journal of Ecology*, 34 (1), 39–47.
- Kreulen, D.A., 1985. Lick use by large herbivores: a review of benefits and banes of soil consumption. *Mammal Review*, 15 (3), 107–123.
- Laity, J., 2008. *Deserts and desert environments*. Chichester, UK: Wiley-Blackwell.
- Lancaster, J., Lancaster, N., and Seely, M.K., 1984. Climate of the central Namib desert. *Madoqua*, 14 (1), 5–61.
- Lancaster, N., 2002. How dry was dry? - Late Pleistocene palaeoclimates in the Namib desert. *Quaternary Science Reviews*, 21 (7), 769–782.
- Landguth, E., Jakes, A., and Hebblewhite, M., 2020. *Testing 'wildlife friendly' fence modifications to manage wildlife and livestock movements*. Helena, MT: Research Programs, Montana Department of Transportation, No. FHWA/MT-20-001/9596-617.
- Landscape Members [online], n.d. *Greater Sossusvlei-Namib Landscape*. Available from: <http://www.landscapesnamibia.org/sossusvlei-namib/landscape-members> [Accessed 17 Feb 2019].
- Laver, P.N. and Kelly, M.J., 2008. A critical review of home range studies. *The Journal of Wildlife Management*, 72 (1), 290–298.
- Lawler, J.J., Ruesch, A.S., Olden, J.D., and McRae, B.H., 2013. Projected climate-driven faunal movement routes. *Ecology Letters*, 16 (8), 1014–1022.
- Lea, J.M.D., Kerley, G.I.H., Hrabar, H., Barry, T.J., and Shultz, S., 2016. Recognition and management of ecological refugees: A case study of the Cape mountain zebra. *Biological Conservation*, 203, 207–215.
- Lee, E., Croft, D.B., and Achiron-Frumkin, T., 2015. Roads in the arid lands: Issues, challenges and potential solutions. In: R. van der Ree, D.J. Smith, and C. Grilo, eds. *Handbook of road ecology*. Chichester, UK: Wiley-Blackwell, 382–390.
- Lehmann, D., Mfunne, J.K.E., Gewers, E., Cloete, J., Aschenborn, O.H.-K., Mbomboro, L., Kasaona, S., Brain, C., and Voigt, C.C., 2020. Spatiotemporal responses of a desert dwelling ungulate to increasing aridity in North-eastern Namibia. *Journal of Arid Environments*, 179 (5), 104193.
- Leuthold, W., 1977. *African ungulates: A comparative review of their ethology and behavioral ecology*. Berlin, Germany: Springer.
- Ley, A.J. and Tynan, B., 2008. Bird casualties in fences in Diamantina National Park, Queensland, 1996 - 2008. *Australian Field Ornithology*, 25 (2), 96–98.

- Li, L., Fassnacht, F.E., Storch, I., and Bürgi, M., 2017. Land-use regime shift triggered the recent degradation of alpine pastures in Nyanpo Yutse of the eastern Qinghai-Tibetan Plateau. *Landscape Ecology*, 32 (8), 2187–2203.
- Liedvogel, M., Chapman, B.B., Muheim, R., and Åkesson, S., 2013. The behavioural ecology of animal movement: Reflections upon potential synergies. *Animal Migration*, 1 (1), 39–46.
- Lightfoot, D.C. and Whitford, W.G., 1991. Productivity of creosotebush foliage and associated canopy arthropods along a desert roadside. *American Midland Naturalist*, 125 (2), 310–322.
- Lindsey, P., 2011. *An analysis of game meat production and wildlife-based land uses on freehold land in Namibia: Links with food security*. Harare, Zimbabwe: TRAFFIC East/Southern Africa.
- Lindsey, P., du Toit, R., Pole, A., and Romañach, S., 2008. Savé Valley Conservancy: A large-scale African experiment in cooperative wildlife management. In: B. Child, H. Suich, and A. Spenceley, eds. *Evolution and innovation in wildlife conservation: Parks and game ranches to transfrontier conservation areas*. London, UK: Routledge, 163–184.
- Lindsey, P.A., Havemann, C.P., Lines, R.M., Price, A.E., Retief, T.A., Rhebergen, T., Van der Waal, C., and 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.
- Lindsey, P.A., Masterson, C.L., Beck, A.L., and Romañach, S., 2012. Ecological, social and financial issues related to fencing as a conservation tool in Africa. In: M.J. Somers and M.D. Hayward, eds. *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* New York, NY: Springer, 215–234.
- Lindstedt, S.L., Miller, B.J., and Buskirk, S.W., 1986. Home range, time, and body size in mammals. *Ecology*, 67 (2), 413–418.
- Linnell, J.D., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., Kusak, J., Majic, A., Skrbinsek, T., Potocnik, H., Hayward, M.W., Milner-Gulland, E.J., Buuveibaatar, B., Olson, K.A., Badamjav, L., Bischof, R., Zuther, S., and Breitenmoser, U., 2016. Border security fencing and wildlife: The end of the transboundary paradigm in Eurasia? *PLoS Biology*, 14 (6), e1002483.
- Linnell, J.D.C., Andersen, R., Kvam, T., Andrén, H., Liberg, O., Odden, J., and Moa, P.F., 2001. Home range size and choice of management strategy for lynx in Scandinavia. *Environmental Management*, 27 (6), 869–879.
- Loarie, S.R., van Aarde, R.J., and Pimm, S.L., 2009. Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, 142 (12), 3086–3098.
- Louw, G.N. and Seely, M.K., 1982. *Ecology of desert organisms*. London, UK: Longman.
- Løvschal, M., Bøcher, P.K., Pilgaard, J., Amoke, I., Odingo, A., Thuo, A., and Svenning, J.-C., 2017. Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Scientific Reports*, 7 (1), 41450.
- Lyons, A., Getz, W., and R Development Core Team, 2019. *T-LoCoH: Time local convex hull homerange and time use analysis*.
- Malakoutikhah, S., Fakheran, S., Hemami, M.-R., Tarkesh, M., and Senn, J., 2020. Assessing future distribution, suitability of corridors and efficiency of protected areas to conserve vulnerable ungulates under climate change. *Diversity and Distributions*, 26 (10), 1383–1396.
- Maloney, S.K., Fuller, A., Mitchell, G., and Mitchell, D., 2002. Brain and arterial blood temperatures of free-ranging oryx (*Oryx gazella*). *Pflügers Archiv - European Journal of Physiology*, 443 (3), 437–445.
- Mannetti, L.M., Götttert, T., Zeller, U., and Esler, K.J., 2019. Identifying and categorizing stakeholders for protected area expansion around a national park in Namibia. *Ecology and Society*, 24 (2), art5.
- Martin, L., 2000. Gazelle (*Gazella* spp.) behavioural ecology: Predicting animal behaviour for prehistoric environments in south-west Asia. *Journal of Zoology*, 250 (1), 13–30.

- Mason, D.R., 1976. Some observations on social organisation and behaviour of springbok in the Jack Scott Nature Reserve. *South African Journal of Wildlife Research*, 6 (1), 33–39.
- Massé, A. and Côté, S.D., 2012. Linking habitat heterogeneity to space use by large herbivores at multiple scales: From habitat mosaics to forest canopy openings. *Forest Ecology and Management*, 285, 67–76.
- Mbaiwa, J.E. and Mbaiwa, O.I., 2006. The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *International Journal of Wilderness*, 12 (3), 17–41.
- McCauley, D.J., 2006. Selling out on nature. *Nature*, 443 (7107), 27–28.
- McInturff, A., Xu, W., Wilkinson, C.E., Dejid, N., and Brashares, J.S., 2020. Fence ecology: Frameworks for understanding the ecological effects of fences. *BioScience*, 70 (11), 971–985.
- McKee, C.J., Stewart, K.M., Sedinger, J.S., Bush, A.P., Darby, N.W., Hughson, D.L., and Bleich, V.C., 2015. Spatial distributions and resource selection by mule deer in an arid environment: Responses to provision of water. *Journal of Arid Environments*, 122, 76–84.
- McLoughlin, P.D. and Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience*, 7 (2), 123–130.
- McNab, B.K., 1963. Bioenergetics and the determination of home range size. *The American Naturalist*, 97 (894), 133–140.
- McNaughton, S.J., 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature*, 334 (6180), 343–345.
- Mechkour, F., Maublanc, M.-L., Bideau, E., Gerard, J.-F., and Pépin, D., 2008. Spatial organization and spatial distribution of activities within home ranges in a springbok (*Antidorcas marsupialis*) captive population. *Zoo Biology*, 27 (1), 19–35.
- Mendelsohn, J., 2014. *Observations on the movements and home ranges of Hartmann's Mountain zebras and oryx in the Greater Sossusvlei-Namib Landscape*. Windhoek: RAISON.
- Mendelsohn, J., Jarvis, A., Roberts, C., and Robertson, T., 2002. *Atlas of Namibia. A portrait of the land and its people*. Cape Town, South Africa: David Phillips Publishers.
- Mendelsohn, J. and Mendelsohn, M., 2014. *Observations on the movements and home ranges of Hartmann's mountain zebras and oryx in the Greater Sossusvlei-Namib Landscape*. Windhoek: RAISON.
- Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., Oates, B.A., Sawyer, H., Scurlock, B.M., and Kauffman, M.J., 2016. Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B*, 283 (1833), 20160456.
- Middleton, A.D., Merkle, J.A., McWhirter, D.E., Cook, J.G., Cook, R.C., White, P.J., and Kauffman, M.J., 2018. Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, 127 (7), 1060–1068.
- Middleton, A.D., Sawyer, H., Merkle, J.A., Kauffman, M.J., Cole, E.K., Dewey, S.R., Gude, J.A., Gustine, D.D., McWhirter, D.E., Proffitt, K.M., and White, P.J., 2020. Conserving transboundary wildlife migrations: recent insights from the Greater Yellowstone Ecosystem. *Frontiers in Ecology and the Environment*, 18 (2), 83–91.
- Miguel, E., Grosbois, V., Caron, A., Boulinier, T., Fritz, H., Cornélis, D., Foggin, C., Makaya, P.V., Tshabalala, P.T., and de Garine-Wichatitsky, M., 2013. Contacts and foot and mouth disease transmission from wild to domestic bovines in Africa. *Ecosphere*, 4 (4), 1–32.
- Ministry of Environment and Tourism, 2013a. Management Plan: Namib-Naukluft Park.
- Ministry of Environment and Tourism, 2013b. Report on the Namibia Tourist Exit Survey 2012-2013.
- Ministry of Environment and Tourism, n.d. A strategic collaborative management and development plan for Greater Sossusvlei-Namib Landscape 2013 – 2018.

- Mitchell, D., Maloney, S.K., Jessen, C., Laburn, H.P., Kamerman, P.R., Mitchell, G., and Fuller, A., 2002. Adaptive heterothermy and selective brain cooling in arid-zone mammals. *Comparative Biochemistry and Physiology Part B*, 131 (4), 571–585.
- Mitchell, M.S., Powell, R.A., and Rachlow, J.L., 2012. Foraging optimally for home ranges. *Journal of Mammalogy*, 93 (4), 917–928.
- Miura, N., Ito, T.Y., Lhagvasuren, B., Enkhbileg, D., Tsunekawa, A., Takatsuki, S., Jiang, Z., and Mochizuki, K., 2004. Analysis of the seasonal migrations of Mongolian gazelle, using MODIS data. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, 35, 418–422.
- Mkanda, F.X. and Chansa, W., 2011. Changes in temporal and spatial pattern of road kills along the Lusaka-Mongu (M9) highway, Kafue National Park, Zambia. *South African Journal of Wildlife Research*, 41 (1), 68–78.
- Moehlman, P.D., King, S.R.B., and Kebede, F., 2016. Status and conservation of threatened equids. In: J.I. Ransom and P. Kaczensky, eds. *Wild equids: Ecology, management, and conservation*. Baltimore, MD: Johns Hopkins University Press, 167–186.
- Moodley, Y. and Harley, E.H., 2005. Population structuring in mountain zebras (*Equus zebra*): The molecular consequences of divergent demographic histories. *Conservation Genetics*, 6 (6), 953–968.
- van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S., and Gaillard, J.-M., 2009. Memory keeps you at home: A mechanistic model for home range emergence. *Oikos*, 118 (5), 641–652.
- Morelle, K., Lehaire, F., and Lejeune, P., 2013. Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. *Nature Conservation*, 5, 53–73.
- Moseby, K.E., Lollback, G.W., and Lynch, C.E., 2018. Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. *Biological Conservation*, 219, 78–88.
- Mueller, T. and Fagan, W.F., 2008. Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos*, 117 (5), 654–664.
- Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Wattles, D., and DeStefano, S., 2011. How landscape dynamics link individual-to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, 20 (5), 683–694.
- Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G., and Leimgruber, P., 2008. In search of forage: Predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, 45 (2), 649–658.
- Muntifering, J.R., Ditmer, M.A., Stapleton, S., Naidoo, R., and Harris, T.H., 2019. Hartmann’s mountain zebra resource selection and movement behavior within a large unprotected landscape in northwest Namibia. *Endangered Species Research*, 38, 159–170.
- Nafus, M.G., Tuberville, T.D., Buhlmann, K.A., and Todd, B.D., 2013. Relative abundance and demographic structure of Agassiz’s desert tortoise (*Gopherus agassizii*) along roads of varying size and traffic volume. *Biological Conservation*, 162, 100–106.
- Nagy, K.A. and Knight, M.H., 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari desert. *Journal of Mammalogy*, 75 (4), 860–872.
- Naidoo, R., Chase, M.J., Beytell, P., du Preez, P., Landen, K., Stuart-Hill, G., and Taylor, R., 2016. A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. *Oryx*, 50 (1), 138–146.
- Naidoo, R., Kilian, J.W., Du Preez, P., Beytell, P., Aschenborn, O., Taylor, R.D., and 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.

- Nam-Place Project [online], n.d. *Landscapes Namibia*. Available from: <http://www.landscapesnamibia.org/namplace-project> [Accessed 17 Oct 2020].
- Nandintsetseg, D., 2019. Nomadic animal movements and their conservation challenges. Doctoral dissertation. Johann Wolfgang Goethe University, Frankfurt am Main.
- Nandintsetseg, D., Bracis, C., Olson, K.A., Böhning-Gaese, K., Calabrese, J.M., Chimeddorj, B., Fagan, W.F., Fleming, C.H., Heiner, M., Kaczensky, P., Leimgruber, P., Munkhnast, D., Stratmann, T., and Mueller, T., 2019. Challenges in the conservation of wide-ranging nomadic species. *Journal of Applied Ecology*, 56 (8), 1916–1926.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105 (49), 19052–19059.
- Nellemann, C., Vistnes, I., Jordhøy, P., and Strand, O., 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. *Biological Conservation*, 101 (3), 351–360.
- Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., and Newton, A., 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological conservation*, 113 (2), 307–317.
- Newmark, W.D., Boshe, J.I., Sariko, H.I., and Makumbule, G.K., 1996. Effects of a highway on large mammals in Mikumi National Park, Tanzania. *African Journal of Ecology*, 34 (1), 15–31.
- Noonan, M.J., Tucker, M.A., Fleming, C.H., Akre, T.S., Alberts, S.C., Ali, A.H., Altmann, J., Antunes, P.C., Belant, J.L., Beyer, D., Blaum, N., Böhning-Gaese, K., Cullen Jr., L., de Paula, R.C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., Ford, A.T., Goheen, J.R., Janssen, R., Jeltsch, F., Kauffman, M., Kappeler, P.M., Koch, F., LaPoint, S., Markham, A.C., Medici, E.P., Morato, R.G., Nathan, R., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., Paviolo, A., Ramalho, E.E., Rösner, S., Schabo, D.G., Selva, N., Sergiel, A., da Silva, M.X., Spiegel, O., Thompson, P., Ullmann, W., Zięba, F., Zwijacz-Kozica, T., Fagan, W.F., Mueller, T., and Calabrese, J.M., 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*, 89 (2), e01344.
- Nott, K. and Savage, M.J., 1985. Observations on the utilization of a dune succulent by Namib faunae. *South African Journal of Zoology*, 20 (4), 269–271.
- Novellie, P., Lindeque, M., Lindeque, P., Lloyd, P., and Koen, J., 2002. Status and action plan for the mountain zebra (*Equus zebra*). In: P.D. Moehlman, ed. *Equids: Zebras, asses and horses. Status survey and conservation action plan*. IUCN/SSC Equid Specialist Group. Gland, Switzerland: IUCN, 28–42.
- Noy-Meir, I., 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4, 25–51.
- Núñez, T.A., Lawler, J.J., McRae, B.H., Pierce, D.J., Krosby, M.B., Kavanagh, D.M., Singleton, P.H., and Tewksbury, J.J., 2013. Connectivity planning to address climate change. *Conservation Biology*, 27 (2), 407–416.
- Oberem, P. and Oberem, P., 2016. *The new game rancher*. 1st ed. Queenswood, South Africa: Briza Publications.
- O’Connell-Rodwell, C.E., Rodwell, T., Rice, M., and Hart, L.A., 2000. Living with the modern conservation paradigm: Can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biological Conservation*, 93 (3), 381–391.
- Odendaal, N. and Shaw, D., 2010. Conservation and economic lessons learned from managing the NamibRand Nature Reserve. *Great Plains Research*, 20 (1), 29–36.
- Olson, D.D., Bissonette, J.A., Cramer, P.C., Green, A.D., Davis, S.T., Jackson, P.J., and Coster, D.C., 2014. Monitoring wildlife-vehicle collisions in the information age: How smartphones can improve data collection. *PLoS ONE*, 9 (6), e98613.

- Olson, K.A., Fuller, T.K., Mueller, T., Murray, M.G., Nicolson, C., Odonkhuu, D., Bolortsetseg, S., and Schaller, G.B., 2010. Annual movements of Mongolian gazelles: Nomads in the eastern steppe. *Journal of Arid Environments*, 74 (11), 1435–1442.
- Ord, J.K. and Getis, A., 1995. Local spatial autocorrelation statistics: Distributional issues and an application. *Geographical Analysis*, 27 (4), 286–306.
- Osmers, B., Petersen, B.-S., Hartl, G.B., Grobler, J.P., Kotze, A., van Aswegen, E., and Zachos, F.E., 2012. Genetic analysis of southern African gemsbok (<i>Oryx gazella</i>) reveals high variability, distinct lineages and strong divergence from the East African *Oryx beisa*. *Mammalian Biology*, 77 (1), 60–66.
- Ottewell, K., Dunlop, J., Thomas, N., Morris, K., Coates, D., and Byrne, M., 2014. Evaluating success of translocations in maintaining genetic diversity in a threatened mammal. *Biological Conservation*, 171, 209–219.
- Oxoli, D., Molinari, M.E., and Brovelli, M.A., 2018. Hotspot Analysis, an open source GIS tool for exploratory spatial data analysis: Application to the study of soil consumption in Italy. *Rendiconti Online Societa Geologica Italiana*, 46, 82–87.
- Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, C., Hanekom, C., Heath, B., Hunter, L., Delongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., MacLennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogotu, J.O., Okot-Omoya, E., Patterson, B.D., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H., and Polasky, S., 2013. Conserving large carnivores: Dollars and fence. *Ecology Letters*, 16 (5), 635–641.
- Paige, C., 2012. *A landowner's guide to wildlife friendly fences*. 2nd ed. Helena, MT: Private Land Technical Assistance Program, Montana Fish, Wildlife & Parks.
- Parry, D., 1987. Wildebeest (*Conchaetes taurinus*) mortalities at Lake Xau, Botswana. *Botswana Notes and Records*, 19, 95–101.
- Parry, D.C. and Campbell, B.M., 1990. Wildlife management areas of Botswana. *Botswana Notes and Records*, 22, 65–77.
- Patten, R.S. and Ellis, J.E., 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. *Vegetatio*, 117 (1), 69–79.
- Peadar, J.M., Nowakowski, A.J., Tuberville, T.D., Buhlmann, K.A., and Todd, B.D., 2017. Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. *Biological Conservation*, 214, 13–22.
- Penzhorn, B., 2013. *Equus zebra* Mountain zebra. In: J. Kingdon and M. Hoffmann, eds. *Mammals of Africa. Volume 5: Carnivores, pangolins, equids and rhinoceroses*. London, UK: Bloomsbury, 438–443.
- Périquet, S., Roxburgh, L., le Roux, A., and Collinson, W.J., 2018. Testing the value of citizen science for roadkill studies: A case study from South Africa. *Frontiers in Ecology and Evolution*, 6, 15.
- Perkins, J.S., 2019. 'Only connect': Restoring resilience in the Kalahari ecosystem. *Journal of Environmental Management*, 249, 109420.
- Peters, J. and Brink, J.S., 1992. Comparative postcranial osteomorphology and osteometry of springbok, *Antidorcas marsupialis* (Zimmermann, 1780) and grey rhebok, *Pelea capreolus* (Forster, 1790) (Mammalia: Bovidae). *Navorsinge van die Nasionale Museum Bloemfontein*, 8 (4), 161–207.

- Pirie, T.J., Thomas, R.L., and Fellowes, M.D.E., 2017. Game fence presence and permeability influences the local movement and distribution of South African mammals. *African Zoology*, 52 (4), 217–227.
- Plante, J., Jaeger, J.A.G., and Desrochers, A., 2019. How do landscape context and fences influence roadkill locations of small and medium-sized mammals? *Journal of Environmental Management*, 235, 511–520.
- Poor, E.E., Loucks, C., Jakes, A., and Urban, D.L., 2012. Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. *PLoS ONE*, 7 (11), e49390.
- Pouya, S. and Pouya, S., 2018. Planning for peace: Introduction of transboundary conservation areas. *Kocaeli Journal of Science and Engineering*, 1 (2), 33–41.
- Powell, R.A., 2000. Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences*, 442.
- Powell, R.A. and Mitchell, M.S., 1998. Topographical constraints and home range quality. *Ecography*, 21 (4), 337–341.
- Powell, R.A. and Mitchell, M.S., 2012. What is a home range? *Journal of Mammalogy*, 93 (4), 948–958.
- QGIS development team, 2021. *QGIS geographic information system*. QGIS Association.
- R Core Team, 2019. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ransom, J.I. and Kaczensky, P., 2016. *Equus*: An ancient genus surviving the modern world. In: J.I. Ransom and P. Kaczensky, eds. *Wild equids: Ecology, management, and conservation*. Baltimore, MD: Johns Hopkins University Press, 1–4.
- Rea, R.V., 2003. Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. *Wildlife Biology*, 9 (4), 81–91.
- van der Ree, R., Smith, D.J., and Grilo, C., 2015. The ecological effects of linear infrastructure and traffic: Challenges and opportunities of rapid global growth. In: R. van der Ree, D.J. Smith, and C. Grilo, eds. *Handbook of road ecology*. Chichester, UK: Wiley-Blackwell, 1–9.
- Relton, C., Selier, J., and Strauss, W.M., 2016. *Oryx gazella* - Gemsbok. In: M.F. Child, L. Roxburgh, E. Do Linh San, D. Raimondo, and H.T. Davies-Mostert, eds. *The Red List of mammals of South Africa, Swaziland and Lesotho*. South Africa: SANBI and Endangered Wildlife Trust, 1–8.
- Rendall, A.R., Webb, V., Sutherland, D.R., White, J.G., Renwick, L., and Cooke, R., 2021. Where wildlife and traffic collide: Roadkill rates change through time in a wildlife-tourism hotspot. *Global Ecology and Conservation*, 27, e01530.
- Rey, A., Novaro, A.J., and Guichón, M.L., 2012. Guanaco (*Lama guanicoe*) mortality by entanglement in wire fences. *Journal for Nature Conservation*, 20 (5), 280–283.
- Rhodes, J.R., Lunney, D., Callaghan, J., and McAlpine, C.A., 2014. A few large roads or many small ones? How to accommodate growth in vehicle numbers to minimise impacts on wildlife. *PLoS ONE*, 9 (3), e91093.
- Riggio, J. and Caro, T., 2017. Structural connectivity at a national scale: Wildlife corridors in Tanzania. *PLoS ONE*, 12 (11), e0187407.
- Ritter, R.C. and Bednekoff, P.A., 1995. Dry season water, female movements and male territoriality in springbok: Preliminary evidence of waterhole-directed sexual selection. *African Journal of Ecology*, 33 (4), 395–404.
- Robinson, T.J., 1975. A comparative study of the three subspecies of springbok, *Antidorcas marsupialis marsupialis* (Zimmermann, 1780), *Antidorcas marsupialis hofmeyri* (Thomas, 1926) and *Antidorcas marsupialis angolensis* (Blaine, 1922). University of Pretoria, South Africa.

- Roche, C., 2008. 'The fertile brain and inventive power of man': Anthropogenic factors in the cessation of springbok treks and the disruption of the Karoo ecosystem, 1865 - 1908. *Africa*, 78 (2), 157–188.
- Rohde, R.F., Hoffmann, M.T., Durbach, I., Venter, Z., and Jack, S., 2019. Vegetation and climate change in the Pro-Namib and Namib desert based on repeat photography: Insights into climate trends. *Journal of Arid Environments*, 165, 119–131.
- Roshier, D., Asmus, M., and Klaassen, M., 2008. What drives long-distance movements in the nomadic grey teal *Anas gracilis* in Australia? *Ibis*, 150 (3), 474–484.
- Rubenstein, D.I., 1989. Life history and social organization in arid adapted ungulates. *Journal of Arid Environments*, 17, 145–156.
- Rytwinski, T., Soanes, K., Jaeger, J.A.G., Fahrig, L., Findlay, C.S., Houlihan, J., van der Ree, R., and van der Grift, E.A., 2016. How effective is road mitigation at reducing road-kill? A meta-analysis. *PLoS ONE*, 11 (11), e0166941.
- Said, S. and Servant, S., 2005. The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, 20 (8), 1003–1012.
- Salomon, M., Cupido, C., and Samuels, I., 2013. The good shepherd: Remediating the fencing syndrome. *African Journal of Range & Forage Science*, 30 (1–2), 71–75.
- Sawyer, H., Kauffman, M.J., Middleton, A.D., Morrison, T.A., Nielson, R.M., and Wyckoff, T.B., 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. *Journal of Applied Ecology*, 50 (1), 68–78.
- Sawyer, H., Middleton, A.D., Hayes, M.M., Kauffman, M.J., and Monteith, K.L., 2016. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. *Ecosphere*, 7 (10), e01534.
- van Schalkwyk, D.L., McMillin, K.W., Witthuhn, R.C., and Hoffman, L.C., 2010. The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability*, 2 (11), 3479–3499.
- Schindler, S., Curado, N., Nikolov, S.C., Kret, E., Cárcamo, B., Catsadorakis, G., Poirazidis, K., Wrbka, T., and Kati, V., 2011. From research to implementation: Nature conservation in the eastern Rhodopes mountains (Greece and Bulgaria), European Green Belt. *Journal for Nature Conservation*, 19 (4), 193–201.
- Schloss, C.A., Nuñez, T.A., and Lawler, J.J., 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences*, 109 (22), 8606–8611.
- Schoenecker, K.A., King, S.R.B., Nordquist, M.K., Nandintsetseg, D., and Cao, Q., 2016. Habitat and diet of equids. In: J.I. Ransom and P. Kaczensky, eds. *Wild equids: Ecology, management, and conservation*. Baltimore, MD: Johns Hopkins University Press, 41–57.
- Schumann, M., Schumann, B., Dickman, A., Watson, L.H., and Marker, L., 2006. Assessing the use of swing gates in game fences as a potential non-lethal predator exclusion technique. *South African Journal of Wildlife Research*, 36 (2), 173–181.
- Scott-Hayward, L.A.S., Oedekoven, C., Mackenzie, M.L., and Rexstad, E., 2017. *MRSea: Marine renewables strategic environmental assessment*. Scotland: University of St Andrews.
- Seaman, D.E. and Powell, R.A., 1990. Identifying patterns and intensity of home range use. In: *Bears: Their biology and management*. Presented at the International Conference of Bear Research and Management, Victoria, British Columbia, Canada.: International Association for Bear Research and Management, 243–249.
- Seely, M. and Pallett, J., 2012. *Namib: Secrets of a desert uncovered*. 2nd ed. Windhoek, Namibia: Venture Publications.

- Seely, M.K., 1978a. Grassland productivity: The desert end of the curve. *South African Journal of Science*, 74 (8), 295–297.
- Seely, M.K., 1978b. Standing crop as an index of precipitation in the central Namib grassland. *Madoqua*, 11 (1), 61–68.
- Seidler, R.G., Long, R.A., Berger, J., Bergen, S., and Beckmann, J.P., 2015. Identifying impediments to long-distance mammal migrations. *Conservation Biology*, 29 (1), 99–109.
- Seiler, A., 2003. Effects of infrastructure on nature. In: M. Trocmé, S. Cahill, J.G. de Vries, H. Farall, L. Folkesson, G.L. Fry, C. Hicks, and J. Peymen, eds. *COST341. Habitat fragmentation due to transportation infrastructure: The European review*. Luxembourg: Office for Official Publications of the European Communities, 31–50.
- Seiler, A., 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology*, 10 (4), 301–313.
- Seiler, A., 2005. Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology*, 42 (2), 371–382.
- Selebatso, M., Maude, G., and Fynn, R.W.S., 2018. Assessment of quality of water provided for wildlife in the Central Kalahari Game Reserve, Botswana. *Physics and Chemistry of the Earth*, 105, 191–195.
- Silva, C.C., Lourenço, R., Godinho, S., Gomes, E., Sabino-Marques, H., Medinas, D., Neves, V., Silva, C., Rabaça, J.E., and Mira, A., 2012. Major roads have a negative impact on the tawny owl *Strix aluco* and the little owl *Athene noctua* populations. *Acta Ornithologica*, 47 (1), 47–54.
- Sinclair, A.R.E. and Fryxell, J.M., 1985. The Sahel of Africa: Ecology of a disaster. *Canadian Journal of Zoology*, 63 (5), 987–994.
- Skinner, J.D., 2013. *Antidorcas marsupialis* Springbok (Springbuck). In: J. Kingdon and M. Hoffmann, eds. *Mammals of Africa. Volume 6: Pigs, hippopotamuses, chevrotain, giraffes, deer and bovids*. London, UK: Bloomsbury, 398–403.
- Skinner, J.D. and Chimimba, C.T., 2005. *The mammals of the southern African subregion*. 3rd ed. Cape Town, South Africa: Cambridge University Press.
- Skinner, J.D., Davies, R.A.G., Conroy, A.M., and Dott, H.M., 1986. Productivity of springbok *Antidorcas marsupialis* and Merino sheep *Ovis aries* during a Karoo drought. *Transactions of the Royal Society of South Africa*, 46 (2), 149–164.
- Skinner, J.D. and Louw, G.N., 1996. *The springbok Antidorcas marsupialis (Zimmermann 1780)*. Pretoria, South Africa: Transvaal Museum.
- Skinner, J.D., van Zyl, J.H.M., and Oates, I.G., 1974. The effect of season on the breeding cycle of plains antelope of the western Transvaal highveld. *South African Journal of Wildlife Research*, 4 (1), 15–23.
- Slotow, R., Garai, M.E., Reilly, B., Page, B., and Carr, R.D., 2005. Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research*, 35 (1), 23–32.
- Smith, D., King, R., and Allen, B.L., 2020. Impacts of exclusion fencing on target and non-target fauna: A global review. *Biological Reviews*, 95 (6), 1590–1606.
- Smith, D.S. and Morton, S.R., 1990. A framework for the ecology of arid Australia. *Journal of Arid Environments*, 18 (3), 255–278.
- Smith, J., 2016. *Terminal Evaluation of the Namibia Protected Landscape Conservation Areas Initiative (NAMPLACE)*. Windhoek: GEF and Ministry of Environment and Tourism.
- Smuts, G.L., 1975. Home range sizes for Burchell's zebra *Equus burchelli antiquorum* from the Kruger National Park. *Koedoe*, 18 (1), 139–146.

- Southern African Institute for Environmental Assessment, 2014. *Strategic Environmental Assessment (SEA) of the Tourism Sector For The Greater Sossusvlei Namib Landscape*. Windhoek, Namibia: Southern African Institute for Environmental Assessment.
- Spanowicz, A.G., Teixeira, F.Z., and Jaeger, J.A., 2020. An adaptive plan for prioritizing road sections for fencing to reduce animal mortality. *Conservation Biology*, 34 (5), 1210–1220.
- Spinage, C.A., 1992. The decline of the Kalahari wildebeest. *Oryx*, 26 (3), 147–150.
- Stabach, J.A., Wittemyer, G., Boone, R.B., Reid, R.S., and Worden, J.S., 2016. Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. *Ecosphere*, 7 (8), e01428.
- Swihart, R.K. and Slade, N.A., 1985. Influence of sampling interval on estimates of home-range size. *The Journal of Wildlife Management*, 49 (4), 1019–1025.
- Swihart, R.K., Slade, N.A., and Bergstrom, B.J., 1988. Relating body size to the rate of home range use in mammals. *Ecology*, 69 (2), 393–399.
- Tabor, K., Hewson, J., Tien, H., González-Roglich, M., Hole, D., and Williams, J.W., 2018. Tropical protected areas under increasing threats from climate change and deforestation. *Land*, 7 (3), 90.
- Tarr, P.W. and Tarr, J.G., 1989. Veld dynamics and utilisation of vegetation by herbivores on the Ganas flats, Skeleton Coast Park, SWA/Namibia. *Madoqua*, 16 (1), 15–22.
- Taylor, C.R., 1969. The eland and the oryx. *Scientific American*, 220 (1), 88–97.
- Taylor, R.D. and Martin, R.B., 1987. Effects of veterinary fences on wildlife conservation in Zimbabwe. *Environmental Management*, 11 (3), 327–334.
- Tear, T.H., Mosley, J.C., and Ables, E.D., 1997. Landscape-scale foraging decisions by reintroduced Arabian oryx. *The Journal of Wildlife Management*, 61 (4), 1142–1154.
- Thomson, G.R., Penrith, M.-L., Atkinson, M.W., Atkinson, S.J., Cassidy, D., and 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.
- Tromp, L.R., 2015. Using remote sensing to explore the role of ambient temperature in determining gemsbok (*Oryx gazella*) usage of a heterogeneous landscape in the Central Kalahari. Master's thesis. University of the Witwatersrand, Johannesburg, South Africa.
- Tufto, J., Andersen, R., and Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *Journal of Animal Ecology*, 65 (6), 715–724.
- Valerio, F., Basile, M., and Balestrieri, R., 2021. The identification of wildlife-vehicle collision hotspots: Citizen science reveals spatial and temporal patterns. *Ecological Processes*, 10 (1), 1–13.
- Vanak, A.T., Thaker, M., and Slotow, R., 2010. Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, 143 (11), 2631–2637.
- Viles, H.A. and Goudie, A.S., 2013. Weathering in the central Namib desert, Namibia: Controls, processes and implications. *Journal of Arid Environments*, 93, 20–29.
- Walter, W.D., Onorato, D.P., and Fischer, J.W., 2015. Is there a single best estimator? Selection of home range estimators using area-under-the-curve. *Movement Ecology*, 3 (1), 1–11.
- Ward, D., 2016. *The biology of deserts*. 2nd ed. UK: Oxford University Press.
- Waters, C.M., McDonald, S.E., Reseigh, J., Grant, R., and Burnside, D.G., 2020. Insights on the relationship between total grazing pressure management and sustainable land management: Key indicators to verify impacts. *The Rangeland Journal*, 41 (6), 535–556.
- Weise, F.J., Wessels, Q., Munro, S., and Solberg, M., 2011. Using artificial passageways to facilitate the movement of wildlife on Namibian farmland. *African Journal of Wildlife Research*, 44 (2), 161–166.
- Welch, R.J. and Parker, D.M., 2016. Brown hyaena population explosion: rapid population growth in a small, fenced system. *Wildlife Research*, 43 (2), 178–187.

- Westoby, M., 1979. Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Plant Sciences*, 28 (3–4), 169–194.
- White, L.C., Moseby, K.E., Thomson, V.A., Donnellan, S.C., and Austin, J.J., 2018. Long-term genetic consequences of mammal reintroductions into an Australian conservation reserve. *Biological Conservation*, 219, 1–11.
- Whitford, W.G. and Duval, B.D., 2020. *Ecology of desert systems*. 2nd ed. London: Academic Press.
- Wilkinson, C.E., McInturff, A., Kelly, M., and Brashares, J.S., 2021. Quantifying wildlife responses to conservation fencing in East Africa. *Biological Conservation*, 256, 109071.
- Williamson, D.T., 1987. Plant underground storage organs as a source of moisture for Kalahari wildlife. *African Journal of Ecology*, 25 (1), 63–64.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70 (1), 164–168.
- Worton, B.J., 1995. A convex hull-based estimator of home-range size. *Biometrics*, 51 (4), 1206–1215.
- Xu, W., Dejid, N., Herrmann, V., Sawyer, H., and Middleton, A.D., 2021. Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. *Journal of Applied Ecology*, 58 (4), 690–698.
- Zhang, L., Liu, J., Mcshea, W.J., Wu, Y., Wang, D., and Lü, Z., 2014. The impact of fencing on the distribution of Przewalski's gazelle. *The Journal of Wildlife Management*, 78 (2), 255–263.
- van Zyl, J.H.M., 1965. The vegetation of the S.A. Lombard Nature Reserve and its utilisation by certain antelope. *Zoologica Africana*, 1 (1), 55–71.

Appendices

Appendix 1 Information on the capture and tracking of ungulates in the GSNL

Species	ID	Sex	Collaring date	Analysis start date	Analysis end date	Tracking duration (total days)	Total telemetry signals	Make	Termination reason
HZ	1092	F	22/11/2013	06/12/2013	14/07/2015	585	2150	AWT	Battery
HZ	1093	F	22/11/2013	06/12/2013	17/09/2015	650	1743	AWT	Battery
HZ	1099	F	22/11/2013	06/12/2013	21/12/2014	380	1424	AWT	Battery
HZ	1100	F	23/11/2013	07/12/2013	30/12/2014	388	1451	AWT	Battery
HZ	1774	F	15/12/2015	29/12/2015	30/12/2017	732	1675	AWT	Battery
HZ	1094	M	22/11/2013	06/12/2013	06/12/2015	730	1728	AWT	Battery
HZ	1095	M	22/11/2013	06/12/2013	17/03/2015	466	1518	AWT	Battery
HZ	1096	M	23/11/2013	07/12/2013	06/04/2015	485	1531	AWT	Battery
HZ	1097	M	22/11/2013	06/12/2013	16/09/2015	649	1753	AWT	Battery
HZ	1098	M	22/11/2013	06/12/2013	07/10/2015	670	1746	AWT	Battery
HZ	1771	M	14/12/2015	28/12/2015	25/11/2017	698	8898	AWT	Battery
HZ	1772	M	14/12/2015	28/12/2015	29/11/2017	702	1845	AWT	Battery
HZ	1773	M	15/12/2015	29/12/2015	26/05/2016	149	390	AWT	Mortality
HZ	1775	M	01/08/2016	15/08/2016	18/03/2018	580	1743	AWT	Battery
HZ	1776	M	01/08/2016	15/08/2016	26/03/2018	588	1736	AWT	Battery
G	1101	F	22/11/2013	06/12/2013	27/10/2015	690	1756	AWT	Battery
G	1102	F	22/11/2013	06/12/2013	08/04/2015	488	1549	AWT	Battery
G	1103	F	22/11/2013	06/12/2013	09/04/2015	489	1565	AWT	Battery
G	1104	F	23/11/2013	07/12/2013	07/10/2015	669	1709	AWT	Battery
G	1105	F	23/11/2013	07/12/2013	16/03/2015	464	1525	AWT	Battery

Species	ID	Sex	Collaring date	Analysis start date	Analysis end date	Tracking duration (total days)	Total telemetry signals	Make	Termination reason
G	1106	F	23/11/2013	07/12/2013	09/04/2015	488	1551	AWT	Battery
G	1108	F	23/11/2013	07/12/2013	08/05/2015	517	1581	AWT	Battery
G	1109	F	23/11/2013	07/12/2013	18/03/2015	466	1506	AWT	Battery
G	1765	F	14/12/2015	28/12/2015	26/06/2018	911	2628	AWT	Battery
G	1766	F	14/12/2015	28/12/2015	05/01/2018	739	2133	AWT	Mortality
G	1768	F	15/12/2015	29/12/2015	28/06/2018	912	2473	AWT	Battery
G	1770	F	16/12/2015	30/12/2015	05/05/2018	857	2486	AWT	Battery
G*	1107	F	23/11/2013	07/12/2013	23/04/2015	502	2383	AWT	Battery
G*	1769	F	15/12/2015	29/12/2015	30/06/2018	914	2681	AWT	Battery
S	2799	F	12/12/2017	26/12/2017	22/06/2018	178	710	ST	Mortality
S	131	M	14/12/2015	28/12/2015	14/08/2016	230	687	AWT	Battery
S	132	M	15/12/2015	29/12/2015	10/03/2016	73	219	AWT	Mortality
S	132.2	M	02/08/2016	16/08/2016	19/12/2016	125	360	AWT	Battery
S	133	M	30/07/2016	13/08/2016	02/01/2017	142	402	AWT	Mortality
S	134	M	16/12/2015	30/12/2015	13/01/2017	380	1161	AWT	Battery
S	135	M	16/12/2015	30/12/2015	28/07/2016	211	629	AWT	Mortality
S	2797	M	12/12/2017	26/12/2017	30/11/2018	339	1375	ST	Mortality
S	2798	M	12/12/2017	26/12/2017	22/05/2018	147	593	ST	Mortality
S	2800	M	19/05/2018	02/06/2018	17/06/2018	15	64	ST	Mortality
S	2801	M	19/05/2018	02/06/2018	09/03/2020	646	2528	ST	Battery
S	2803	M	20/05/2018	03/06/2018	02/03/2020	638	2514	ST	Battery

*SAT1107 and SAT1769 was the same gemsbok individual.