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Abstract of thesis entitled

ECOLOGY OF WILDLIFE REINTRODUCTION:
HABITAT SELECTION OF REINTRODUCED LIONS (*PANTHERA LEO*)
AND BEHAVIOURAL RESPONSES OF THEIR PREY

Submitted by

YIU SZE WING

for the degree of Doctor of Philosophy
at The University of Hong Kong
in February 2017

Reintroduction is used for re-establishing species in their former ranges where they had been extirpated. In South Africa, the growth in tourism industry in recent years has resulted in rapid establishment of wildlife reserves, where the land was historically used for livestock farming. Large carnivores are often reintroduced in these reserves for conservation and tourist attractions. However, long-term monitoring on post-release behaviour that is critical for reintroduction success remains limited. The reintroduction of lions (*Panthera leo*) to Dinokeng Game Reserve has provided an opportunity to investigate the behaviour of reintroduced large carnivores and their impact on prey behaviour.

The early post-release period is critical for reintroduced animals to learn the locations of essential resources for fitness and survival. In this study, early post-release movement of lions was investigated. Movement patterns varied greatly between individuals. Post-release dispersal from the release site was observed, but some groups returned to the area of release while others settled further away. Rates of movements differed at different times of the day and some of the lions avoided buildings while others showed a sign of habituation over time. Despite individual variations, the movement patterns started to stabilise by the end of the first season, suggesting that the animals had been exploring the environment before settlement.
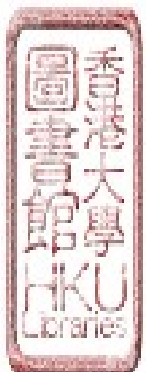
To understand the space use of reintroduced lions, their second and third order of habitat selections, home range utilisation and home range resource selection, respectively, were examined. Exploratory behaviour was found in space use patterns. The rates of expansion in home range sizes were the highest after release, and declined over time. Resource selection patterns showed consistent change in trends but also stabilized over time. All lions established home ranges at their release area and selected for landscape features with low topographic roughness, high prey availability and accessibility, and low human disturbance. The locations and order of release had great impact on spatial behaviour by influencing inter-group interactions. Lions avoided the home ranges of those released earlier at the same site and their selected vegetation.

The presence of predators generates a "landscape of fear" in which prey adjust anti-predatory behaviour according to the levels of perceived predation risk. Intense and routine vigilance response of wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga burchellii*) to the "landscape of fear" topographies were tested in this study to assess the impact of predator reintroductions. Response was species-specific, but in general, intense vigilance increased with higher predator encounter rate, higher predator lethality and lower effectiveness of the vigilance behaviour. In contrast, routine vigilance response related more to the amount of time the animals could potentially spare when foraging under different environmental conditions.

This study indicates the usefulness of monitoring animal movement and patterns of habitat selection in assessing post-release wildlife dynamics. It highlights the importance of adequate spatial planning of release sites when multiple releases are to occur, to minimise inter-group competition and maximise the reintroduction success; and the application of focal sampling of prey behaviour as indicator of the intensity of predator impact.
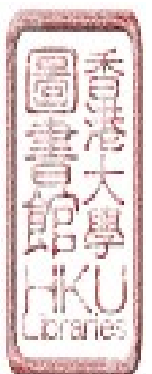
ECOLOGY OF WILDLIFE REINTRODUCTION:

HABITAT SELECTION OF REINTRODUCED LIONS

(*PANTHERA LEO*) AND

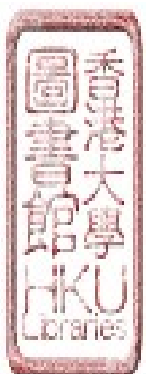# BEHAVIOURAL RESPONSES OF THEIR PREY

by

YIU SZE WING

B.Sc. The University of Hong Kong

A thesis submitted in partial fulfilment of the requirements

for the degree of Doctor of Philosophy
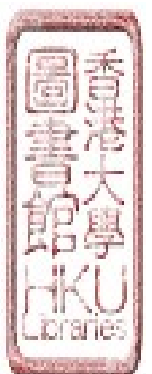
at The University of Hong Kong

February 2017

To God, who has saved my life from the feet of a furious elephant and accompanied me through the best and the worst.
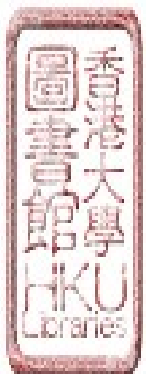
"With man this is impossible, but with God all things are possible."

– Matthew 19:26

"God blessed them and said to them, 'Be fruitful and increase in number; fill the earth and subdue it. Rule over the fish in the sea and the birds in the sky and over every living creature that moves on the ground.'" – Genesis 1:28
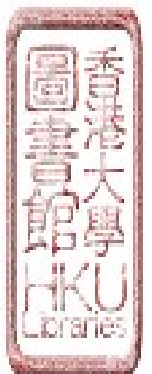
Declaration

I declare that this thesis represents my own work, except where due acknowledgement is made, and that is has not been previously included in a thesis, dissertation or report submitted to this University or to any other institution for a degree, diploma or other qualifications.

Signed ………………………………………….
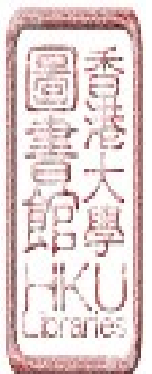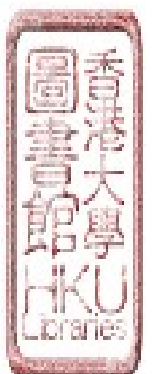
Yiu Sze Wing

Acknowledgements

guarding and protecting me from getting eaten or trampled by the wild animals when I was conducting fieldwork on foot.

I am grateful to the Centre for African Ecology of University of the Witwatersrand, where I was based for a prolonged period of time, for the provision of research vehicle and working space. I would also like to extend my sincere thanks to Dr. Jodie Martin, Dr. Jason Marshal and Dr. Thulani Tshabalala for their guidance and advices on statistics and modelling and insightful discussions on research. I thank all my Wits labmates and friends, especially Wendy Panaino, Christopher Rankin, Elena Mariotti, Giacomo D'Ammando, Claire Relton, Kim Mordecai, Melinda Boyers and Dr. Lochran Traill, for their suggestions on research, and kindness and friendship that made me feel welcomed and for all the fun and laughter we shared.

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driving me to the middle of the bush and asking me to drive us home without a GPS on my second day of arrival), assisting me with my fieldwork, and all meaningful and interesting conversations. I also want to thank Robin Cook, Ivan Annandale, Sumeshni Pillay and Felicia Morgan for their friendship, kindness, support and care which mean a whole lot to me. My stay in South Africa would not have been so pleasant and unforgettable without the love from my friends.

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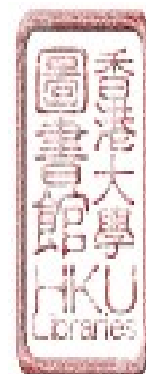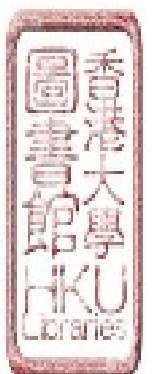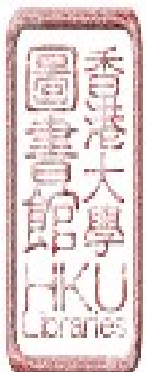
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Chapter 1
General introduction

With a rapid growth in human population, conflicts between human and wildlife species arise. Exploitation of resources destroys and fragments natural habitats, shrinks species distribution and abundance and accelerates species extinction (Happold 1995; Sitati et al. 2003; Thuiller et al. 2006). In order to re-establish populations of a species in areas within their historical range from which they had gone extinct or to maintain existing populations of species in their remaining habitats, reintroductions and translocations are being used increasingly as conservation practices (IUCN 1998; Ripple and Beschta 2003; Armstrong and Seddon 2007). Translocation is defined as an artificial movement of wildlife, either an individual or a population, from one part of their range to another (IUCN 1998). Reintroduction involves the translocation of animals, either wild and captured from a viable population elsewhere or bred and reared in captive facilities, from their original range (or facilities) to another site for releases. Reintroductions have been used across species and taxa in different geographic regions; for example, the endangered and endemic stitchbird (*Notiomystis cincta*) in New Zealand (Armstrong et al. 2002), the giant tortoises (*Chelonoidis nigra*) in the Galápagos (Gibbs et al. 2008), and the African wild dogs (*Lycaon pictus*) in South Africa (Gusset et al. 2010) have all been reintroduced to their former ranges. At the same time, more research efforts have been put into the field of reintroduction biology, from population level to ecosystem level, to gain knowledge on the ecology of reintroduced animals, the effects of the reintroduction on the environment, and factors that affect reintroduction success (Sarrazin and Barbault 1996; Sutherland 1998; Seddon 1999; Armstrong and Seddon 2007).

The definition of a successful reintroduction varies and depends on the specific aim of the reintroduction attempt, but in general it includes the persistence of the introduced animals until breeding and the establishment of a self-sustaining population (Seddon 1999). Numerous factors influence reintroduction success, e.g. the capturing and handling procedures, sex and age composition of the reintroduced animals, habitat quality, food availability and inter-specific interactions at the release site, and most importantly, post-release monitoring (Scheepers and Venzke
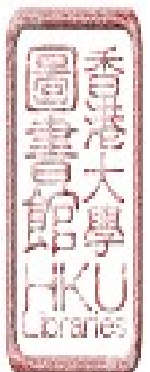
1995; Moorhouse et al. 2009; Moseby et al. 2011; Ewen et al. 2012). Post-release monitoring allows one to assess the habitat utilisation by the reintroduced animals and the influence of different environmental factors on the survival and population dynamics of the animals, which indicate the adaptation progress of the animals to the new environment (Boyd and Bandi 2002; Nichols and Armstrong 2012). The information collected is therefore critical for informed management decisions to enhance post-release survival and future reintroduction planning (McCarthy and Possingham 2007; Bernardo et al. 2011; McCarthy et al. 2012).

Behavioural and spatial ecology are two important aspects in studying and monitoring reintroduced animals (Sutherland 1998; Seddon et al. 2007). Once released, the reintroduced animals need to learn the location of resources that are essential for their survival in the new environment. The processes of learning and adapting to the change in environment in reintroduced animals are reflected in their post-release movement and habitat selection (Vickery and Mason 2003; Bose and Sarrazin 2007). These in turn affect their fitness, reproductive success and survival probability (Morales et al. 2010), thus reintroduction success. Extensive post-release dispersal could result in the reintroduced animals leaving the release site, as shown in translocated wolves (*Canis lupus*) in Minnesota (Fritts et al. 1984), black bear (*Ursus americanus*) in Arkansas (Wear et al. 2005) and white-tailed deer (*Odocoileus virginianus*) in Texas, U.S. (Roger 1988). On the other hand, movement and range expansion within the release site could facilitate population growth and establishment (Saltz et al. 2000; Dolev et al. 2002; Benson and Chamberlain 2007). According to Johnson (1980), animal habitat selection is a hierarchical process: first order selection of geographic range; second order selection of home range; third order selection of habitat components within the home range; and forth order selection of food items. A successful establishment of home ranges and selection for desired habitat features and food resources are therefore important for the reintroduced animals to survive. Signs of stabilization in movement and habitat selection patterns were mostly observed after a year of reintroduction in previous studies, in some cases after more than 2 years (Bernardo et al. 2011; de Hoog 2014). It suggests that long-term post-release monitoring of the spatial behaviour of reintroduced animals are necessary for assessing reintroduction success.
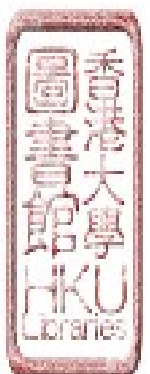
Research focus is also being placed on the interactions between reintroduced animals and the local animals, particularly on reintroduced large carnivores and prey. Predators regulate prey through direct predation and predation risk effect (Creel and Christianson 2008). The risk effect influences the morphology and behaviour of prey, and could have a greater impact on prey reproduction and survival than direct predation. Creel et al. (2007) reported a decline in elk fecal progesterone concentration and recruitment of calves in the Greater Yellowstone Ecosystem, resulting from changes in habitat selection, aggregation and foraging patterns of elk after the reintroduction of wolves. The risk effect is also discussed in Laundré et al. (2001): predators regulate their prey non-lethally by establishing a "landscape of fear", within which the prey adjust their behaviour in response to the different levels of predation risk in the landscape (Brown et al. 1999; Laundré et al 2010). The predation risk indicates and quantifies the level of "fear" of being captured by predators that the prey is experiencing. Also, behavioural changes of prey and its impacts on population dynamics could ultimately cascade into environmental changes (Nelson et al. 2004; Preisser et al. 2005). The most well-known example is the reintroduction of wolves in Yellowstone National Park, U.S., which has led to an increase in vigilance behaviour and use of open meadows habitat by elk (*Cervus Canadensis*), and resulted in a reduction in diet quality for the elk and an increase in the abundance of quaking aspen (*Populus tremuloides*) and willow trees (*Salix spp.*) (Laundré et al 2001; Hernández and Laundré 2005). The increase in vegetation has, in turn, provided habitats for beavers (*Castor canadensis*) and led to their population increase (Ripple and Beschta 2004). Therefore, the reintroduction of a top-order predator could influence not only the prey population, but the entire ecosystem dynamics. The impacts could be extensive on a naïve prey population that lacks experience in interacting with a long extinct predator (Sih et al. 2010). The monitoring of prey behaviour is thus needed for identifying and preventing potential adverse impacts of predator reintroduction on prey and ultimately the environment.

Africa has a high level of mammal species extinction, with its species abundance in protected areas decreased by half in 35 years since 1970 (Ceballos and Enrlich 2002; Craigie te al. 2010). Top-order predators often have high risk of extinction due to their large body size thus requirement of large and intact habitat

3

to survive, and vulnerability to human disturbances and exploitation (Cardillo 2003; Duffy 2003; Cardillo et al. 2004). It is predicted that the current population of African lion (*Panthera leo*), estimated between 32,000 and 35,000 (Riggio et al. 2013), will decrease by 50% in the next two decades (Bauer et al. 2015). Among the geographic areas that have existing lion populations, South Africa has been identified as one of the lion stronghold area (Riggio et al. 2013).

In South Africa, the rapid development of agriculture in the last century has led to a three-fold increase in the cultivated land area (Biggs and Scholes 2002). This has resulted in a great extent of habitat fragmentation and the subsequent restriction of movement of the remaining wildlife in fenced protected areas (Hayward and Kerley 2009). At the same time, the fast-growing tourism industry in the country in recent decades has led to the rapid establishment of small private wildlife reserves ($<1000 \text{ km}^2$) from lands that were previously used for livestock farming (Hoffman and Rohde 2007; Di Minin et al. 2013). To compensate for the exploitation of wildlife and to attract tourists, considerable efforts have been made to reintroduce flagship large carnivores such as lions, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and African wild dogs in the protected areas and private reserves (Hayward et al. 2007b). Starting from 1991, at least 45 small, fenced reserves have reintroduced lions with the total lion population within these reserves reaching 700 (Miller and Funston 2014). Management of lions is especially challenging in small and enclosed systems because of the difficulties in maintaining the ecological integrity with fast growing lion populations and high abundance of naïve prey (Ferreira and Hofmeyr 2013; Miller et al. 2013). Intense intra-specific competitions for resources could arise in these small areas and the potential impacts of predator reintroductions on the local prey species could be high (Lehmann et al. 2008a; Miller and Funston 2014). However, studies have been focusing on population control while information on the behavioural ecology of reintroduced lions and the behavioural dynamics between lions and their prey remain limited (Hayward et al. 2007a; Hunter et al. 2007).

With the cooperation between Gauteng Provincial Government, landowners and local communities, a reintroduction project was recently initiated at the 185km^2 Dinokeng Game Reserve (DGR), situated in the north-eastern Gauteng Province, South Africa. The major objective of the DGR project is to establish a wildlife
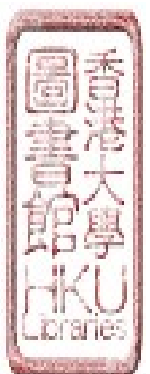
reserve that provides job opportunities and community enrichment, and promote economic growth through conservation. Lions were extirpated from the area before the reintroductions of 11 lions into the reserve since 2011. Without any resident population of other large carnivores, such a situation provides a great research opportunity for studying the ecology and impact of lion reintroduction on the local prey species in a small fenced ecological system. With the potential of expanding the reserve into the greater Dinokeng area, this study may have long-lasting implications on future management practices.

In this study, I aim to: (1) investigate the post-release movement patterns and habitat selection of reintroduced lions; (2) assess the impacts of lion reintroductions on the behaviour of their prey, with the following objectives in the different chapters:

Chapter 2

1. To document the geography, climate, and species composition of the study area and the history of lion reintroductions.

Chapter 3

1. To test for the presence of homing behaviour (a continuous movement towards the direction of capture sites) in the reintroduced lions.
2. To investigate the early post-release movement patterns of the reintroduced lions in relation to landscape and environmental features.

Chapter 4

1. To assess the second order habitat selection by the reintroduced lions, including home range establishment and changes in home range utilisation over time.
2. To investigate the influence of territorial conflicts and new introductions on the home range utilisation of reintroduced lions.

Chapter 5

1. To investigate the changes in third order habitat selection, i.e. resource selection within home ranges, by the reintroduced lions over time.
2. To assess the impacts of territorial conflicts and new introductions on the third order habitat selection of the reintroduced lions.
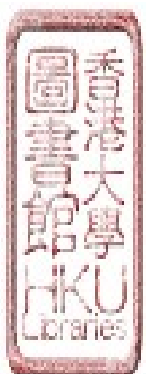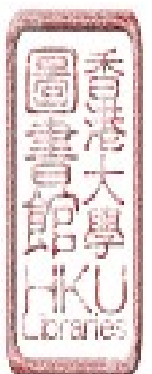
Chapter 6

1. To quantify predation risks at the study site using lion home range maps and predicted probability of occurrence of lions.
2. To examine two types of vigilance behaviour of Burchell's zebra (*Equus quagga burcelli*) and blue wildebeest (*Connochaetes taurinus*) in response to the predation risks and different environmental features relating to the landscape of fear topographies.

Chapter 7

1. To summarize the findings from the study and its implications for the conservation management of large carnivore reintroduction.
2. To identify limitations of the study and suggest future research directions.

The results from this research will allow a better understanding of the behavioural responses of reintroduced large carnivores to a new environment, the processes of adapting to this environment and the impacts of reintroducing a top-order predator on the behaviour of naïve prey. It will likely prove valuable in the informed management decisions for small enclosed reserves and contribute to the fast developing field of reintroduction and restoration ecology, ultimately benefitting future reintroduction practices.

Chapter 2
Study area

Location, topography and history

The study was undertaken in Dinokeng Game Reserve (DGR), situated in the Gauteng and Limpopo province of South Africa between latitudes 25°15'28" S and 25°28'12" S and longitudes 28°17'55" E and 28°28'25" E (Fig. 2.1). DGR is entirely enclosed by a predator-proof electric fence, spanning an area of 185 km^2 that ranges from 1025 m above sea level (a.s.l) in the northwest to 1258 m a.s.l. in the southeast (Appendix A, Fig. A-1). The Kaallaagte Spruit in the southwest and the Boekenhout Spruit in the southeast flow into the Pienaars River in the north, providing perennial source of water in the reserve together with more than 40 natural and artificial dams (Fig. 2.1). The road network is extensive, with the tarred Rust de Winter Road (D48) running from west to east and dividing the reserve into two parts (Appendix A, Fig. A-2). There are more than 180 fenced-in private residential areas, lodges and camps in the reserve (Fig. 2.1).

DGR is a key component of a development project initiated by the Gauteng Provincial Government to promote tourism through conservation in the greater Dinokeng area which encompasses Roodeplaat Dam and Nature Reserve, and the towns of Cullinan and Rayton (Contour Project Managers 2009). DGR is the first initiative in South Africa to involve more than 250 private landowners in removing fences and incorporating their land into a larger reserve. Before the establishment of the reserve, most of the lands were used for agriculture, livestock farming, game viewing and hunting purposes. DGR was officially opened in September 2011 and is still at a stage of expansion into the Mpumalanga Province, expecting to span an area of 1200km^2 after completion. The reserve is currently managed by the Dinokeng Game Reserve Management Association (DGRMA) represented by elected landowners and government officials.
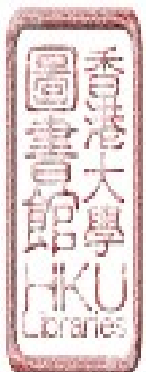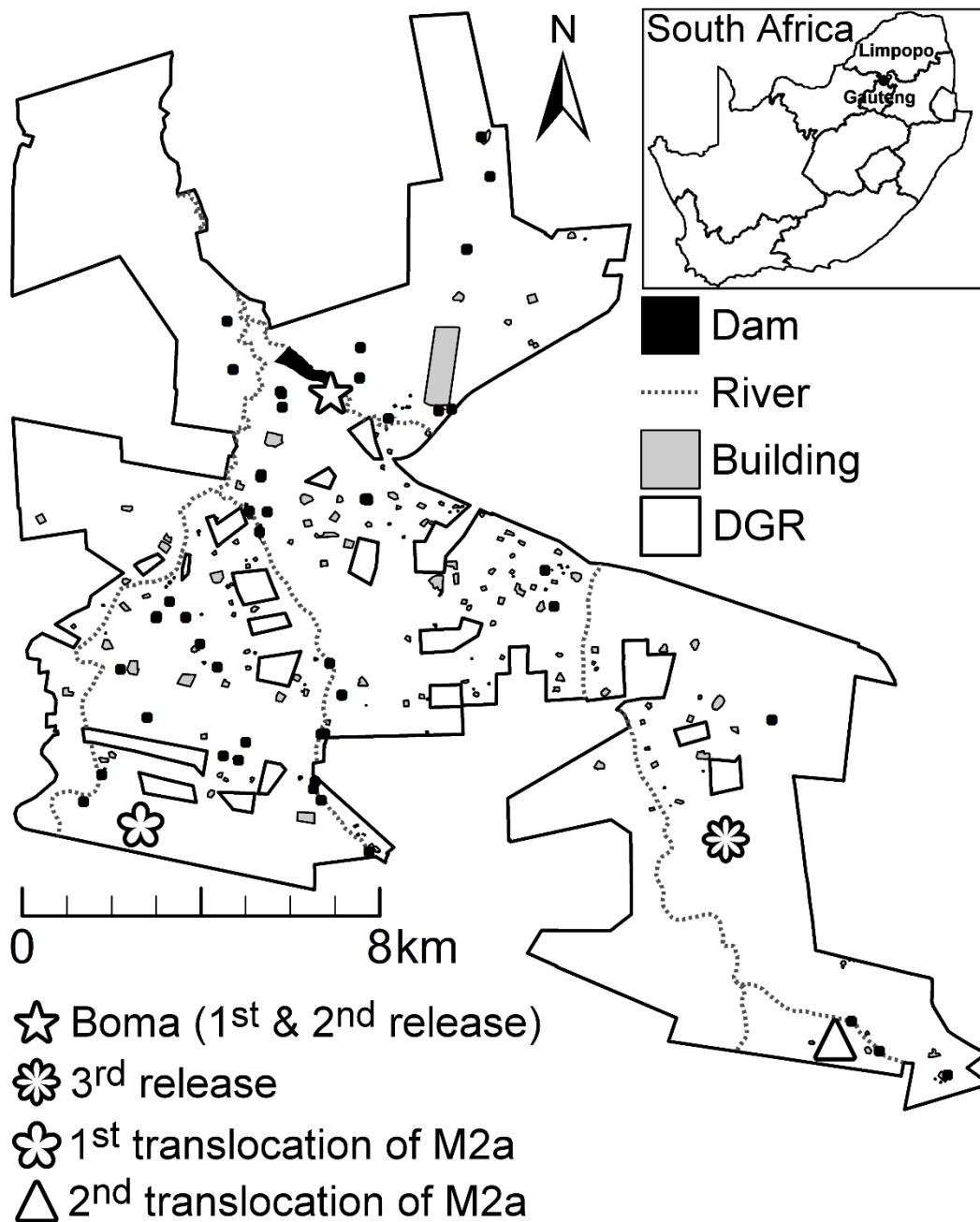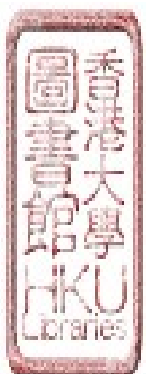
Fig. 2.1 Dinokeng Game Reserve (DGR) with indicated locations of boma and release and translocation sites. Inset map: location of DGR in South Africa.

Climate

DGR is located within the South Temperate Zone. The average annual rainfall in the area is 626 mm from 1961 to 1990, with distinct wet (October-April) and dry (May-September) seasons (New et al. 2002) (Fig. 2.2). Average maximum temperature ranges from 21°C to 30°C and minimum temperature from 5°C to 18°C

(WWO 2012) (Fig. 2.3). Temperature is the highest from December to February in the wet season and the lowest from June to July in the dry season.
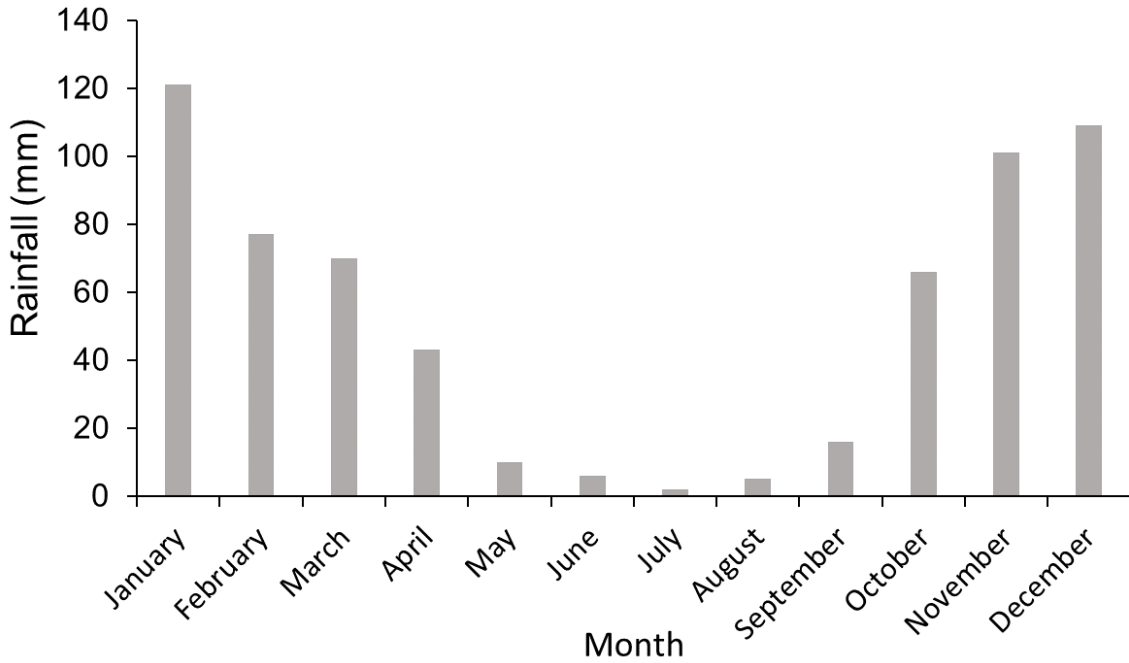
Fig. 2.2 Average annual rainfall (mm) in Dinokeng Game Reserve, 1961-1990. (Source: New et al. 2002).
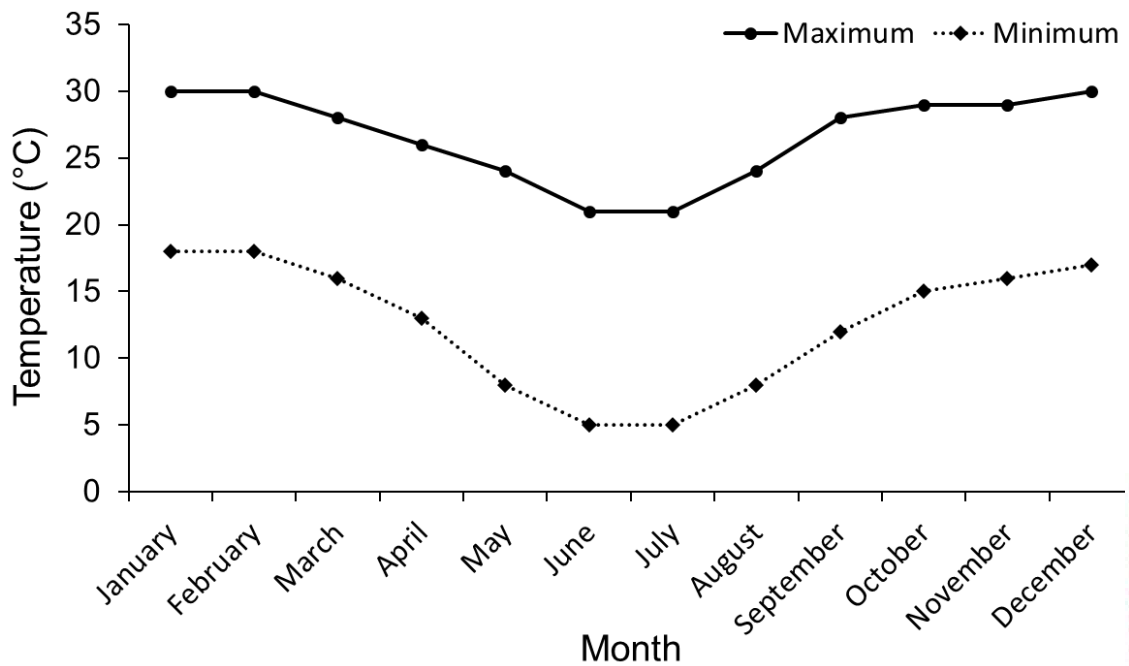
Fig. 2.3 Average annual maximum and minimum temperature (°C) in Dinokeng Game Reserve, 2000-2012. (Source: World Weather Online 2012).
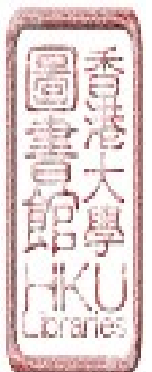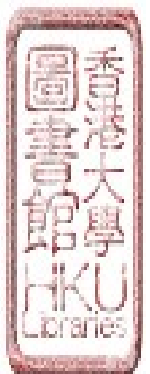
Vegetation types

DGR is situated within the savanna biome, consisting primarily of mixed Bushveld, Kalahari thornveld and sourish mixed Bushveld (Mucina and Rutherford 2006). Fifteen vegetation types were identified in the reserve from a vegetation conducted in 2009 (Contour Project Managers 2009), each type representing a distinguished plant community with varied vegetation structure (Fig. 2.4):

1. Open *Combretum apiculatum* veld on rhyolite. Open grassland with scattered trees and shrubs on shallow soils. Common grass species includes *Schizachyrium sanguineum*, *Loudetia simplex*, *Themeda triandra*, *Trachypogon spicatus* and *Tristachya leucothrix*, with low grazing capacity.

2. Dense *Combretum apiculatum*/*Combretum zeyheri* bushveld on rhyolite. Dominant grass species includes Schizachyrium sanguineum, *Loudetia simplex* and *Themeda triandra*. *Brachiaria serrata* and *Digitaria eriantha* are also common, resulting in a fair grazing capacity.

3. Open *Mundulea sericea*/*Combretum molle* shrubveld on rocky rhyolite ridges. Open shrubveld vegetation on rolling hills and ridges with rocky outcrops. Grass species are sourish mixed dominated by *Loudetia simplex* and *Themeda triandra* with low grazing capacity.

4. Rhyolitic floodplains and riparian vegetation complex comprised of a mix of open grassland, sparsely wooded grassland and woody riparian vegetation. Grass layer is dense with the most prominent grasses being *Aristida congesta*, *Heteropogon contortus* and *Cynodon dactylon*. Grazing capacity is fair.

5. Dense *Combretum apiculatum* bushveld on granite. Dense broad-leaved bushveld on shallow granite. *Eragrostis rigidior*, *Eragrostis lehmanniana* and *Enneapogon cenchroides* dominate the grass layer and provide high grazing value.

6. *Terminalia sericea*/*Burkea Africana* bushveld on granite. Dense woody vegetation. Grass layer is well developed and dense but with low grazing capacity comprising mainly *Schizachyrium sanguineum*, *Pogonarthria squarrosa*, *Setaria sphacelata*, *Loudetia simplex* and *Hyperthelia dissolute*.

7. *Peltophorum africanum*/*Terminalia sericea* bushveld on granite and sandstone. Dense and tall tree veld on very deep sandy soils. Common grass species include *Digitaria eriantha*, *Panicum maximum* and *Setaria sphacelata* with high grazing capacity.
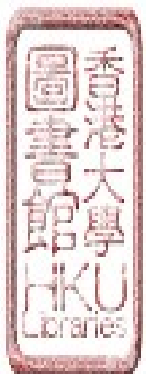
8.	Grassy floodplains with scattered *Terminalia sericea* veld on granite. Open grassland floodplains with low cover of trees and shrubs on deep sandy soils. Grass species are diverse and include *Hyperthelia dissoluta*, *Eragrostis rigidior*, *Cynodon dactylon* and *Urochloa mosambicense* with fair grazing capacity.

9.	Floodplains and riparian vegetation complex on granite and Karoo Sediments. Dense and tall woody vegetation on deep sandy soils. Common grass species include *Panicum maximum*, *Cynodon dactylon* and *Setaria megaphylla* of high grazing value, but grass layer is poorly developed under the dense tree layer.

10.	*Tarchonanthus camphoratus*/*Boscia albitrunca* bushveld on Karoo Sediments. Fairly open tree layer but dense shrub layer on deep clay soils. Dominant grass species include *Themeda triandra*, *Cymbopogon* excavatus, *Eragrostis rigidior*, *Panicum maximum* and *Urochloa mosambicense*, forming a grass layer with high grazing capacity.

11.	Open *Vachellia tortilis* floodplains on shales. Open bushveld with scattered trees and shrubs on clay soils. Grasses are of high grazing capacity and dominated by *Heteropogon contortus*, *Urochloa mosambicense* and *Panicum maximum*.

12.	Dense *Vachellia tortilis*/*Combretum apiculatum* bushveld on Karoo Sediment elevations. Dense thornveld on sandy soils. Grass layer is of high grazing capacity with prominent grass species including *Eragrostis rigidior*, *Urochloa mosambicense* and *Themeda triandra*.

13.	*Vachellia tortilis*/*Senegalia mellifera*/*Terminalia sericea* complex on Karoo Sediments. A mosaic of thornveld and *Terminalia sericea* on deep sandy or clay soils. Common grass species include *Hyperthelia dissoluta*, *Sporobolus pyramidalis*, *Eragrostis rigidior*, *Themeda triandra* and *Urochloa mosambicense*, providing high grazing capacity.

14.	Mixed Bontveld with bush clumps on Karoo Sediments. A mosaic of dense trees and shrubs clumps. *Themeda triandra*, *Eragrostis rigidior* and *Urochloa mosambicense* form the grass layer with high grazing value.

15.	*Vachellia robusta*/*Euclea undulata* brak thornveld on shales. Short, dense shrubveld on brackish soils. Grass layer is open and has high grazing capacity. *Aristida congesta*, *Enneapogon scoparius*, *Sporobolus nitens*, *Eragrostis rigidior*, *Themeda triandra* and *Urochloa mosambicense* are the dominate grass species.

Dam

– – – River

Building

1. Open *Combretum apiculatum* veld
2. Dense *Combretum apiculatum* & *Combretum zeyheri* bushveld
3. Open *Mundulea sericea* & *Combretum molle* veld
4. Rhyolitic floodplains and riparian vegetation complex
5. Dense *Combretum apiculatum* bushveld
6. *Terminalia sericea* & *Burkea africana* bushveld
7. *Peltophorum africanum* & *Terminalia sericea* bushveld
8. Grassy floodplains with scattered *Terminalia sericea*
9. Floodplain and riparian vegetation complex
10. *Tarchonanthus camphorates* & *Boschia albitrunca* veld
11. Open *Acacia tortilis* floodplains
12. Dense *Acacia tortilis* & *Combretum apiculatum* bushveld
13. *Acacia tortilis* & *Acacia mellifera* & *Terminalia sericea* complex
14. Mixed Bontveld with Bushclumps
15. *Acacia robusta* & *Euclea undulata* Brackish Thornveld

Fig. 2.4 The distribution of vegetation types in Dinokeng Game Reserve. (Data source: Contour Project Managers 2009)

Mammal species

DGR supports more than 20 species of large herbivores (see Table 2.1 for complete species list); the most common species are blue wildebeest (*Connochaetes taurinus*) and impala (*Aepyceros melampus*) (over 1000 individuals each), and Burchell's zebra (*Equus quagga burchelli*) and blesbock (*Damaliscus pygargus phillipsi*) (over 600 individuals each) (unpublished DGR aerial census data 2012). Other common lion prey species include warthog (*Phacochoerus africanus*) and South African porcupine (*Hystrix africaeaustralis*). White rhinoceros (*Ceratotherium simum*), African elephants (*Loxodonta africana*) and African buffalo (*Syncerus caffer*) were reintroduced into the reserve in October 2008, October 2011 and August 2012 respectively.

Prior to the reintroduction of lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*), leopard (*Panthera pardus*) and brown hyaena (*Hyaena brunnea*) were the only large carnivores confirmed to exist but sightings of leopards are rare and information on the possible number present is unavailable (Contour Project Managers 2009). One male and one female cheetah were reintroduced into DGR in October 2012.

Reintroduction of lions (*Panthera leo*)

Eleven lions, four males and seven females of different ages and genetic relatedness, were introduced by DGRMA in three different release events between 2011 and 2013 (individual and group ID referred to Table 2.2 thereafter). Lions were captured and translocated from Welgevonden Game Reserve (Limpopo Province), Pilanesberg Game Reserve (North West Province), Madikwe Game Reserve (North West Province) and Tembe Elephant Park (KwaZulu-Natal Province). All of the lions were fitted with satellite collars (African Wildlife Tracking, Pretoria, South Africa) by DGRMA in compliance with the ethical standard as advised by recognised authorities including the Department of Environmental Affairs and Tourism (DEAT) and the Gauteng Department Agriculture, Conservation and Environment (GDACE). Individuals released together were kept in a 45 x 85 m boma (Fig. 2.1) for one month prior to the release. Keeping the animals in captivity before release is a procedure widely recommended in carnivore reintroduction to facilitate recovery from the shock of capture and
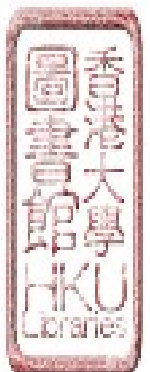
translocation, and to allow for acclimation to a new environment and enhance bonding formation between unrelated individuals (Miller et al. 2013). Lions in the first and second reintroduction were released directly from the boma, while animals in the third reintroduction were first translocated from the boma to the southeast of the reserve and released (Fig. 2.1). The boma was situated next to the biggest dam in the reserve surrounded by reed beds (*Phragmites australis*) and floodplain and riparian vegetation complex (vegetation type 9) that is also the major vegetation type at the release site of the third reintroduction located closely to the river. Females in the first and second releases were injected with reversible contraceptives; a management decision by DGRMA for controlling population growth during early stage of reserve development. The effects of the contraceptives are reversed once the hormones within the implant are depleted, which takes approximately two years. M2a (one of the males from the second release) was translocated to the south-eastern part of the reserve in October 2012, after a territorial conflict between M1 and M2 during February 2012 that had resulted in the death of M2b (Table 2.3).
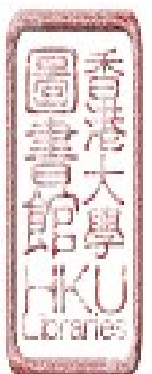
Table 2.1 Total area counts of antelope species in Dinokeng Game Reserve by helicopter-based aerial census in August 2012. (Data source: Dinokeng Management Association 2012).

Species	Count
Browser	
Greater kudu (*Tragelaphus strepsiceros*)	454
South African giraffe (*Giraffa camelopardalis giraffe*)	104
Nyala (*Tragelaphus angasii*)	1
Bushbuck (*Tragelaphus sylvaticus*)	0
Common duiker (*Sylvicapra grimmia*)	10
Grazer	
Blue wildebeest (*Connochaetes taurinus*)	1635
Burchell's Zebra (*Equus quagga burchellii*)	818
Waterbuck (*Kobus ellipsiprymnus*)	122
African buffalo (*Syncerus caffer*)	9
White rhinoceros (*Ceratotherium simum*)	17
Hippopotamus (*Hippopotamus amphibius*)	7
Blesbuck (*Damaliscus pygargus phillipsi*)	686
Red Hartebeest (*Alcelaphus caama*)	161
Tsessebe (*Damaliscus lunatus lunatus*)	25
Gemsbuck (*Oryx gazella*)	6
Common reedbuck (*Redunca arundinum*)	15
Mountain reedbuck (*Redunca fulvorufula*)	0
Warthog (*Phacochoerus africanus*)	327
Bushpig (*Potamochoerus larvatus*)	12
Mixed feeder	
Eland (*Taurotragus oryx*)	152
Impala (*Aepyceros melampus*)	1239
Steinbuck (*Raphicerus campestris*)	0
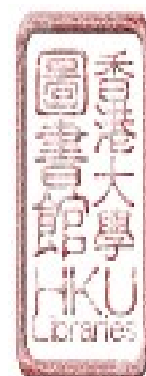
Table 2.2 Details of the lions reintroduced into Dinokeng Game Reserve during three reintroduction events between 2011 and 2013. * indicates individual group members with GPS locations used to representing the group.

Date of release	Group structure after release (Group id: lion id)	Sex	Age at release (years)	Genetic relationship	Capture site	Wet season 2011-12	Dry season 2012	Wet season 2012-13	Dry season 2013	Wet season 2013-14	Dry season 2014
19/10/2011	M1: M1a*, M1b	Males	2.5	Brothers	Welgevonden Game Reserve	X	X	X		X	X
	F1: F1a*, F2b	Females	2	Sisters (unrelated to M1)		X	X	X	X	X	X
14/11/2011	M2: M2a*, M2b	Males	2	Brothers	Pilanesberg Game Reserve	X	X	X		X	X
	F2: F2a*, F2b	Females	2	Sisters	Madikwe Game Reserve	X					
02/11/2013	F3: F3a*, F3b	Females	5	Sisters	Tembe Elephant Park					X	X
	F3c: F3c*		2	Offspring of F3a						X	X
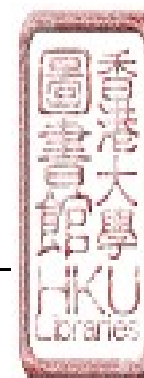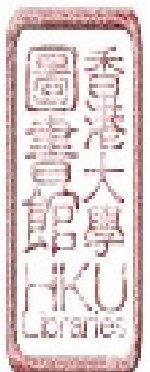
Table 2.3 Events of management practices and sighting information on the interactions between lion groups in Dinokeng Game Reserve.

Date	Event
24/2/2012	M1 and M2 were involved in a territorial conflict, resulting in M2b being killed by M1.
27/2/2012	M2a was translocated from the northwest to the southwest, but it returned to the northwest within 24 hours.
23/4/2012	F2b was killed by M1.
5/5/2012	F2a was killed by M1.
10/8/2012	M2a was attacked by M1.
30/8/2012	M2a was translocated from the northwest to the southeast and kept in a boma (Fig. 2.1)
4/10/2012	M2a was released from the boma in the southeast
21/3/2013	M1a was re-collared and the collar of M1b was taken off. M1b went missing after this re-collaring event.
13/9/2013	Mating between M1a and F1a was observed for the first time.
26/11/2013	Positive interactions (head rubbing and licking) between M2a and F3 were observed.

Chapter 3

Early post-release movement of reintroduced lions
(*Panthera leo*)

Introduction

Dispersal is a key process in animal movement ecology and can happen more than once at any stage in an animal's lifespan (Santini et al. 2013). It can be defined as an animal moving away from its natal or current home range to settle in another area (Bowler and Benton 2005). Dispersal behaviour allows animals to optimize their fitness and breeding opportunities with a trade-off between resource exploration and exploitation (Bonte et al. 2012). Before deciding to settle in a new area, animals typically perform exploratory movements that allow them to learn and compare habitat quality and distribution of competitors and predators (Delgado et al. 2009, 2010; Debeffe et al. 2013). However, exploration cost could be high because of the unfamiliarity with the environment, which leads to fitness reduction and high mortality risk due to misadventures (Bonte et al. 2012). Animals therefore need to balance the time and energy spent between exploration and exploitation to maximise benefits gained in dispersal.

While natural dispersal occurs in wild populations, early post-release movement of reintroduced animals can be viewed as 'forced-dispersal' (Stamps and Swaisgood 2007). Reintroduction has been increasingly used to re-establish species in their former ranges in which they have been extirpated (Seddon et al. 2007; Armstrong and Seddon 2008). During a reintroduction, an animal bred in captivity or captured from a wild population is translocated to a new area (IUCN 1998). The process resembles natural dispersal as the animals have to balance the trade-off between exploration and exploitation in both situations, but 'forced-dispersal' implies bigger challenges and risks for reintroduced animals because they are forced to learn as efficiently as possible, the landscape, environmental conditions and resource distributions that are completely new to them (Berger-Tal and Saltz 2014). Due to the lack of knowledge in landscape features, predators and

competitors, mortality risk during exploration is even higher than in natural dispersals (Spinola et al. 2008), particularly for territorial species like lions (*Panthera leo*) which defend against intruders aggressively. In addition, homing behaviour is a common occurrence in reintroductions, when animals tend to travel towards the direction of their capture sites upon release (Rogers 1988). Such behaviour has been interpreted as a rejection to the 'forced-dispersal' and typically results in low site fidelity, i.e. animals are unwilling to settle in the new area (Miller et al. 1999). Understanding movement patterns in the early post-release period is thus critical for the survival and re-establishment of reintroduced animals (Preatoni et al. 2005; Berger-Tal and Saltz 2014).

Large carnivores are frequent subjects of reintroductions due to their predisposed risk of extirpation because of high ecological demands, sensitivity to habitat loss and high potential for human conflicts (Woodroffe 2000; Cardillo et al. 2004; Hayward and Somers 2009). In South Africa, there has been an increase in establishment of small reserves and demand for reintroducing flagship carnivores including lions, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*) and spotted hyaenas (*Crocuta crocuta*) in recent years (Hayward et al. 2007a, b). Most studies on reintroduced carnivores have focused mainly on population control, inbreeding, diseases and human-wildlife conflicts (Ferreira and Hofmeyr 2013; Miller and Funston 2014), while information on post-release movement behaviour is limited (Hayward et al. 2007a; Hunter et al. 2007). Post-release movement pattern allows us to understand the exploration-exploitation trade-off of reintroduced animals during establishment stage and individual variation in movement strategies in adapting to a new environment, which can be used as a tool to assess establishment success (Berger-tal and Saltz 2014). On the other hand, individual movement decisions do not only affect individual fitness but also the behaviour and the interactions of conspecifics and sympatric species (Fortin et al. 2005), which could ultimately have important implications on community structure and population dynamics (Hawkes 2009; Morales et al. 2010). Studying individual animal movement, particularly of large mammalian species that are able to undertake long-distance movement and have large home ranges, is therefore crucial in understanding their spatial dynamics and broader population processes (Tilman and Kareiva 1997).

In this chapter, I investigated space use and movement patterns of reintroduced lions subjected to 'forced dispersal' during their early post-release period and to assess the potential of using movement patterns to identify successful reintroductions. Directions of movements, daily movement rates and distances from release sites were compared over time, as well as animal locations in relation to human settlements. I expected movement rates to be highest upon release, decrease over the study period and eventually stabilize, together with an initial increase in distances from the release site during exploration and stabilisation or reduction when the animals had settled. An increase in distances from buildings over time was expected in avoidance to human disturbances, a factor found to influence carnivore behaviours in various studies (Kerley et al. 2002; Ngoprasert et al. 2007). I also compared movements at different times of the day to test if 'forced dispersal' increases diurnal activities of lions due to the need to explore the environment and avoid previously released conspecifics. Lastly, I constructed utilisation distributions, a statistical representation of home ranges, and expected a positive relationship between movement rates and cumulative home range sizes for as long as the lions still display exploratory behaviours.

Material and methods

Data collection

GPS locations of all lions were recorded regularly by the satellite collars once every four hours for the lions in the first two releases and every five hours for the lions in the third release (recording frequency was controlled by DGRMA). The locations were sent via satellite to an online centralised database and downloaded from there. The location data collected for analyses in this chapter span the first season of release of the lions: October-April 2011-12 for lions from the first and second release and October-April 2013-14 for lions from the third release.

I documented changes in group structure and interactions between groups that could have affected the movement and spatial behaviour of the lions by observing the animals in the field whenever possible and gathering additional sighting information from rangers, landowners and the DGRMA (Table 2.3).
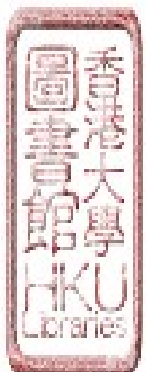
Data analyses

Analyses were performed using the lion GPS location data collected as explained in chapter 2. I defined early post-release period as the first wet season (Oct-Apr; first and second release: 2011-12; third release: 2013-14) after release to control for potential seasonal effects on lion movements due to seasonal distribution of prey (Hunter 1998; Hayward et al. 2009). Movement was analysed as the movements of groups, based on association of animals after release (see Table 2.2 in chapter 2). GPS locations of the group member that had the most regular fixes were used and movements were compared between each 30-day period. Six time periods were included for all groups except lions in the second release that had five time periods only, as they were released in mid-November 2011.

Distance and bearing between consecutive locations, bearing between release and capture site of each group and distance between each location and the release site and nearest buildings were calculated using Hawth's Analysis Tools 3.27 (Beyer 2004) and ArcGIS 10.2 (ESRI, Redlands, Calif.). Distances between locations were separated into six different time slots and defined as: 04-08hr (sunrise), 08-12hr (morning), 12-16hr (afternoon), 16-20hr (sunset), 20-00hr (night) and 00-04hr (midnight), for the lions in first and second release. Because of the 5-hour recording interval, locations for lions in the third release were taken at different time in each day and I defined 04-09hr as sunrise, 08-13hr as morning, 12-17hr as afternoon, 15-20hr as sunset, 19-00hr as night and 23-04hr as midnight. Daily distances travelled were calculated by summing up the distances between locations in each day. Distances to release sites and buildings were averaged across each day, using only the first location when animals remained stationary for more than one location (when distance to the next location was <100 m, a distance used to identify GPS clusters of potential feeding sites of carnivores; Tambling et al. 2010; Wilmers et al. 2013) to prevent pseudo-replication.

Rayleigh test of uniformity (one-sample test for mean angles, Zar 1984) was performed to test the bearings of movement against random distribution separately for each 30-day period using R 3.1.1 (R Core Team 2015) and the R package 'CircStats' (Lund and Agostinelli 2014). Homing behaviour was assumed to be

present if the direction from release to capture site fell within the confidence interval of significant direction of travel.

Daily distances travelled were square root transformed and compared between the 30-day periods for each lion group using one-way ANOVA with post-hoc Tukey's HSD test. Due to violation of model assumptions of normality and equal variances even after data transformation, comparison of distances travelled at different times of day and distances between locations and release site and nearest building were done using Kruskal-Wallis non-parametric ANOVA with post-hoc Bonferroni–Dunn test. Apart from the 30-day periods, distances to buildings were also compared between weekdays (Monday to Thursday) and weekends (Friday to Sunday; Fridays were included into weekends because of local customary reasons) using Mann-Whitney U test, because human disturbances might be higher on weekends due to higher number of visitors. Kruskal-Wallis non-parametric ANOVA compares data by ranks therefore results were reported in box plots showing medians, minimum and maximum values and first and third quartile (Kruskal and Wallis 1952). All statistical tests were performed in R 3.1.1 (R Core Team 2015).

The k-LoCoH (local convex hull; Getz and Wilmers 2004) method was used to construct 50% core and 95% full home range utilisation distributions using R package 'adehabitat' in R2.13.0 (Calenge 2006). Values for k were selected as $\sqrt{n}/2$ where n equals number of locations (Getz and Wilmers 2004). To investigate the process of expansion and stabilization of home ranges over time, I constructed cumulative utilisation distributions by adding the locations of the previous time period, i.e. number of locations was cumulated over time.

Results

Post-release group structure and survival

Lions kept in boma and released together showed varied post-release association (see Table 2.2 in Chapter 2). In the first and second release, the animals split into pairs of brothers and sisters and these pairs remained together throughout the early post-release period. In the third release, the youngest female roamed alone most of the time but occasionally joined the two adult females that remained
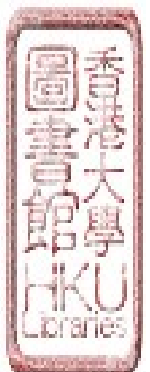
associated. Movement analyses were therefore done separately for these 6 groups (M1, F1, M2, F2, F3 and F3c).

The F2 and M2b (one of the males from M2) were killed in their 7th and 4th month of release, respectively by the M1 (see Table 2.3 in Chapter 2). Consequently, from the 5th time period, movement of M2 represented only the one survived individual.

Direction of movements and homing behaviour

None of the lions were found to have movement directions different from random (Rayleigh test of uniformity, $p \geq 0.15$). Consequently, no lions were moving towards a specific direction and no homing behaviour was detected.

Daily movement rate

Average daily distance travelled by lions ranged from 2.42 ± 0.44 km to 6.64 ± 0.57 km (mean $\pm$ SE, Fig. 3.1). Movements through time varied greatly between groups, with an increase in distance travelled observed in M1 in 4th time period (one-way ANOVA, $F_{5,174}=5.49$, $p<0.001$; Tukey's HSD test, $p<0.05$) and F1 in 2nd time period (one-way ANOVA, $F_{5,174}=4.01$, $p<0.01$; Tukey's HSD test, $p<0.05$). On the contrary, F2 and F3c significantly reduced their distance travelled in 3rd (one-way ANOVA, $F_{4,145}=2.68$, $p<0.05$; Tukey's HSD test, $p<0.05$) and 4th time period respectively (one-way ANOVA, $F_{5,173}=2.94$, $p<0.05$; Tukey's HSD test, $p<0.05$). Movement of these four lion groups stabilized after the initial increases and decreases. A significant increase in distance travelled was found in M2a in 5th time period after M2b was killed (one-way ANOVA, $F_{4,144}=11.92$, $p<0.001$; Tukey's HSD test, $p<0.05$) while F3 had similar travel distances throughout the early post-release period.

Movement rates at different times of the day

Lions moved different distances during different times of the day (Fig. 3.2) and in general moved more at sunrise, night and midnight. The least movements occurred in the morning and afternoon. The animals in the first and second release, had travelled significantly less in the morning and afternoon than in other times of the day (Kruskal-Wallis test, $\chi^2>46.73$, *df*=5, $p<0.001$; Bonferroni–Dunn test,
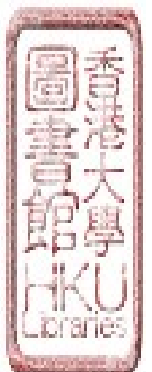
p<0.05) during which individual variation was low throughout the entire early post-release period (Fig.3.2).

In comparison, lions in the last release travelled significantly less in mornings and afternoons only in the 1st time period (Kruskal-Wallis test, $\chi^2 > 23.28$, $df=5$, p<0.001; Bonferroni-Dunn test, p<0.05). Their movement remained similar through the day from 2nd time period onwards.
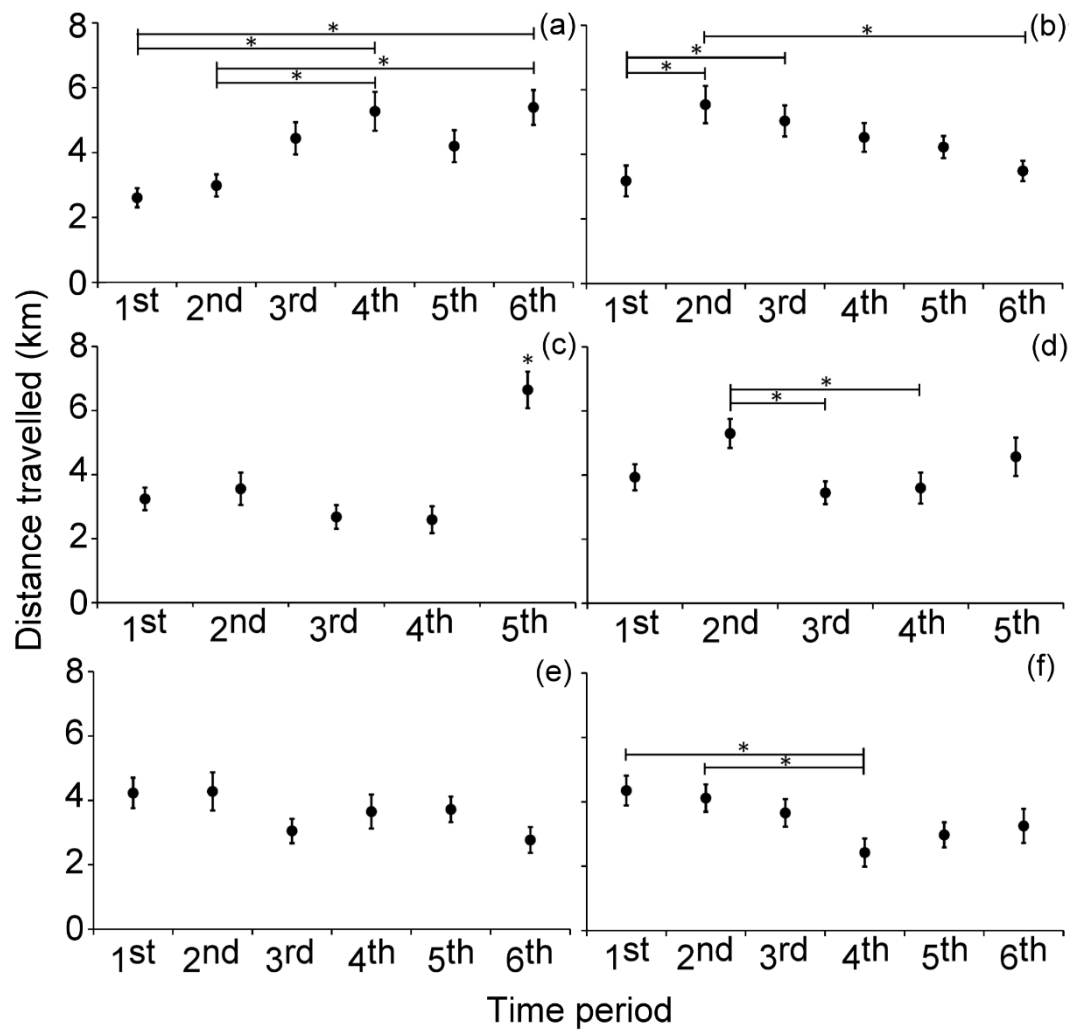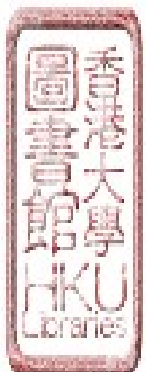
Fig. 3.1 Average daily distance travelled by lions (mean ± SE) during early post-release period in 2011-12 and 2013-14 in the Dinokeng Game Reserve. * indicates significant difference. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.
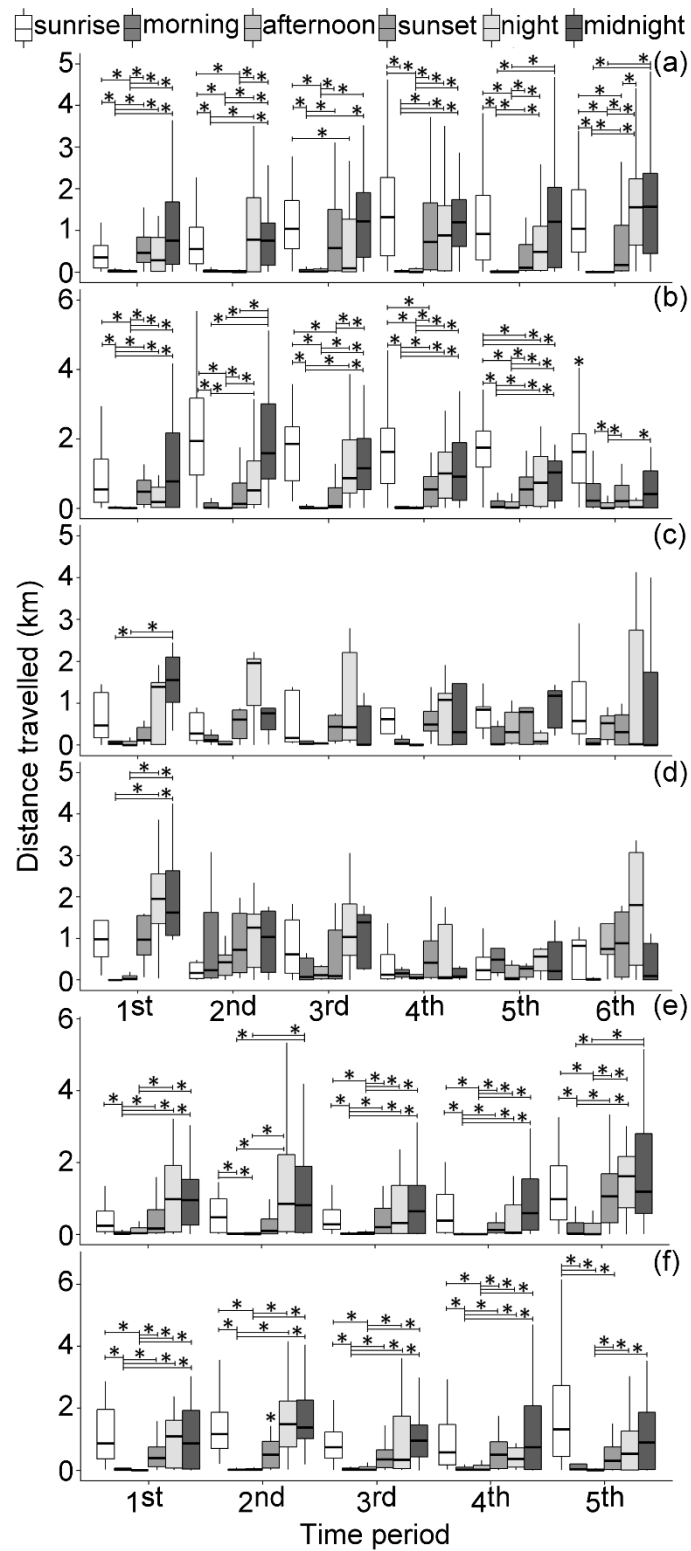
Fig. 3.2 Average distance travelled by lions in different time of a day during early post-release period in 2011-12 and 2013-14 in the Dinokeng Game Reserve. Box plot shows median, minimum and maximum values, and first and third quartile. * indicates significant difference. (a) M1, (b) F1, (c) F3, (d) F3c, (e) M2, (f) F2.
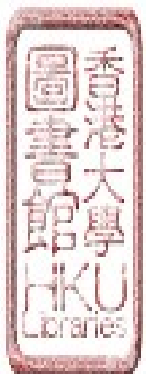
Distance from release site

Variation among lions in dispersal behaviour upon releases was large. Medians of distances from release site ranged from 1.50 to 7.18 km, first quartile from 0.81-6.68 km and third quartile from 1.68-8.18 km (Fig. 3.3), and in all cases but one (F2) these distances differed between time periods (Kruskal-Wallis test, M1 and F1 and F3: $\chi^2 > 40.77$, $df=5$, p<0.001; M2: $\chi^2=90.06$, $df=4$, p<0.001) but what varied was the pattern of these changes. Two lion groups (M2, F3b) dispersed, resulting in an increase in distance from the sites through time, while three groups (M1, F1, F3) travelled back to the area of release sites after initial dispersal, which led to a decrease in distances after an initial increase.

Distance to buildings

Distances to nearest buildings significantly differed between weekdays and weekends only in certain time periods (M1: 1st time period, F1 and M2: 3rd time period, F2: 1st and 3rd time period, F3: 5th time period, F3c: 6th time period; Mann-Whitney U test, U>35, p<0.05).

The effects of the presence of buildings on lion movements changed through time. The distance from buildings kept by males increased significantly over time in both weekdays and weekends (Kruskal-Wallis test, M1: $\chi^2 > 44.32$, $df=5$, p<0.001; M2: $\chi^2 > 29.25$, $df=4$, p<0.001; Bonferroni-Dunn Test, p<0.05) (Fig. 3.4). Among females, some retained a similar distance to buildings during weekdays throughout the entire period (Kruskal-Wallis test, F2: $\chi^2=6.68$, $df=4$, p=0.15; F3 and F3c: $\chi^2 < 8.11$, $df=5$, p>0.15) while others showed a more varied pattern, with their distance to buildings decreased from the 1st to 3rd time period but increased from 4th time period onwards. (Kruskal-Wallis test, F1: $\chi^2=39.27$, $df=5$, p<0.001). On weekends, with the exception of a significant decrease in distance from the 5th to 6th time period in F3 and F3c (Kruskal-Wallis test, $\chi^2 > 14.38$, $df=5$, p≤0.01; Bonferroni-Dunn Test, p<0.05), no obvious difference was seen from one time period to the next. However all females displayed a pattern of a gradual decrease in distances over time, even though the differences were not statistically significant (Fig. 3.4).
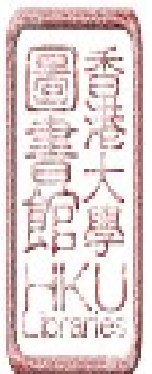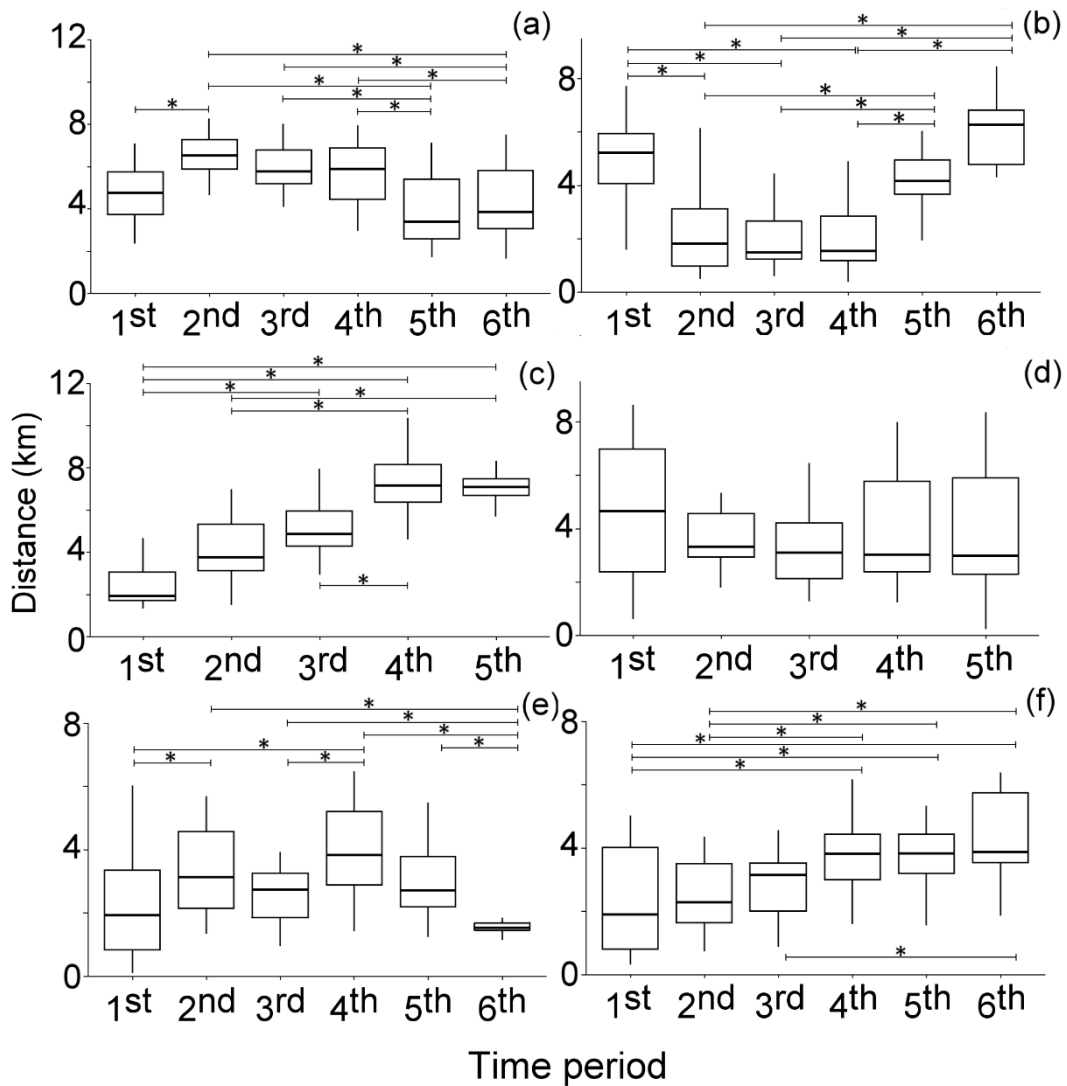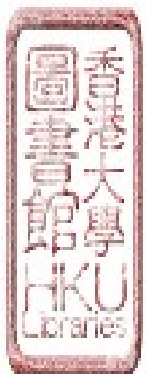
Fig. 3.3 Average daily distance of lions from release sites during early post-release period in 2011-12 and 2013-14 in the Dinokeng Game Reserve. Box plot shows median, minimum and maximum values, and first and third quartile. * indicates significant difference. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.
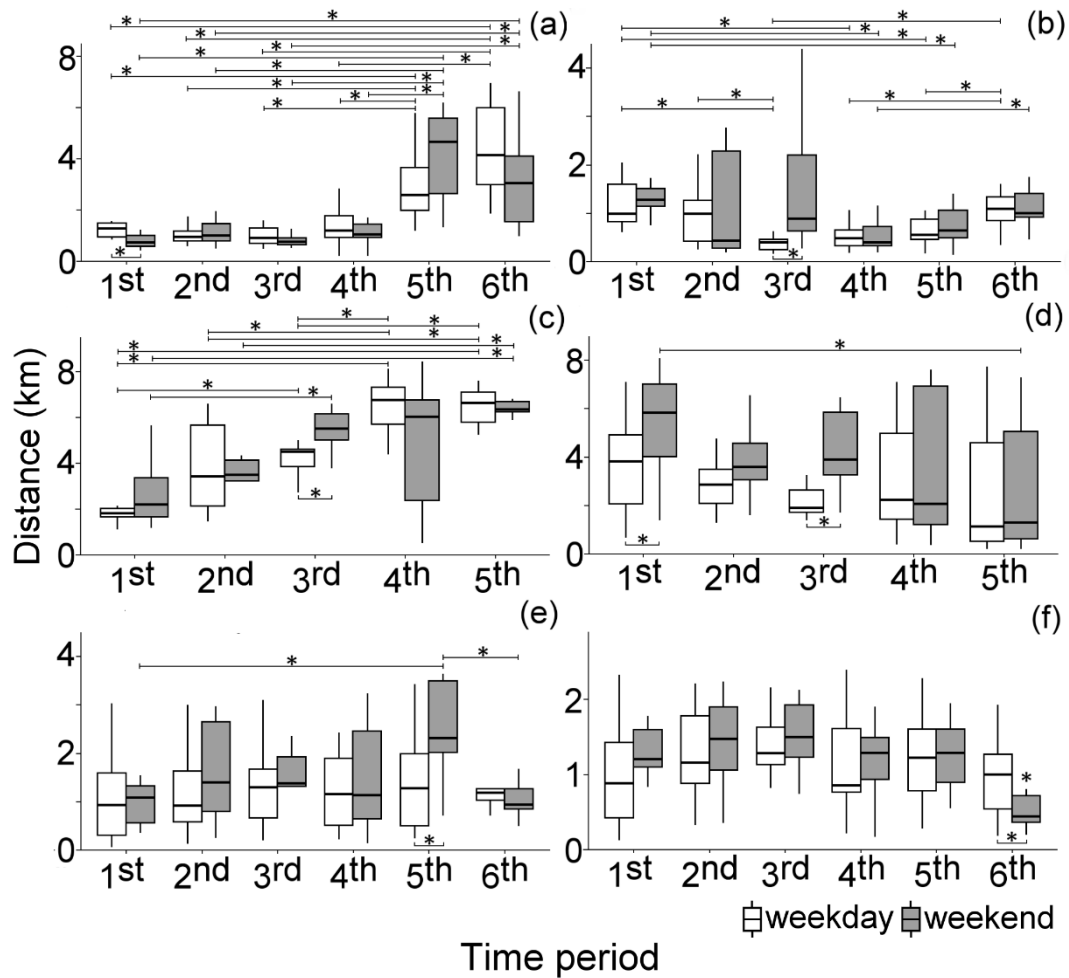
Fig. 3.4 Average daily distance of lions from nearest building during early post-release period in 2011-12 and 2013-14 in the Dinokeng Game Reserve. Box plot shows median, minimum and maximum values, and first and third quartile. * indicates significant difference. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.

Utilisation distribution and home range establishment

Cumulative area of 50% core UD and 95% full UD of all lions continued to increase through the early post-release period, indicating an expansion in home range (Fig. 3.5). However the rates of increase from the first to last time period differed between groups, with F1 having the largest increase of both 50% core (from 0.06 to 2.71 km^2) and 95% full UD (from 2.45 to 26.75 km^2); while M2 and M1 had the smallest increase of 50% core (from 0.03 to 0.54 km^2) and 95% full UD (1.82 to 13.38 km^2), respectively, in the entire early post-release period (Fig. 3.5).

Although no sign of stabilization in cumulative area was detected, home range expansion appeared to slow down from 5th time period (Fig. 3.5).
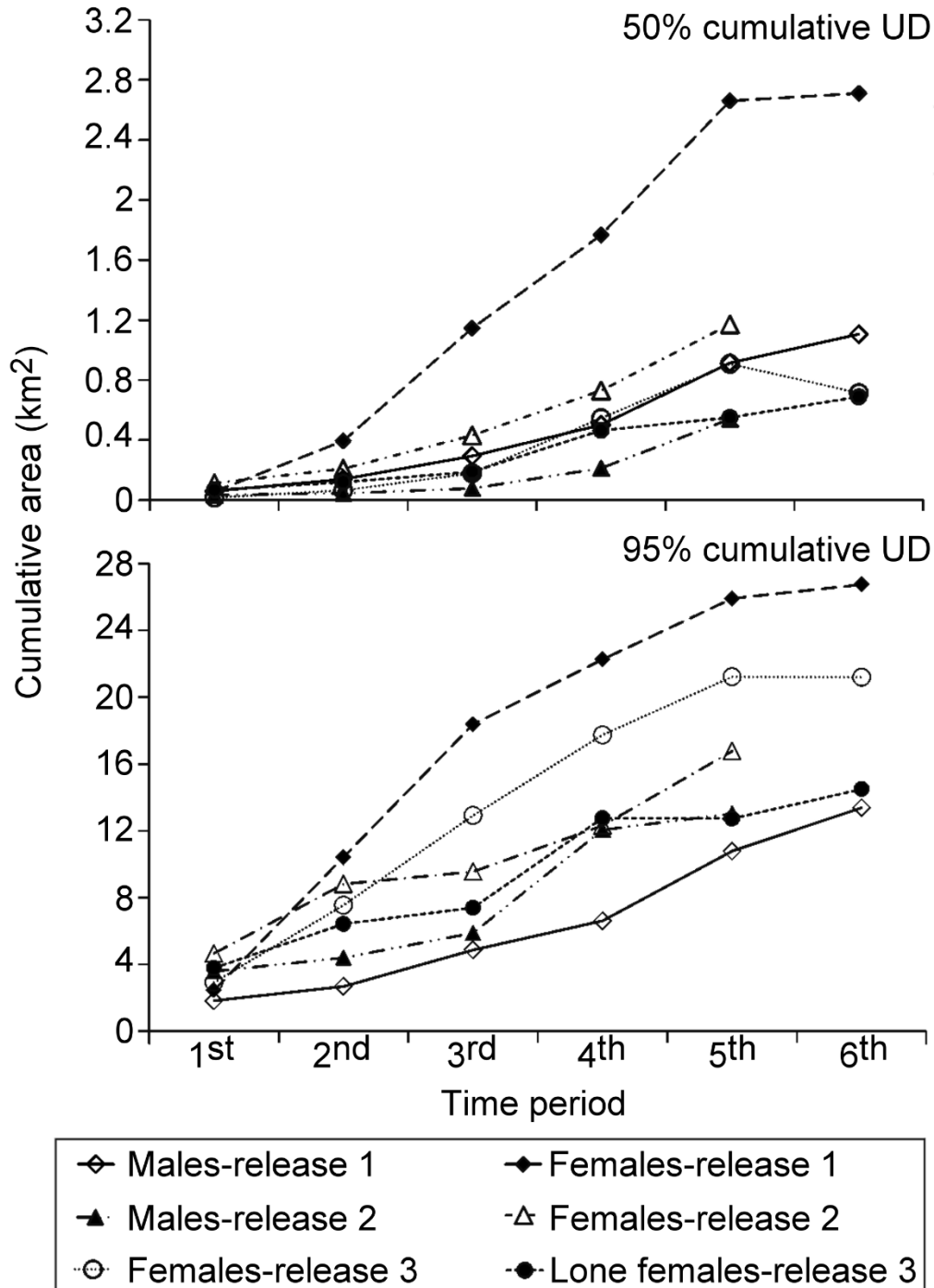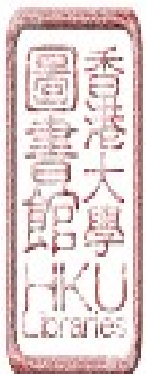
Fig. 3.5 Cumulative area of 50% core and 95% full utilisation distribution of lions during early post-release period in 2011-12 and 2013-14 in the Dinokeng Game Reserve.
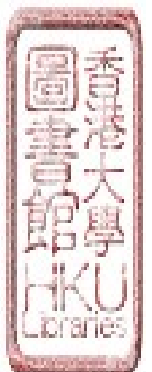
Discussion

As the results show, individual movement patterns can vary greatly between sexes and individual groups of lions. I found no evidence of homing behaviour, indicating that the animals did not reject the 'forced-dispersal' by attempting to break away from the reserve. However, the one dominant pattern in early post-release movement was that of an overwhelming variability. Even though all individuals displayed exploratory behaviour, they performed exploratory movements differently such that certain groups increased while other groups decreased their rates of movement upon release. However, changes in movement rates all occurred in either the 2nd or 4th time period and movements remained similar thereafter. Previous studies in Phinda (Hunter 1998) and Welgevonden Game Reserve (Kilian 2003) both found a general trend of increase in daily movements of reintroduced lions, but these studies were conducted only for the first three months of release. Results in DGR suggest that reintroduced lions might take up to 120 days in exploration before making decisions on the most cost effective movement pattern, which then lead to stabilization of movement rates as I expected.

Increase in rates of movement was found only in lions in the first release. In later releases, the animals had in general lower movement rates than those in the first release, and these rates either decreased or remained relatively unchanged. These differences are likely due to the fact that lions released first were at an advantage of being able to explore a competitor-free environment. As territorial carnivores, in natural populations lions are less likely to disperse from or remain close to their natal prides during dispersal when the numbers of unrelated lions in the surrounding areas is high, as exploration in a landscape with high density of competitors could lead to territorial conflicts between groups and result in fatality (Funston et al. 2003). Without other lions to compete with, individuals released first had an opportunity to explore and establish territories with no intra-specific constraints. Low intra-specific competition also explains the general increase in movement found in Phinda Game Reserve (Hunter 1998) where lions were released in different areas and in Welgevonden Game Reserve (Kilian 2003) where there was only one release. In contrast, lions released later avoided the already released lions by having lower rates of movements and establishing home ranges that were non-overlapped with the animals released earlier (see Chapter 4).

After the death of one male in M2, the remaining one male increased its movement during sunrise and sunset. This coincides with the behaviour observed previously in lions and other carnivores where nomadic individuals became more active diurnally to minimise interactions with dominant competitors (Hayward and Hayward 2006; Hayward and Slowtow 2009). The increase in movement might also result from the animal relocating itself more frequently to minimise the chance of being detected, as highlighted by a shift in home range of the surviving male away from its original range taken by M1 after the death of the coalition member (see Chapter 4). Avoidance of conspecifics could also explain why lions released in the last reintroduction had similar movement rates across different time of a day, compared to lions in the first release that had the lowest rate of movement during day time throughout the study period.

Dispersal from the release sites varied between lion groups and did not coincide with changes in movement rates. This differs from the increase in distance of released lions from boma reported by Hunter (1998) and Kilian (2003) but is similar to the diverse dispersal patterns found in other translocated or reintroduced carnivores (Linnell et al. 1997; Preatoni et al. 2005). Various factors including intraspecific interactions, internal states of individuals, habitats quality and experiences in natal habitats are suggested to influence dispersal and settlement decisions of animals (Benard and McCauley 2008; Stamps et al. 2009; Santini et al. 2013). The boma in DGR is situated next to the biggest dam in the reserve (Fig. 2.1) which attracts different herbivores, with vegetation in the area consisting mainly of dense reed beds and riparian vegetation that are ideal for lions to ambush their prey and rest (Spong 2002). During the first release, the behaviour of lions returning to and settling in the area around the boma after initial dispersals was likely because of a preference for the reed beds after initial exploration of the environs. In fact, the core home ranges with high frequencies of revisit of the animals were centred at the dam throughout their first three years of release (see Chapter 4) and they were observed to hunt and rest continuously and hide their cubs in the area. In contrast, males in the second release dispersed continuously while females in the same release settled in an area at least 3 km away from the boma after initial dispersal. The differences in dispersal upon release indicate that lions released later did not only move differently as mentioned before but also used the space differently in

order to avoid conflicts with the lions released first. The lions released last were translocated and released in open *Combretum molle* vegetation in the south east side of the reserve. They then dispersed and settled 3-4 km away from the site close to rivers with floodplains and riparian vegetation, two vegetation types preferred by the lions in the study site (see Chapter 5) that are known to favour lions hunting (Spong 2002; De Boer et al. 2010).

The presence of buildings affected males and females differently. Upon release, males continued to move away from buildings, while females, after initial increase, generally decreased distance to building over time. Results coincide with the behaviour of reintroduced elephants in DGR that selected areas away from buildings (De Hoog 2014) and other species in several studies elsewhere that avoided human activities (Ngoprasert et al. 2007; Vanthomme et al. 2013), suggesting that human settlement was perceived as a disturbance by lions and elephants reintroduced to the reserve. While initial responses of females were to move away from buildings, the decrease in distance over time likely indicates their habituation to the disturbance which was not observed in males. Differences of distance to buildings between weekdays and weekends were found in certain time periods. DGR was still newly established with visitors and tourists consisting mainly of local people who came to visit during weekends (S-W Yiu, personal observation). Thus, higher disturbances during weekends could have contributed to the larger distances of lions to buildings in weekends than in weekdays. Differences in the number of weekend visitors staying in different lodges and residences during different time could have led to continuous changes in the intensity of disturbances and explained why lions behaved differently between time periods.

Despite the highly varied movement patterns, cumulative home ranges of all lion groups continued to increase in size over time. Space use is mostly driven by resource availability that determines the size of animal home ranges (Herfindal et al. 2005; Hayward et al. 2009). Previous studies of home ranges of reintroduced carnivores focused primarily on seasonal ranges (Hunter 1998, Druce et al. 2004), not the process of establishment and expansion of home ranges after release. My investigation of cumulative home ranges suggests that reintroduced lions were continuously expanding their range of exploration, with different movement strategies used by different group. Although lions expanded both core and full home
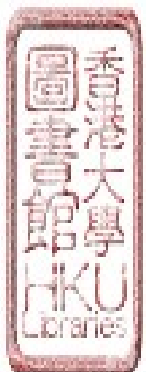
ranges, their core home range remained below 3 km^2 which indicate that they were able to acquire resources for survival within small areas, and the presence of fence did not impose a constraint on their movement. Hayward et al. (2009) suggested that fencing does not affect predator behaviour and home range sizes remained correlated with prey abundance in fenced reserves. DGR has high prey abundance (unpublished DGR aerial census data 2012; see Chapter 2 and Table 2.1), therefore the lions did not have to establish large home ranges to secure food. The decline in home range expansion upon the 5th time period indicates that lions begun reducing their exploration and starting to settle in the established home ranges.

To summarize, the reintroduced lions displayed highly complex and diverse post-release movements, where rates of movement do not necessarily correlate with spatial exploration. Optimal movement decisions of animals are to a certain extent influenced by individual ability to learn and navigate through a landscape of heterogeneous resource patches (Bélisle 2005; Roshier et al. 2008), which in DGR was shown by the varied movement patterns of different lions. As this chapter demonstrates, behavioural responses of lions to 'forced dispersal' of reintroduction, their subsequent ways in exploring and adapting to a new habitat and optimal movement decisions can differ greatly between individuals, depending on intra-specific interactions, habitat preferences, human disturbances, and individual experiences that vary in spatial and temporal scales. The absence of homing behaviour, stabilization in movement rates, habituation to human disturbances and decline in rates of home range expansion all together suggest release site fidelity and successful establishment of reintroduced lions. An absence of homing behaviour and a sign of stabilization in movement patterns could potentially be used as criteria for assessing early establishment success in future reintroductions. However, I show how movements can be disrupted by inter-group interactions as evidenced by the changes in movement of a male after the coalition member was killed. The behavioural differences between lions in different releases show that the presence of competitors greatly affects the exploratory movement of reintroduced animals, with intra-specific competition being the most important driver of movement decisions for those released later. Therefore, the order and release site of lion reintroductions should be planned to minimise intra-specific competition

and direct conflict between groups in early establishment stages which could otherwise lead to selection of sub-optimal resources and reduction in fitness.

Chapter 4
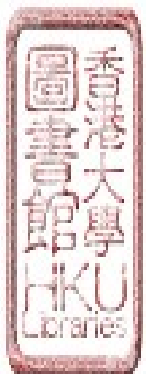
Second order habitat selection: home range establishment and utilisation of reintroduced lions (*Panthera leo*)

Introduction

Animal habitat selection is a central topic in spatial ecology studies and is fundamental to understanding animal behaviour in response to a heterogeneous environment. Habitats are selected by animals hierarchically from geographic range (first order selection) to home range (second order selection), within which habitat components (third order selection) and specific sites for feeding or breeding (forth order selection) are selected (Johnson 1980).

A home range, i.e. second order selection, is generally defined as the area where an animal acquires resources, mates, reproduces, and takes care of its offspring (Burt 1943). It can be quantified by a utilization distribution [UD] that describes the frequency distribution of the locations of an animal at the landscape level (Worton 1987); the 50% utilization distribution is often viewed as the core and most important area within the entire home range (Powell 2000). The ranging behaviour of animals is complex, depending not only on resource availability but also on landscape features, climate, population density, inter- and intra-specific interactions, social structure and status, life stages and history of the animals, and individual differences (Schradin et al. 2010; Bjornlie et al. 2014; Tuqa et al. 2014). For carnivores, food availability is one major factor that influences the location and size of animal home ranges as it determines the minimum area required for an animal to survive (Herfindal et al. 2005; Hayward et al. 2009; Loveridge et al. 2009; Van Beest et al. 2011). Under these influencing factors, animals optimize their energy expenses in movement and space use by varying their frequency and duration of visits in different areas to maximise fitness and survival, resulting in changes in their broad-scale home range extent (Moorcroft et al. 2006; Benhamou and Riotte-Lambert 2012; Van Moorter 2015). Although home range studies are numerous across species and geographic ranges, few empirical studies have coupled

home ranges with movement components such as residence time and revisitation frequencies (e.g. see Benhamou and Riotte-Lambert 2012 and Van Moorter 2015).

Reintroduction has been increasingly used as a conservation tool in species recovery and re-establishment (Hayward and Somers 2009). The study of home range utilisation of reintroduced animals is important for informed reintroduction planning and management (Armstrong and Seddon 2007; Ewen et al. 2012). Reintroduction involves the relocation of animals to an area from which they had been extirpated (IUCN 1998). Reintroduced individuals are therefore released in a new environment where they need to explore and learn the resource locations and establish their home ranges in order to survive (Stamp & Swaisgood 2007). Exploratory movement is energetically expensive and dangerous for reintroduced animals as their lack of knowledge of the local environment, such as distributions of predators and competitors could lead to death (Bélichon et al. 1996; Travis et al. 2012). On the other hand, the animals must acquire resources in order to gain energy for fitness and survival. The ranging behaviour of reintroduced animals thus represents a trade-off between time spent on resource exploration and exploitation (Bartumeus and Levin 2008; Bonte et al. 2012). Their ability to optimize movement and their space utilization decisions directly affects the reintroduction success. The behaviour of reintroduced animals is influenced both directly and indirectly by the reintroduction procedures and subsequent management protocols that affect the social interactions between individuals, environmental conditions and resource provisions (Dunham 2001; Clark et al. 2002). For examples, the introduction of new individuals, artificial provisioning or removal of resources including food, water and physical boundaries (e.g. fence lines) could potentially affect the movement and space use of reintroduced animals but have been rarely addressed in previous studies (Druce et al. 2004; Steury and Murray 2004; Hayward et al. 2009).

In South Africa, the establishment of small fenced reserves (<1000 km2) and reintroduction of large predators to these reserves have increased rapidly in recent years (Hayward et al. 2007*a*, *b*). Lions are often the subject of reintroductions for the purposes of both conservation, as they face high risk of extirpation, and tourism, as they are often perceived as the African flagship species (Hunter 1998; Kilian 2003). Long-term post-release monitoring, however, which is critical for reintroduction success, is lacking despite the increase in reintroduction efforts and
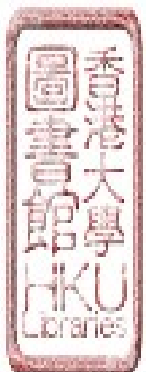
studies on home range establishment and utilization of reintroduced lions remain limited (Hayward et al. 2007a; Hunter et al. 2007). Lions are highly territorial, often leading to fatal intergroup fights (Mosser and Packer 2009). As lions are capable of long-range movement (Hunter 1998, Kilian 2003), competition for resources and territorial conflicts between different groups are both unavoidable in small fenced reserves and important in shaping individual ranging behaviour (Elliott and Cowan 1978; Hayward and Kerley 2009), ultimately affecting reintroduction success. An understanding of the spatial behaviour and inter-group spatial interactions of lions reintroduced in these small reserves is therefore essential for effective management practices to enhance lion establishment and long-term survival (Hayward and Somers 2009; Ewen et al. 2012).

In this Chapter, I investigate the ranging behaviour of lions of both sexes introduced in a small reserve less than 200 km^2 in size. I modelled cumulative home ranges from introduction to investigate the process of expansion and stabilization over time, estimated core and 95% seasonal and total home ranges sizes of the whole study period and explored frequency and duration of visits for areas within the home ranges. Finally, I tested the response of lions to the death of their competitors which resulted from territorial conflicts and to management interventions (introduction of new individuals) by comparing their home ranges before and after the events. I expected home ranges sizes to increase as the animals explored the new environment upon release, but the rates of increase to decline over time and stabilize. Revisitation frequency was expected to be higher and duration to be longer in core areas compared to the remainder of the home range. I also expected the dominant groups to take over the home ranges of the subordinate groups after territorial conflicts, and the lions to avoid the home ranges of other groups of the same sex but overlap with the ranges of the opposite sex.

Material and methods

Data collection

GPS locations of all lions were recorded regularly by the satellite collars once every four hours for the lions in the first two releases and every five hours for the lions in the third release (recording frequency was controlled by DGRMA). The locations were sent via satellite to an online centralised database and downloaded
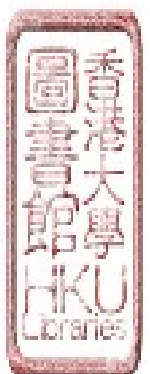
from there. Location data span from October 2011 to September 2014 consisting of three wet seasons (October-April 2011-12, 2012-13, 2013-14) and three dry seasons (May-September 2012, 2013, 2014). The location data of males were not available during the dry season 2013 due to failures of their collars.

I documented changes in group structure and interactions between groups that could have affected the movement and spatial behaviour of the lions by observing the animals in the field whenever possible and gathering additional sighting information from rangers, landowners and the DGRMA (Table 2.3).

Data analyses

I analysed home ranges by group based on the association of lions after the releases using the GPS location data collected as described in Chapter 2 (see Table 2.2 in Chapter 2). Females in the second release (F2) were killed in May 2012 by the males in the first release (M1), consequently, home range of F2 was analysed only for wet season 2011-12 (see Table 2.2 & 2.3 in Chapter 2). One of the males in the second release (M2b) was killed in February 2012 by M1, while one of the males (M1b) in M1 went missing in March 2013 (see Table 2.3 & 2.3 in Chapter 2). Therefore, data of the individual that remained alive throughout the study in each group were used for analyses (see Table 2.2 in Chapter 2).
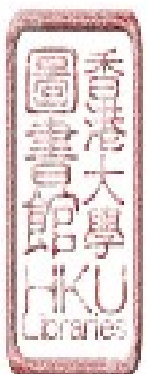
Home ranges were modelled using Time Local Convex Hull (T-LoCoH) in R package 'tlocoh' in R3.1.3 (Lyons et al. 2013). T-LoCoH advances the traditional LoCoH method by integrating not only space but also time differences in home range modelling (Lyons et al. 2013). The time-space scaling factor, *s*, was selected such that the diffusion distance (time) and spatial terms were equalled for 50% of the locations (i.e. temporal and spatial differences between points were balanced during nearest-neighbours selections). Values were chosen using time intervals of 72 hours for animals in the first and second release and 75 hours for those in the third release, based on the natural movement cycles observed in distances of each location to the centroid of the dataset. The adaptive method was used to identify nearest neighbours with cumulative time-scaled distance less than or equal to the value of *a* (Lyons et al. 2013). I computed values of *a*, so that 95% of locations had at least three nearest neighbours (the minimum number of points needed to create a hull) and used the values as starting points in selecting the final values. A range of

values were then used to create isopleths and plotted against isopleths areas and edge to area ratios. The plots were examined and values of *a* selected for constructing the final 50% core and 95% home ranges when isopleths areas stabilized with low edge to area ratios (i.e. when spurious holes not used by the animals were excluded and holes in core areas covered) (see Getz et al. 2007; Lyons et al. 2013).

To estimate cumulative home ranges, I modelled lion home ranges during the first 30 days of release and constructed subsequent home ranges over the study period by adding the locations of the next 30 days, i.e. the number of locations were cumulated over time. I also calculated the rate of change (slope) over time. Since all reintroductions happened at the beginning of the wet season, I assumed that cumulative home ranges from the day of release were comparable between lions released in different years. Total home ranges were modelled using all locations in the study period. Frequency and duration of visits for each hull in the total home ranges were calculated with inter-visit gap periods (the time that must past before the next occurrence is considered as a separate visit) set the same as the time intervals used in the *s* values selection. Seasonal home ranges were modelled separately for the wet and dry season each year, resulting in different numbers of seasonal home ranges for animals from different releases (see Table 2.2 in Chapter 2). The effects of season and sex and the interaction between the two factors on home range sizes were then tested using two-way ANOVA. I did not include the dry season 2013 home range of M1 and M2 in the test since data were unavailable due to collar failures.

To examine the effects of death of a competitor which resulted from a territorial conflict, I tested if the death of lions (M2b and F2) had led to home range takeovers by the remaining lion groups. I did this by calculating and comparing the home range overlap percentages of lion groups before and after each conflict events. For each event, pre-event home range overlap was compared to the overlap between pre-event home range of the killed individuals and post-event home range of the other lion groups (Table 4.1). A 67-day home range was used in the comparison for the death of M2b, because this time period was the maximum number of days before and after the event that still fell within the same season, such that any possible seasonal effect could be removed. Comparison was made between the wet

season 2011-12 (pre-death) and the dry season 2012 (post-death) for the event of death of F2, because F2 was killed at the end of the wet season 2011-12. I also tested for the effect of death of a group member on the ranging behaviour of the remaining member by calculating the overlap between the 67-day home range of M2 before and after the event.

In the case of the reintroductions, the overlap between pre-release home range of the existing lions and post-release home range of the new lions was compared to the overlap between existing and new lions post-release home ranges (Table 4.1). In the case of the second reintroduction, I used a 26-day home range because that was the time interval between first and second reintroduction. For the third reintroduction, to test if existing lions avoided the areas they had been utilising before, that were now utilised by the new individuals, I compared the wet season 2013-14 (after reintroduction) and the dry season 2013 (before introduction) because the introduction was carried out at the start of the wet season 2013-14. All percentages of home range overlaps were calculated using the equation (Miller 2012):

$$\frac{2(OZ) \times 100}{(HRa + HRb)}$$

Where OZ is the area of the overlapping zone between two home ranges, and HRa and HRb are the areas of the 95% home range of each lion group.

Table 4.1 Home range overlap comparison of lions in Dinokeng Game Reserve before and after territorial conflicts and introduction of new individuals.

Event	Home range overlap		
Death of M2b	M1 − M2	F1 − M2	M2
Before	M1(pre-death) x M2 (pre-death)	F1(pre-death) x M2(pre-death)	
After	M1(post-death) x M2(pre-death)	F1(post-death) x M2(pre-death)	M2(pre-death) x M2(post-death)
Death of F2	M1 – F2	F1 – F2	
Before	M1(pre-death) x F2 (pre-death)	F1(pre-death) x F2(pre-death)	
After	M1(post-death) x F2(pre-death)	F1(post-death) x F2(pre-death)	
Third reintroduction	M1 – F3	F1 – F3	
Before	M1(pre-release) x F3 (post-release)	F1(pre-release) x F3 (post-release)	
After	M1(post-release) x F3 (post-release)	F1(post-release) x F3 (post-release)	
	M1 – F3c	F1 – F3c	
Before	M1(pre-release) x F3c (post-release)	F1(pre-release) x F3c (post-release)	
After	M1(post-release) x F3c (post-release)	F1(post-release) x F3c (post-release)	

Results

Cumulative home range

Changes in the size of core and 95% home ranges were similar through time. As expected, the rates of increase in home range sizes were the highest upon release and decreased over time (Fig. 4.1). Time taken to reach the steadily increasing stage varied from 180 to 330 days. A sign of long-term stabilization was only found in F1 after 630 days and in M2 after 180 days of release. However, M2 resumed its
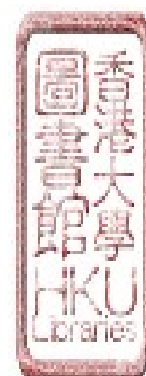
home range expansion after the third reintroduction (780 days of release), when M1 also showed an increase in home range expansion rate (Fig. 4.1). Home ranges of lions in the first release were larger than those in the second and third release throughout the study period.

Total home range, revisitation frequencies and duration of visit

The 50% and 95% total home range sizes were 16.42 ± 0.47 km^2 (mean $\pm$ SD) and 62.10 ± 6.00 km^2 for males and 12.27 ± 4.64 km^2 and 41.33 ± 15.29 km^2 for females respectively (Table 4.2). The core home ranges of all animals were established exclusively at their areas of release (first and second release: northern DGR, third release: southeast DGR), except M2 that included both northern and southeast DGR, where the surviving individual (M2a) was translocated in the dry season 2012 by DGRMA (Fig. 4.2). M2 continued to utilise the northern DGR even after the translocation. The central DGR was utilised only by lions in the first release as a part of their 95% home ranges (Fig. 4.2a and 4.2b) and the southwest and central southern DGR was excluded from the home ranges of all animals (Fig. 4.2).

For all lions, hulls with the longest durations of visit were visited only once (Fig. 4.3). Most of the hulls with low revisitation frequencies (green, turquoise and blue points) were scattered within the 95% home ranges and those with high revisitation frequencies (orange, purple and red points) clustered within the core areas (Fig. 4.4). Lions in the first release showed an increase in duration of visit when revisitation frequencies increased (Fig. 4.3a and 4.3b), with the most often revisited hulls (number of separate visits [nsv] >100) clustering around the biggest dam in the reserve (Fig. 4.3a and 4.3b). In comparison, revisitation rates of other lions did not exceed 40 nsv and durations of visit remained similar in different locations (Fig. 4.3c-f). The hulls with higher revisitation frequencies (orange, purple and red points) were clustered along the rivers or in the seasonal floodplains (areas that were flooded during wet season) (Fig. 4.4d-f), except M2 which were clustered also at the northwest corner of the reserve consisting of *Tarchonanthus camphorates* and *Boschia albitrunca* vegetation (Fig. 4.4c).
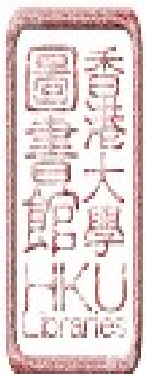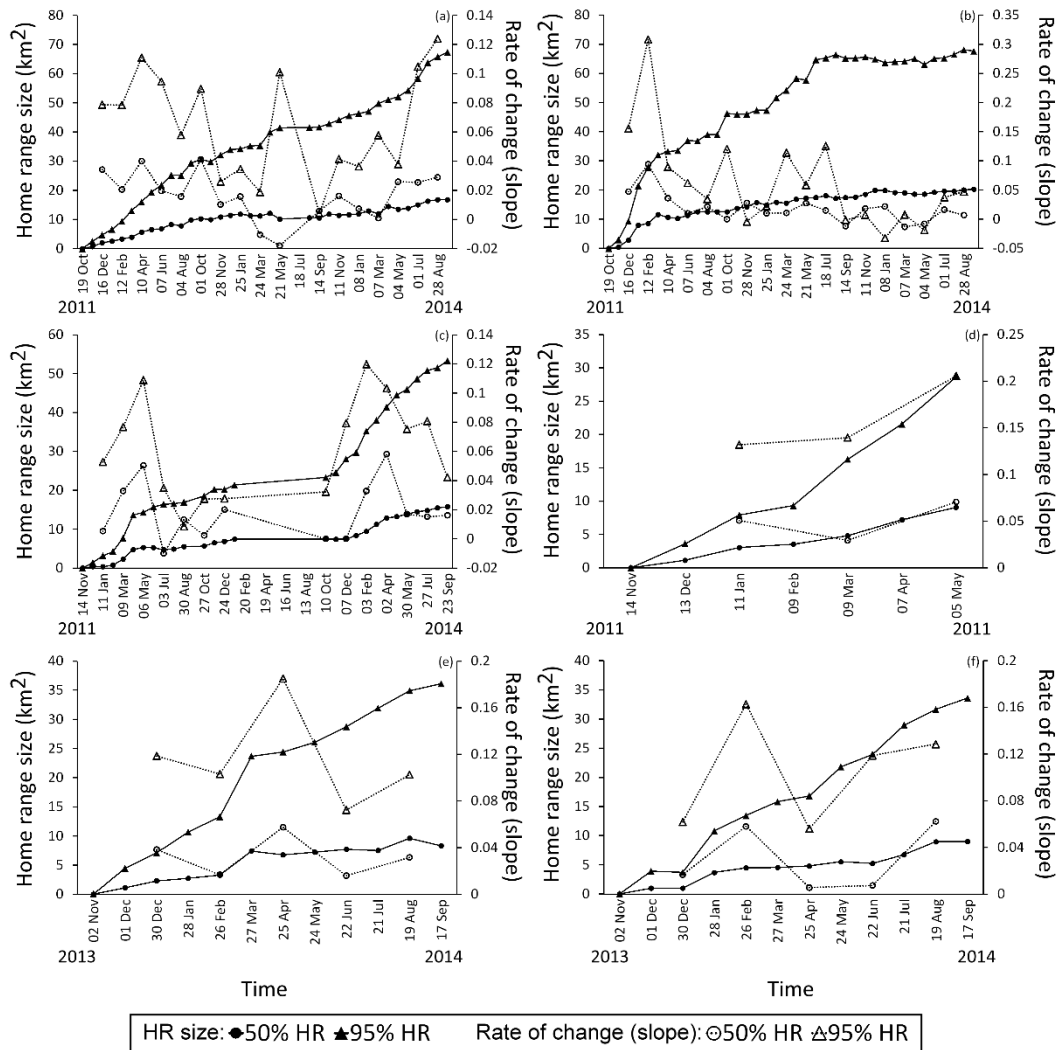
Fig. 4.1 Cumulative home range size and the rate of change in cumulative home range sizes of lions in Dinokeng Game Reserve, 2011-2014. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.
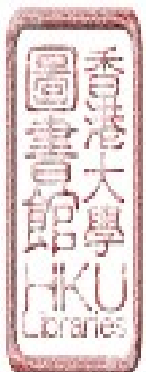
Table 4.2 The 50% core and 95% seasonal and total home range size (km^2) of lions in Dinokeng Game Reserve, 2011-2014.

Group	HR (%)	Home range size (km^2)						
		Wet season 2011-12	Dry season 2012	Wet season 2012-13	Dry season 2013	Wet season 2013-14	Dry season 2014	Total
M1	50	6.55	8.72	11.98		11.03	9.34	16.89
	95	20.91	28.47	40.80		54.02	48.62	68.10
F1	50	9.42	8.50	18.46	12.02	10.29	9.49	20.24
	95	33.27	37.25	48.35	41.58	33.93	42.82	67.45
M2	50	5.89	2.96	1.42		8.25	20.25	15.94
	95	17.39	5.81	9.84		29.10	54.40	56.10
F2	50	9.24						9.04
	95	28.52						28.62
F3	50					6.13	11.60	9.26
	95					24.01	31.43	35.64
F3c	50					5.24	12.68	10.52
	95					21.06	32.26	33.61
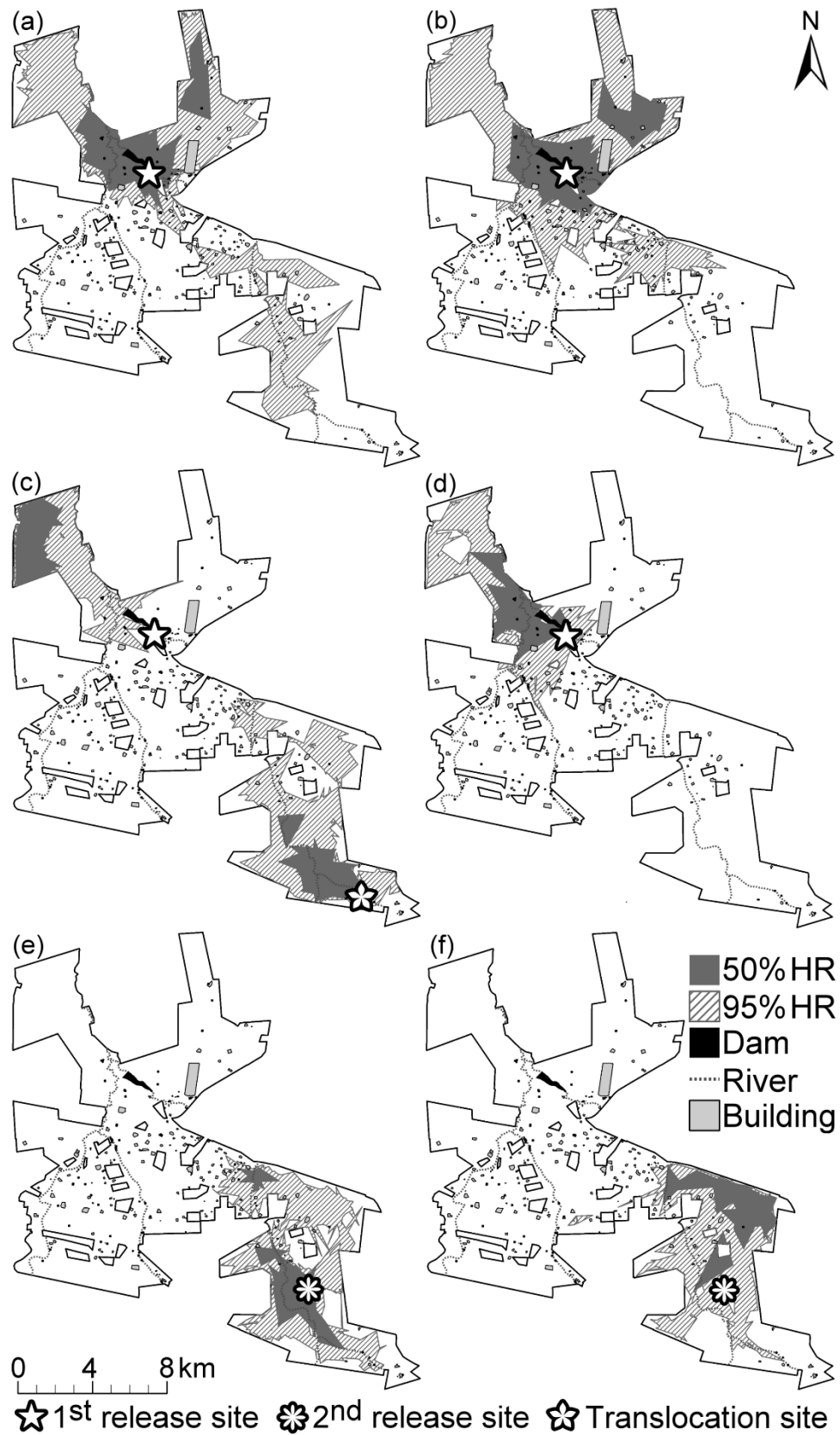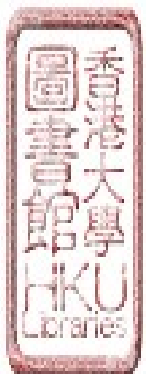
Fig. 4.2 Total home range of lions in Dinokeng Game Reserve, 2011-2014. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.
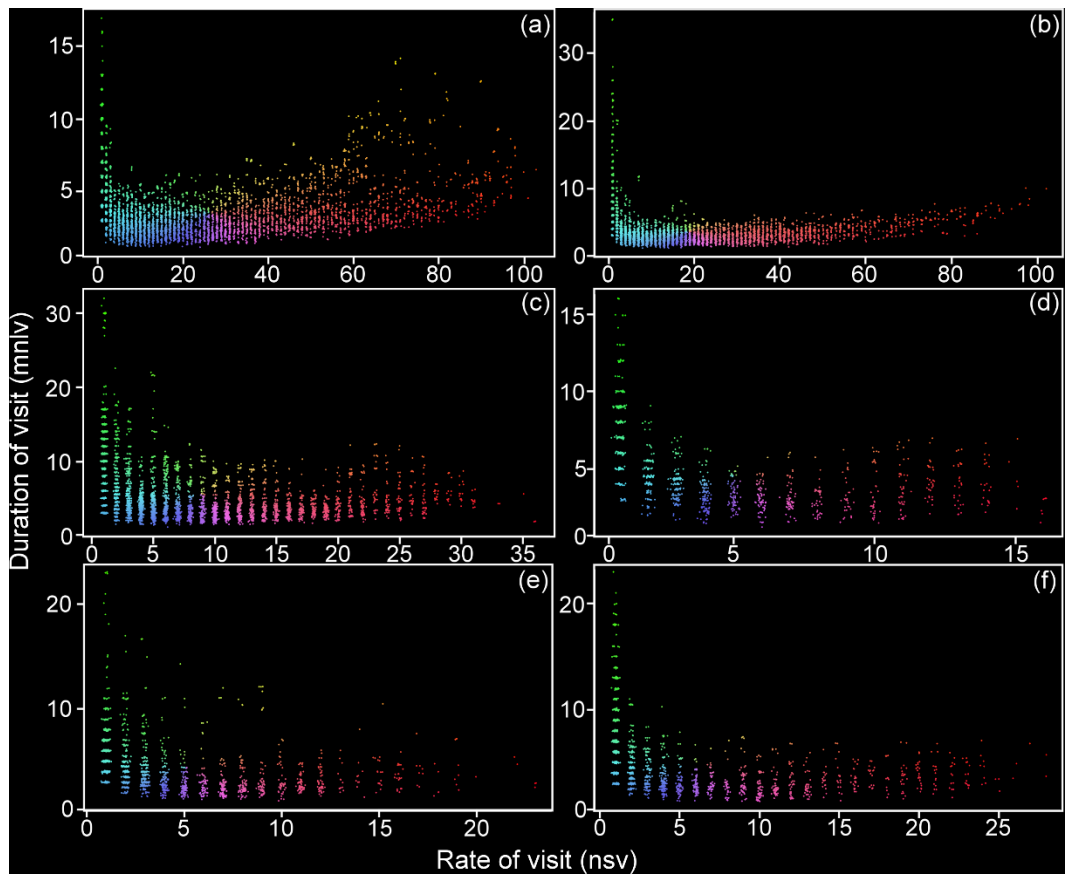
Fig. 4.3 Rates (number of separate visit [nsv]) and duration of visits (mean number of locations per visit [mnlv]) of different hulls in total home ranges of lions in Dinokeng Game Reserve, 2011-2014. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.
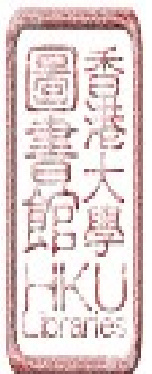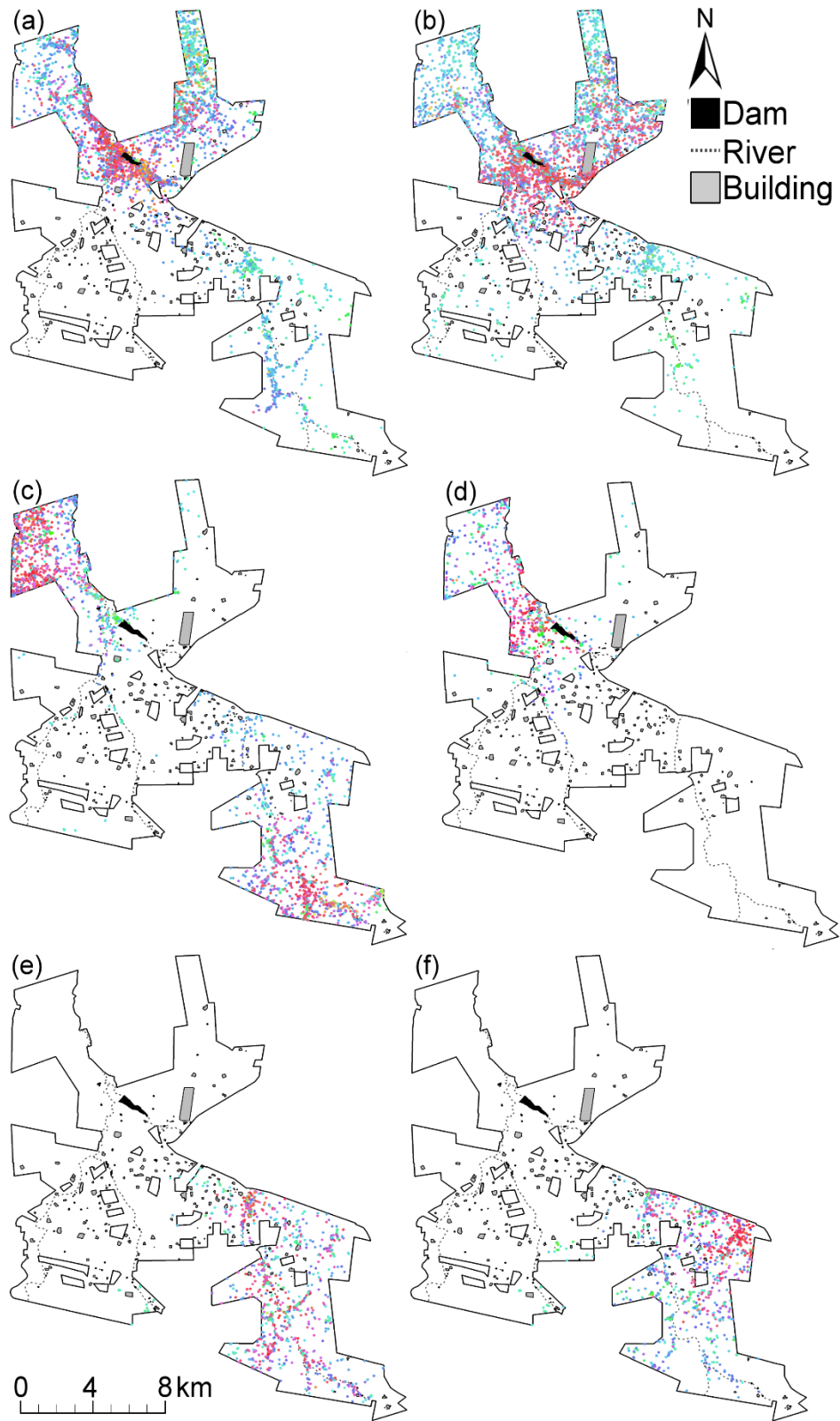
Fig. 4.4 Rates (number of separate visits [nsv]) and duration of visits (mean number of locations per visit [mnlv]) of different hulls in total home ranges of lions in Dinokeng Game Reserve, 2011-2014, in accordance with Fig. 4.3. (a) M1, (b) F1, (c) M2, (d) F2, (e) F3, (f) F3c.
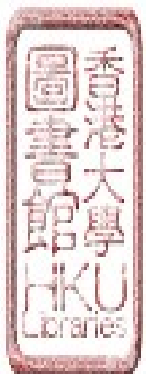
Seasonal home range

The core and 95% home ranges of the animals did not differ between seasons (50%: $F_{1,17} = 0.95$, p = 0.34; 95%: $F_{1,17} = 0.86$, p = 0.37) or sexes (50%: $F_{1,17} = 0.60$, p = 0.45; 95%: $F_{1,17} = 0.21$, p = 0.654) (Table 4.2) and the interaction between the two main factors was non-significant (50%: $F_{1,17} = 0.19$, p = 0.67; 95%: $F_{1,17} = 0.18$, p = 0.68).

Effect of territorial conflicts and introduction of new individuals

Territorial conflicts affected ranging behaviour differently in males and females. The overlap between the home ranges of M1 and M2 (pre-M2b death) increased by 18.89% after M2b was killed while the home range of the surviving member in M2 (M2a) showed little overlap (4.51%) with its original home range prior to the death of M2b (Table 4.3), i.e. M1 had taken over the area used by M2 while M2a had shifted away from its original home range. Similar behaviour was shown following the death of F2, when M1 increased its home range overlap with the F2 home range (pre-death) by 24.38%, and F1 by 22.59% (Table 4.3). On the contrary, the home range overlaps between F1 and M2 were negligible both before and after the death of M2b (Table 4.3).

Sexual differences were also shown in the response of lions to a new introduction. Lions in the second release (M2 and F2) established their home ranges in the northwest DGR, away from the northeast DGR where the home ranges of lions in the first release (M1 and F1) were located (Fig. 4.5). Following the third introductions (F3 and F3c), M1 increased the overlap between their home ranges and the area utilised by the new introduced lions (by 21.38% with F3 and by 17.44% with F3c), while F1 decreased the overlap (by 11.74% with F3, and by 10.86% with F3c) (Table 3), i.e. M1 expanded its home range towards the areas utilised by the newly introduced females (F3 and F3c), while F1 abandoned the areas utilised by the new females.
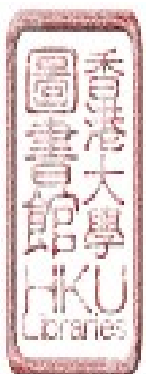
Table 4.3 Percentage of home range overlap of lions in Dinokeng Game Reserve before and after territorial conflicts and introduction of new individuals, 2011-2014.

Event	Percentage of home range overlap (%)		
Death of M2b	M1 – M2	F1 − M2	M2
Before	4.95	0.10	
After	23.84	0	4.51
Death of F2	M1 – F2	F1 – F2	
Before	36.54	33.44	
After	60.92	56.03	
Third reintroduction	M1 – F3	F1 – F3	
Before	0	13.87	
After	21.38	2.13	
	M1 – F3c	F1 – F3c	
Before	0	12.19	
After	17.44	1.33	
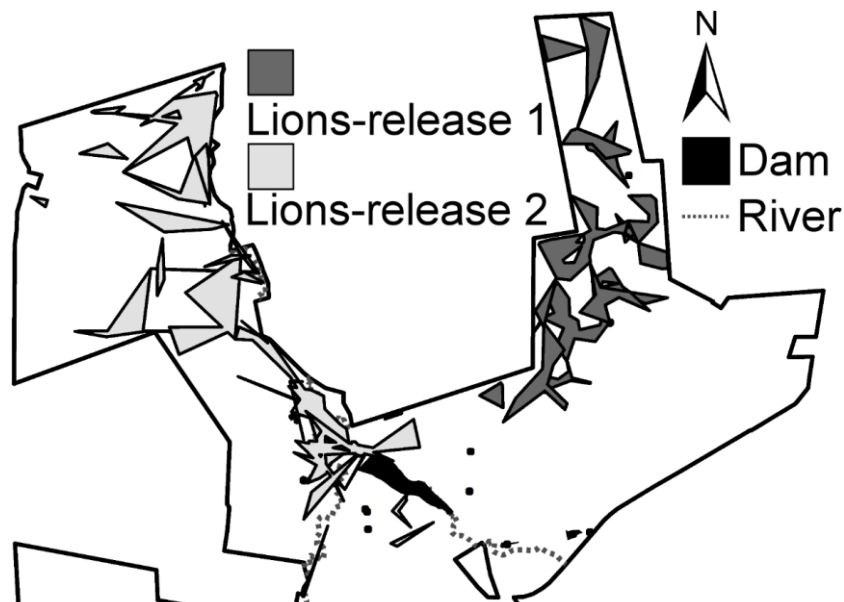
Fig. 4.5 The 95% home ranges of lions in the first release 26 days before the second reintroduction (19 October - 13 November 2011) and lions in the second reintroduction 26 days after released (14 November - 9 December 2011) in Dinokeng Game Reserve.
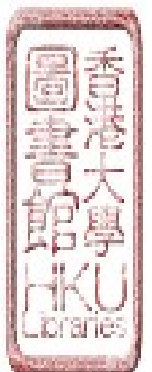
Discussion
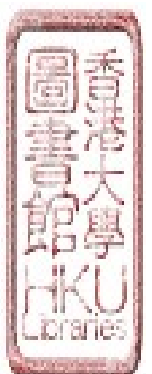
The results presented in this chapter show that home range expansion of reintroduced lions is a long process that can last more than three years. However, despite their continuous expansion during the study period, home range sizes of all lions remained below half the size of the reserve (<70 km^2). It suggests that hard boundary (fencing) of the reserve did not define the home range establishment of the lions, and the animals were able to acquire essential resources within small areas. The rates of increase in cumulative home range sizes were highest upon release and declined over time. The changes in the rates of home range expansions implies a change in movement behaviour from large scale exploration during early stages of release to smaller scale exploration after initial home ranges were established and the animals became more familiar with the environment. Similar behaviour was found in previous studies on reintroduced carnivores that had the highest rates of movement in the first few months of release (Hunter 1998; Preatoni et al. 2005). The cumulative home ranges of two of the lion groups (F1 and M2) reached a long-term stabilization while M1 continued to expand its home range over the entire study period. Male lions tend to aggressively expand their territories in order to maximise their chances of encountering and mating with females, while females are more risk sensitive and often avoid the costs of territorial conflicts particularly when in small groups (McComb et al. 1994; Mosser and Packer 2009). Therefore, F1 settled in a defined home range when the costs and benefits in maintaining its territory were balanced, instead of continuing the expansion which could lead to an increase in potential injuries and intergroup fights. On the other hand, since the females in the first and second release were injected with contraceptive and non-receptive, the males might have been expanding their home ranges extensively in order to search for other females. In comparison, the stabilization of the home range of M2 was likely due to the loss of its group member and subsequent translocation, resulting in ceased exploration. Restriction of movement is often observed in subordinate individuals in large carnivores to minimize territorial competition (Mosser and Packer 2009; Vanak et al. 2013). M2 resumed home range expansion after the third reintroduction when it sought for the newly released females.

All animals established their core home ranges at the area of their releases, except M2 which established a part of its core home range in southeast DGR, where
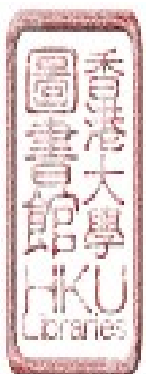
it was translocated. However, M2 continued to utilise the area where it was first released despite the translocation. The lack of utilisation of southwest and central southern DGR showed that the animals expanded their home ranges outwards from their release sites instead of elsewhere inside the reserve, despite their capability of travelling over 15 km in a single day (Hunter 1998; Kilian 2003). The pattern of home range establishment and expansion might result from the animals trying to optimize their energy expenses (Rosenbaum et al. 1991; Lenore 2007), by exploring and utilising the areas they were more familiar with and where they were less likely to move into unfamiliar landscapes or encounter competitors unexpectedly, which could result in injuries and decrease in fitness. The importance of release site in affecting movements was also revealed by the behaviour of the lions in returning to the area of their release site after initial dispersal during their early post-release movement (see Chapter 3). Although studies on various reintroduced mammal species had shown successful home range establishments (Preatoni et al. 2005; Hayward et al. 2009; Wauters et al. 2015), the location of home ranges in relation to the sites of release over time have rarely been addressed. Results suggest a considerable influence of the location of the release site on subsequent home range establishment and utilization. Moreover, the death of the three lions from the second introduction caused by the males released a month earlier in the same location, further highlights the importance of careful planning of the sites of release in lion reintroductions to ensure a successful establishment of the animals.
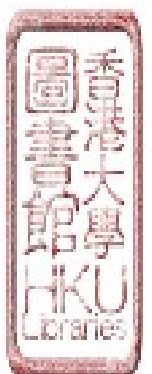
The areas in central DGR were utilised only by lions in the first release in their 95% home ranges, and M1 was likely using the area only as a transit zone for travelling between the north and the south. DGR incorporates privately owned land that belongs to more than 250 landowners, many of whom reside in the reserve. There is a high density of residential infrastructure in the reserve, with central DGR representing the most densely populated area (74 buildings in 26 km^2). It suggests that human related disturbance had influenced the space utilization of the lions, which agrees with several previous studies of carnivores (Kerley et al. 2002; Ngoprasert et al. 2007), had influenced the space utilisation of the lions. Different responses between groups were likely due to individual variations in behaviour (Schuett et al. 2010).

A core home range of an animal constitutes generally the area of most valuable resources for fitness and survival (Samuel et al. 1985; Vander Wal and Rodgers 2012), and was most intensely revisited by the reintroduced lions. Frequent revisitations may allow the animals to maximise their access to important resources and to defend their core territories against intruders. Locations with the highest revisitation rates were clustered around the largest dam in the reserve, which is surrounded by reed beds (*Phragmites australis*), or in the riparian vegetation complex along the rivers and seasonal floodplains. Results coincide with the preferred vegetation selection by lions in the study site (see Chapter 5). The dam and rivers are perennial water supplies that attract various herbivores, as well as the seasonal floodplains that attract the animals during wet season, while the dense vegetation around the water bodies could facilitate lions in ambushing their prey and provide shelters for the animals to rest during daytime. Similar types of vegetation are known to be preferred by lions elsewhere, and the distribution of water sources and vegetation structure are known to affect the space use of lions across geographic range (Hunter 1998; Spong 2002; Hopcraft et al. 2005; Lehmann et al. 2008b). Lions in the first release increased not only the frequencies but also their duration of visits around the biggest dam, showing that the area was of particular importance.

I found no seasonal difference in home range sizes, which differs from findings of previous studies in Phinda (Hunter 1998) and Karongwe Game Reserve (Lehmann et al. 2008b) in South Africa, where lions' home ranges were larger during wet season than dry season. These differences were explained by the restricted distributions of prey close to water sources during the dry season when water is a limiting factor, leading to smaller home ranges of the predators compared to the wet season pattern. In contrast, DGR has widely distributed perennial water sources and high abundance of prey species preferred by lions (e.g. 1635 blue wildebeest, 818 Burchell's zebra, 1239 impala; see Chapter 2 and Table 2.1), which likely removes any restrictions to the movement of lions in the dry season.

Home ranges of males were larger than that of females in the last two seasons of the study (wet season 2013-14 & dry season 2014), although overall differences between male and female home range sizes throughout the study period were not statistically significant. Results could potentially be explained by the application of
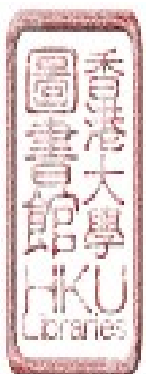
contraceptives to the females. Sexual selection is a driving force of behavioural differences between sexes (Cox and Le Boeuf 1977; Krebs and Davies 1997), and males increase their fitness by mating with multiple females (Emlen and Oring 1977). Movement of male lions are therefore influenced directly by the availability of females and were found in previous studies to utilise larger ranges to maximise mating opportunities by defending multiple prides (Loveridge et al. 2009; Mosser and Packer 2009). The females in the first and second release were non-receptive, which was likely the cause for males not defending the home ranges of these females during the initial two post-release years. However, the contraceptives on F1 were no longer effective in the last two seasons (estrous behavior was observed and cubs were born after mating with M1). At the same time in those seasons, the males were also likely trying to maximize their chances of mating with the females in the third release which were not injected with contraceptives.

Males and females in the first release responded differently to death of competitors and new introductions. Males were found to take over some parts of the original home ranges of the lions they killed during territorial conflicts. On the other hand, females did not engage in intergroup fights and their home ranges were expanded only after the death of F2 but not the member of M2 (M2b) which happened at an earlier time. As discussed earlier, female lions are more cautious and risk sensitive than males (McComb et al. 1994, Mosser & Packer 2009), which explains their range expansion into the previously occupied areas only after three of the lions in the second release were killed, i.e. when the probability of encountering a competitor has lowered. This also explains the home range expansions of males in the areas utilised by the females in the third release while females introduced earlier avoided those areas. I also found that lions in the second release avoided the areas occupied by lions in the first release, and that the surviving member of M2 shifted its entire home range after the other member was killed. This suggests that the lions released later were at a disadvantage because they were forced to explore in a new environment with existing competitors that were released earlier in the same area, which had likely imposed restrictions on their movements. Similar behaviour was shown in the early post-release movement patterns of the animals (see Chapter 3) and movements of lions in natural populations when less-fit individuals often become nomadic to avoid dominant individuals (Grinnell and
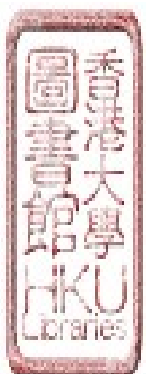
McComb 2001; Funston et al. 2003). It is further supported by the fact that lions in the first release developed larger home ranges than those of the same sex in the second release. These effects might have been lessened if the second introduction was to take place in another area away from the location of the first introduction, such that intra-specific competition could have been minimised at an early stage of release.

Post-release monitoring of movement and space utilisation is critical for reintroduction success, yet information on spatial behaviour of reintroduced lions remain limited despite the increase in their reintroduction. Research in this chapter shows that home range utilisation of reintroduced lions is a highly dynamic process, shaped by their movement strategies in exploration and territorial defence. Home range expansion and exploration in a new environment can take more than three years, and the animals change their ranging behaviour during this process in response to intergroup interactions, territorial conflicts and introduction of new individuals. Management decisions pertaining to reintroductions, such as the consecutive order and site of release, sexual composition, application of contraceptives and potential further translocation can influence the home range establishment utilization of the animals both directly and indirectly through affecting intergroup interactions. Reintroductions of lions should therefore be planned so that intra-specific competition and potential territorial conflicts are minimised during early stage of release to allow the animals to explore the environment and exploit resources with less constraint, therefore increasing reintroduction success.

Chapter 5

Third order habitat selection: within home range resource selection of reintroduced lions (*Panthera leo*)

(This chapter is currently submitted to the journal *Applied Animal Behaviour Science* as Yiu, S.W., Karczmarski, L., Parrini, F., & Keith, M., 2016. Habitat selection by reintroduced lions (*Panthera leo*) in a South African reserve)

Introduction

Studies of the processes and patterns of habitat selection by animals facilitate a greater understanding of how animals acquire resources within a heterogeneous landscape (Lima and Zollner 1996). Johnson (1980) defined habitat selection as a hierarchical process in which, within a geographic range (first order), animals establish their home ranges (second order), within which they select for preferable habitat components (third order), and eventually obtain food (forth order). Therefore, the process of habitat selection is a function of time and space and is influenced by ecological processes that determine the spatio-temporal resource distribution (Boyce 2006; Ciarniello et al. 2007; Mayor et al. 2009). The third order of habitat selection, within home range, is of particular importance as it indicates the animal preferences for habitat features and specific resources. Such information is in turn important for informed habitat management decisions and wildlife conservation (Johnson et al. 2004; Hebblewhite et al. 2011; Squires et al. 2013). Various factors, including topography, food availability, types and density of vegetation, human disturbances, and inter- and intra-specific interactions, have been identified as affecting the third order habitat selection of mammals (Simcharoen et al. 2008; Godvik et al. 2009; Vanak et al. 2013). However, studies on large carnivores have primarily focused on food (i.e. prey) abundance and accessibility, while the selection for other landscape features have rarely been addressed (Hopcraft et al. 2005; Balme et al. 2007; Davidson et al. 2012).

Reintroduction is a management practice commonly used in conservation projects aiming to re-establish species in areas where they had become extirpated (IUCN 1998; Hayward and Somers 2009). In this practice, however, the newly introduced animals, translocated from their original range and released in a new environment, lack any prior knowledge of the resource distribution. Reintroduced
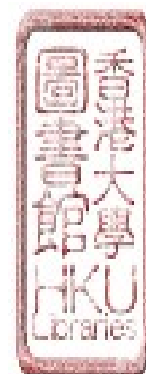
animals, therefore, face increased challenges in selecting optimal habitats and costs to their fitness and survival because of their need to explore and learn the distribution and accessibility of resources (Berger-Tal et al. 2014). Time taken by reintroduced animals to learn an unfamiliar environment varies and depends largely on individual behavioural plasticity and experience (Stamps and Swaisgood 2007; Berger-Tal et al. 2014). Selection for suboptimal habitats after introduction to a new environment has been seen in several species and proven to influence survival rates (Steffens et al. 2005; Roe et al. 2010; Bennett et al. 2012). Successful establishments of reintroduced animals thus depend directly on individual ability to optimize selections of suitable resources (Le Gouar et al. 2012). Therefore, studying habitat selection of reintroduced animals through time provides insights into the processes and patterns of how animals learn and adapt to a new environment.

Habitat selection affects not only individual fitness and survival but also inter- and intra-specific behavioural interactions. Landscape heterogeneity shapes predator-prey dynamics by influencing the habitat selection of predators and thus the predation risk perceived by the prey (Hebblewhite et al. 2005; Kauffman et al. 2007). The best known example is in Yellowstone National Park, U.S. where the utilisation of riparian areas and grasslands by reintroduced wolves (*Canis lupus*) had led to a shift in habitat selection of elks (*Cervus elaphus*) away from those areas, which then cascaded into vegetation changes (Ripple and Beschta 2004; Creel et al. 2005; Kauffman et al. 2007). Habitat selection patterns could also affect interactions between inter- or intra-specific competitors, resulting in the selection of suboptimal resources by subordinate individuals or subdominant species. For example, resident reintroduced black-footed ferrets (*Mustela nigripes*) has stronger preference for habitat with high densities of burrows than those that were newly released (Biggins et al. 2004); and, Alpine chamois (*Rupicapra rupicapra*) increases its habitat specialization in the presence of the Himalayan tahr (*Hemitragus jemlahicus*) (Forsyth 2000), while least weasel (*Mustela nivalis*) selects for less productive habitats compared to that of stoat (*Mustela erminea*) (Aunapuu and Oksanen 2003). Consequently, species-specific habitat selection provides information not only on the habitat requirement of that particular species but also on the overall ecosystem dynamics.

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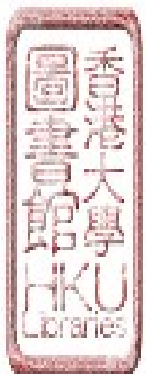
The establishment of small reserves (<1000 km^2) and reintroduction of large carnivores, such as lions (*Panthera leo*), has been increasing in recent years in South Africa due to growing demand for ecotourism (Di Minin et al. 2013; Hayward et al. 2007a, b). Most of these South African reserves are entirely fenced and heavily managed (Kettles and Slotow 2008; Ferreira and Hofmeyr 2014). Large carnivores, on the other hand, are long-ranging and highly territorial, and often require high quality habitats due to their large body size (Crook 2002; Hayward et al. 2007c). Competition for resources between large carnivores and their impacts on other local species could therefore be intense within small and enclosed areas (Mosser and Packer 2009; Thaker et al. 2011). However, despite a growing number of reintroduction projects, studies on habitat selection of reintroduced large carnivores remain limited (Hunter et al. 2007) and there is therefore a need for a greater understanding of the behavioural response of reintroduced large carnivores to a new environment and the environmental determinants of their habitat selection.

I studied the third order habitat selection of reintroduced lions in a small reserve using resource selection function (RSF) (Manly et al. 2002). The objectives were to (1) investigate environmental determinants of habitat selection, (2) examine temporal habitat selection patterns, (3) compare selection patterns between large extent (95%) and small extent (50%) home range scale, and (4) test the response of lions to the predicted probability of occurrence of potential mates and competitors, before and after each territorial conflict and new introduction event. I expected the lions to select landscape features that could facilitate movement (low topographic roughness), attract prey (areas close to water sources and floodplains and riparian vegetation) and low level of human disturbances (areas away from roads and buildings). I anticipated the selection patterns to become more consistent with time. I also expected the lions to select areas with low probability of occurrence of individuals they had territorial conflicts with, but select areas with high predicted probability of occurrence of potential mates.

Material and methods

Data collection

GPS locations of all lions were recorded regularly by the satellite collars once every four hours for the lions in the first two releases and every five hours for the

lions in the third release (recording frequency was controlled by DGRMA). The locations were sent via satellite to an online centralised database and downloaded from there. The location data span from October 2011 to September 2014 consisting of three wet seasons (October-April 2011-12, 2012-13, 2013-14) and three dry seasons (May-September 2012, 2013, 2014). The location data of males were not available during the dry season 2013 due to failures of their collars. I documented changes in group structure and interactions between groups that could have affected the movement and spatial behaviour of the lions by observing the animals in the field whenever possible and gathering additional sighting information from rangers, landowners and the DGRMA (Table 2.3).

Environmental variables that could potentially affect habitat selection of lions (Abade et al. 2014) were categorized into features related to: topographic roughness (elevation, slope, Vegetation Continuous Fields [VCF]); prey availability and accessibility (distance to the nearest river, distance to the nearest dam, VCF, vegetation types); human disturbance (density of roads, distance to the nearest buildings). I created shapefiles of DGR and rivers, dams, roads and buildings within the reserve using satellite image from Google Earth (2005). Distribution of the 15 vegetation types were sourced from Contour Project Managers (2009) and mapped (Fig. 2.4). All shapefiles were projected as UTM WGS1984 35S coordinate system in ArcGIS 10.2 (ESRI, Redlands, Calif.). I obtained elevation data at 30 m spatial resolution from the ASTER Global Digital Elevation Model (GDEM) (NASA LP DAAC 2009), and derived the slope using the Slope tool in ArcGIS 10.2 (Appendix A, Fig. A-3). I downloaded the 250 m Terra MODIS Vegetation Continuous Fields (VCF) imagery (Townshend et al. 2011), representing the annual percentage of tree cover, from 2011 to 2015 and resampled the data to the same spatial resolution as the GDEM. Each VCF image was produced with data between 5th June of a year and 4th June the next year, therefore 2011-12 image represented the wet season 2011-12, 2012-13 image represented the dry season 2012 and wet season 2012-13, 2013-14 image represented the dry season 2013 and wet season 2013-14, and 2014-15 image represented the dry season 2014 (Appendix A, Fig. A-4). I mapped the rivers, dams, roads, buildings and the distribution of 15 vegetation types (see Fig. 2.4 in Chapter 2) within the reserve as described in Chapter 2. Road density at 30 m resolution was calculated using the kernel density tool in ArcGIS 10.2, with
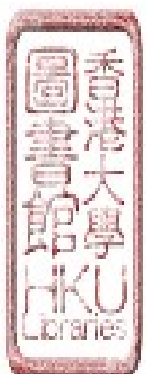
radius defined as the average distance between roads. I counted the Rust de Winter Road twice due to its much higher traffic flow compared to other dirt roads (Appendix A, Fig. A-5).

Data analyses

Lion data (data were collected as explained in Chapter 2) were analysed based on the association of the animals after release. Data of the individuals that remained alive throughout the study were chosen to represent the group and used for the analyses (see Table 2.2 in Chapter 2).

I assessed habitat selection of all lions by building resource selection functions (RSFs) using mixed-effects logistic regression (generalised linear mixed model [GLMM]) (Gillies et al. 2006) implemented in R package 'lme4' (Bates et al. 2014) and R3.1.3, with lion groups as random. Models were built under the used-availability design, defining the locations of animals as used resources and random points created within their home ranges estimated by minimum convex polygon (MCP) as available resources (Manly et al. 2002). I sampled random points at a ratio of 1:1 to the number of used locations to ensure that the random points representing the available resources were accessible to the animals at that particular spatial and temporal scale (Recio et al. 2014). The values of the different environmental variables (Table 5.1) at each used and random location were then calculated and extracted. RSFs were estimated at two spatial scales: (1) 95% home range, and (2) 50% home range (home range estimates derived from Chapter 4).

A set of seven a priori models of different combinations of the three environmental variables categories (Topographic roughness, prey availability and accessibility, human disturbance), including the global model, was constructed for the two spatial scales and each season (Table 5.1). Multicollinearity between variables was tested using the variance inflation factor (VIF) with a cut-off value of 10 (O'Brien 2007). I calculated the Akaike weights (ω) of the models based on their AIC values and selected the model with the best fit using $\omega \geq 0.95$ (Burnham and Anderson 2002). When none of the models had $\omega \geq 0.95$, i.e. model selection was uncertain, I used the multi-model inference approach by computing the average model parameters weighted by the Akaike weights of each model (Burnham et al. 2011). Model fit was assessed using 10-fold cross validation (Boyce et al. 2002;
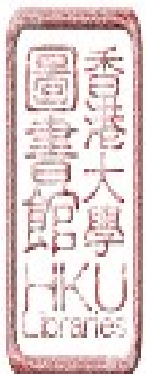
Koper and Manseau 2010). By treating individual group as a random factor, GLMM controls the non-independent behaviour between groups and provides accurate resource selection inference for the entire population (i.e. all of the lions) (Gillies et al. 2006). However, results from this approach do not show the individual differences in resource selection patterns. Therefore, in order to understand individual variation in habitat selection of lions, I also built RSFs separately for each lion group using logistic regression (generalised linear model [GLM]) following the same procedures just described.

To evaluate the impacts of territorial conflicts and introduction of new individuals on habitat selection by lions, logistic regression was used to build RSFs that tested the effects of the interaction between two independent variables: 1) predicted probability of occurrence of other lion groups (continuous variable), and 2) the time in the events of conflicts or introduction (categorical variable coded as before or after). The time period and probabilities used for each event are illustrated in Table 5.2. A 67-day time period before and after the death of M2b was selected to remove any possible seasonal effects, as it was the maximum number of days that fell within the same season. For the event of F2 killed by M1, RSFs were built for the wet season 2011-12 (before event) and the dry season 2012 (after event) because F2 was killed at the start of the dry season 2012, therefore potential seasonal effect cannot be removed. Similar to the death of F2, the third introduction was carried out at the start of a season (wet season 2013-14), therefore we defined the time period before and after the introduction as the dry season 2014 and the wet season 2013-14 respectively. To build the RSFs, lion GPS locations and random points used for the seasonal RSF analyses were extracted for the time period before and after each event. Values of the predicted probability of occurrence associated with each points were extracted from predictive maps created using the raster calculator in ArcGIS 10.2 and the equation (Manly et al. 2002):

$$P = \frac{e^{a+bx_1+bx_2+\cdots+bx_\infty}}{1 + e^{a+bx_1+bx_2+\cdots+bx_\infty}}$$

Where P is the predicted probability of a lion group, a is the intercept and b is the coefficient of each independent variable x extracted from the seasonal RSF built for that group. To obtain the value of the combined probabilities of F3 and F3c, I used the equation (Ash 2008):

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$$P(\text{females from the third release}) = P(F3) + P(F3c) - P(F3) \times P(F3c)$$

Table 5.1 Environmental variables and a prior model set used for estimating the resource selection function (RSF) of lions in Dinokeng Game Reserve, 2011-2014.

Feature categories	Variable
Topographic roughness	Elevation, slope, Vegetation Continuous Fields (VCF)
Prey availability and accessibility	Distance to the nearest river, distance to the nearest dam, VCF, vegetation types
Human disturbances	Density of roads, distance to the nearest building
Model number	**A priori model set**
1	Elevation + slope + VCF
2	Distance to river + distance to dam + VCF + vegetation types
3	Density of roads + distance to building
4	Elevation + slope + VCF + distance to river + distance to dam + vegetation types
5	Elevation + slope + VCF + density of roads + distance to building
6	Distance to river + distance to dam + VCF + vegetation types + density of roads + distance to building
7 (global model)	Elevation + slope + VCF + distance to river + distance to dam + vegetation types + density of roads + distance to building
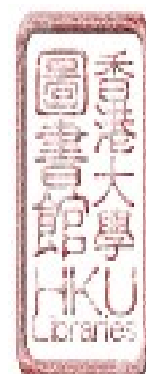
Table 5.2 The time of event and probabilities of occurrence of lion groups used as independent variable in the resource selection function (RSF) modelling of lions in Dinokeng Game Reserve, 2011-2014.

Event/Lion group	Time of event/Probability
Death of M2b	Before: 67 days before death
	After: 67 days after death
M1	M2 (wet season 2011-12)
M2	M1 (wet season 2011-12)
Death of F2	Before: wet season 2011-12
	After: dry season 2012
M1	M2 (wet season 2011-12)
F1	M2 (wet season 2011-12)
3rd reintroduction	Before: dry season 2013
	After: wet season 2013-14
M1	F3 & F3c (wet season 2013-14)
F1	F3 & F3c (wet season 2013-14)

Results

Model selection

The global model which includes all variables related to topographic roughness (elevation, slope and VCF), prey availability and accessibility (distance to river and dam, VCF and vegetation types), and human disturbances (density of roads and distance to building) was the best model ($\omega \geq 0.99$) in explaining habitat selection of all lions together (GLMM) and each group (GLM) in 50% and 95% home range scales for most of the seasons (Table 5.3).
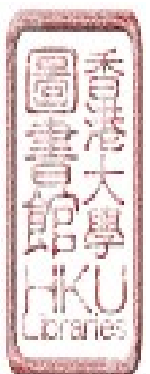
Model averaging was performed for the seasons when model selection was uncertain (none of the candidate models had ω ≥ 0.95 (Table 5.3). For these averaged models, the sum of the Akaike weights of model 7 (global model), model 2 (features related to prey) and model 4 (features related to topographic roughness and prey) was greater than 0.95, i.e. model 7, model 2 and model 4 had similar weights in explaining the resource selection of the lions.

Distance to buildings was removed from the analyses for M2 for the dry season 2012 due to multicollinearity with distance to dams.

Features related to topographic roughness

Selections for different topographic roughness features by lions remained similar in their 50% and 95% home ranges over time (Fig. 5.1a-c). All lions selected lower elevations over the duration of study period (Fig. 5.1a), except for M2 which changed from selecting lower elevation to higher elevation after the translocation from northwest to southeast DGR at the start of the wet season 2012-13 (Fig. 5.2a). Selections for steeper slope were found only in 50% HR during the wet season 2011-12, with a change to selection for less steep slope over time after this season (Fig. 5.1b). Although the animals increased their magnitude (i.e. an increase in the value of the coefficient) in selecting higher VCF after their releases (Fig. 5.1c), the trend was reversed for males and the selection became negative for females, i.e. the females avoided dense vegetation, after the third reintroduction in the wet season 2013-14 (Fig. 5.3b).
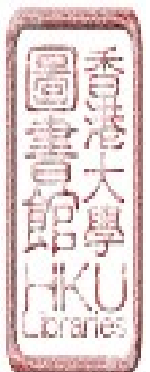
Table 5.3 Model selection for resource selection function (RSF) of lions in Dinokeng Game Reserve, 2011-2014.

Season	Wet season 2011-12		Dry season 2012		Wet season 2012-13		Dry season 2013		Wet season 2013-14		Dry season 2014	
Home range (%)	50	95	50	95	50	95	50	95	50	95	50	95
All lions	7	7	7	7	6,7	7,4	7	4,7	7,6	4,7	7,4	7
M1	4,7	6,7	7	4,7	7	4,7			2,7,6	4,7	4,7	4,7
F1	2,6,4,7	7	7,6	7	7	7	4,7	4,7	7,6	4,7	7	4,7
M2	7	7	7	7,4	4,7	7			7	6,7	7,6	6,7
F2	7	7										
F3									6,7	4,2,7,6	7,4	7
F3c									7	2,4,6,7	7	4,7
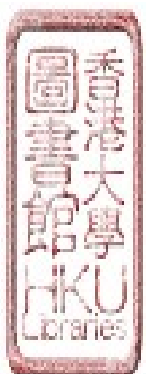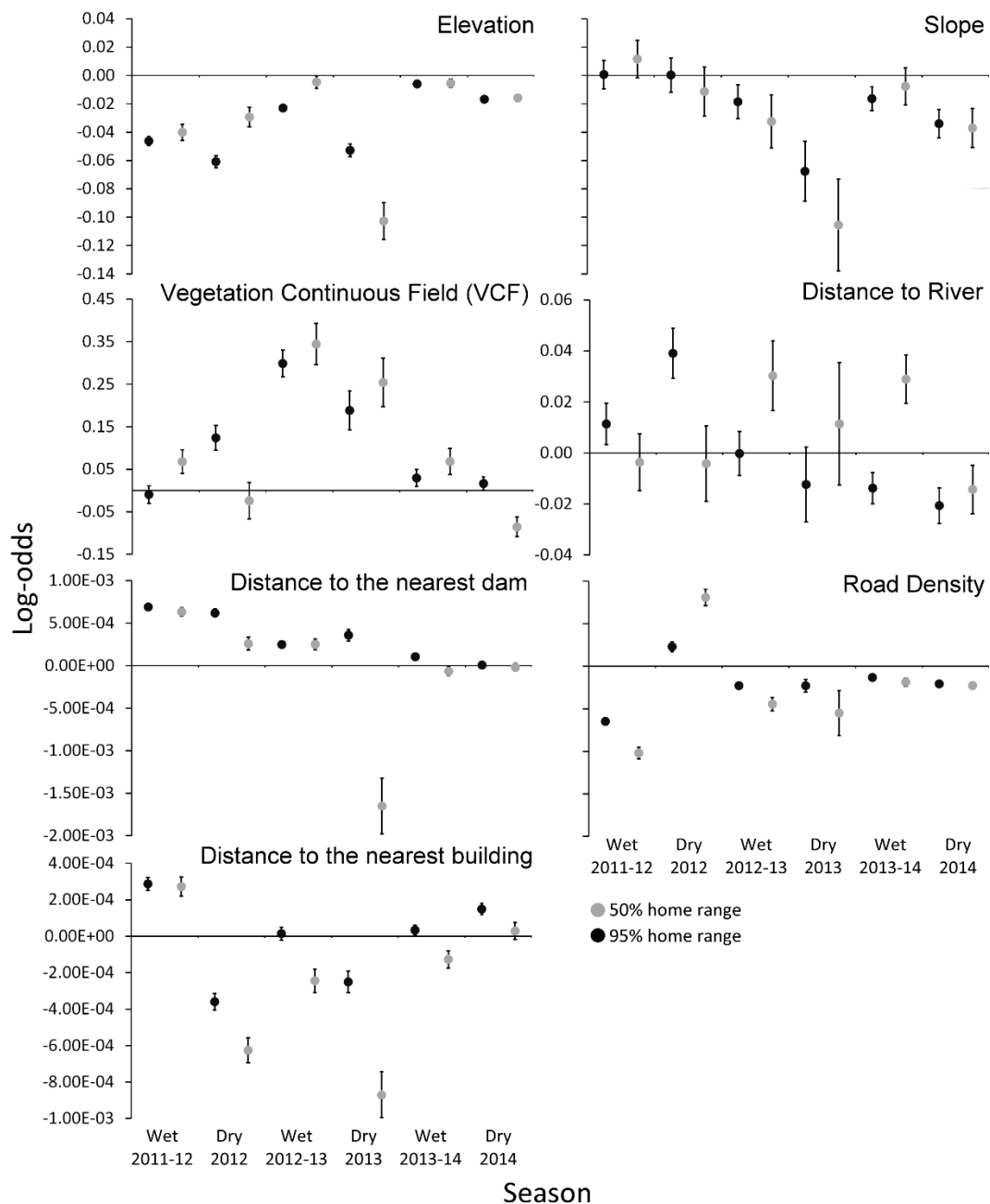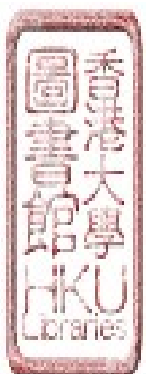
Fig. 5.1 Resource selection within 50% and 95% home range by lions in Dinokeng Game Reserve, 2011-2014. Regression estimates and 95% confidence intervals of different environmental variables (continuous variables) from GLMM model are presented.
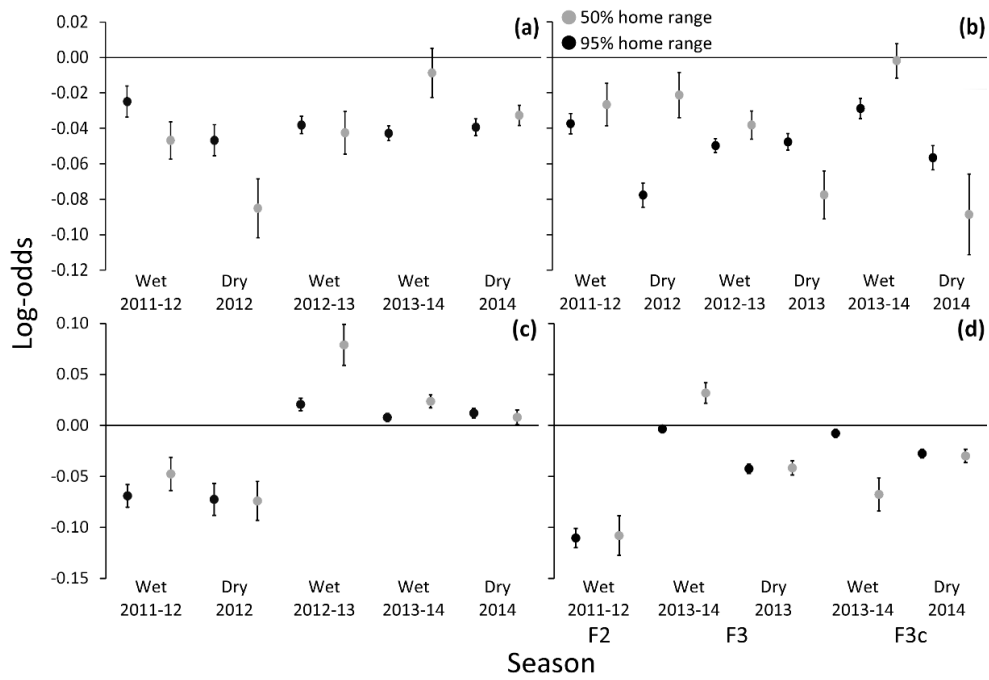
Fig. 5.2 Selection of elevation within 50% and 95% home range by each lion group in Dinokeng Game Reserve, 2011-2014. Regression estimates and 95% confidence intervals from GLM model are presented. (a) M1, (b) F1, (c) M2, (d) F2, F3 and F3c.
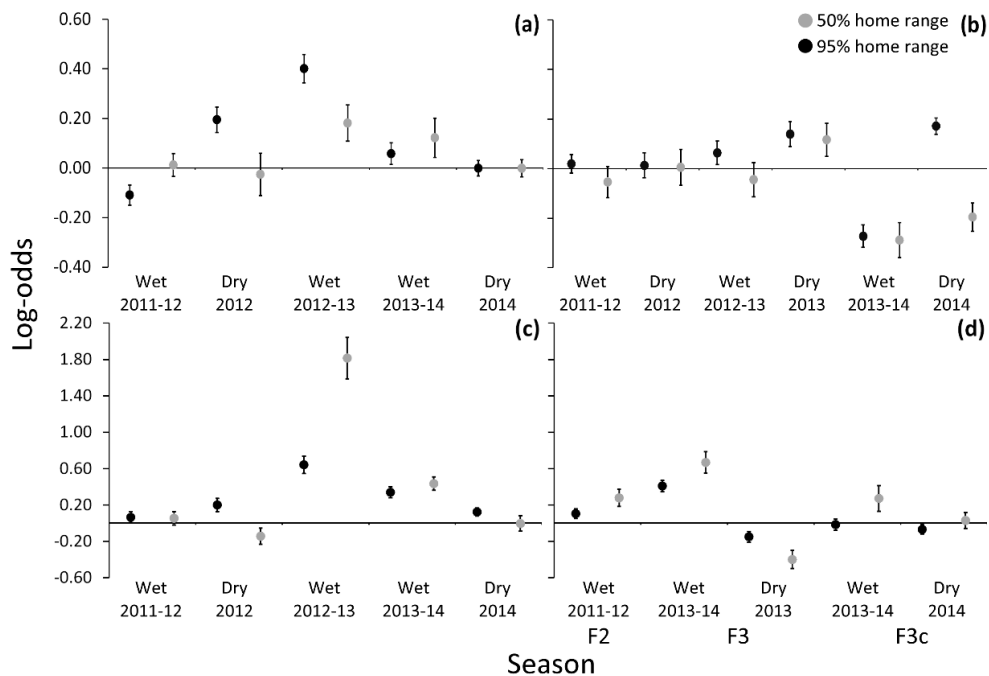
Fig. 5.3 Selection of Vegetation Continuous Fields (VCF) within 50% and 95% home range by each lion group in Dinokeng Game Reserve, 2011-2014. Regression estimates and 95% confidence intervals from GLM model are presented. (a) M1, (b) F1, (c) M2, (d) F2, F3 and F3c.
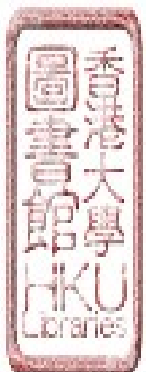
Features related to prey availability and accessibility

Lions selected areas further away from rivers after release, but the magnitude of selection decreased over time, and the animals switched to selecting areas close to rivers within their 50% HR after the dry season 2013 (Fig. 5.1e). The probability of occurrence of lions decreased when distance from dams increased (Fig. 5.1f) throughout the study period, except during the dry season 2012 when the animals stayed away from the dams.

Lions selected floodplains and riparian vegetation (vegetation type 4 and 9, reference levels; see Fig. 2.4 in Chapter 2) more than other vegetation types at both home range scales, except during the wet season 2012-13, dry season 2013 and wet season 2013-14 when the animals selected other vegetation types over the floodplains and riparian vegetation in their 50% home ranges (Table 5.4). Number of vegetation types used by M2 in its 50% home range decreased from six in the wet season 2011-12 to two, floodplains and riparian vegetation (type 9) excluded, in the dry season 2012 (Appendix B). Within its dry season 2012 95% home range, M2 selected floodplains and riparian vegetation less than or equal to all other vegetation types that were avoided in the previous season, except for the avoidance of type 11 (open *Vachellia tortilis* floodplains) which remained unchanged (Appendix B). The floodplains and riparian vegetation were strongly selected for by F1 in its 50% home range during wet season 2012-13 but F1 avoided this vegetation type in the following season (Appendix B).

Features related to human disturbances

Resource selection in response to human disturbances differed between male and female lions (Fig. 5.4 and 5.5). Males selected areas with high road density in general, while females avoided these areas except in certain seasons (F1: 50% home range, dry season 2014; F2: 95% home range, wet season 2011-12; F3: 50% and 95% home range, wet season 2013-14) (Fig. 5.4). Behavioural differences also existed between groups of the same sex, with M1 showing a stronger selection for higher road density in the 50% home range compared to 95% home range whereas the opposite was true for M2 (Fig. 5.4).

Females selected areas closer to buildings in general but moved away over time (Fig. 5.5). On the other hand, males responded to buildings differently, with

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M1 showing a sign of habituation (i.e. selecting for areas closer to buildings with time) and M2 a sign of increased avoidance of buildings over the study period.

Table 5.4 Selection for vegetation types by lions in Dinokeng Game Reserve, 2011-2014. - indicates avoidance, 0 indicates no significant selection, + indicates preference. Ref. = reference level.

Season	Wet 2011-12		Dry 2012		Wet 2012-13		Dry 2013		Wet 2013-14		Dry 2014	
Home range	95 %	50 %	95 %	50 %	95 %	50 %	95 %	50 %	95 %	50 %	95 %	50 %
1					-		0	+	-	-	-	-
2					-	-	-	+	-	-	-	-
3					-	0	-	0	-	-	-	-
4					+	+	0	+	ref.	ref.	ref.	ref.
5	0				-	0					-	
6	-	-	-	-	-	0	-	+	-	+	-	-
7	-	-	-	-	-	-	-	+	-	+	-	-
8	-	-	-	-	-	+	-	+	-	+	-	-
9	ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.	-	+	-	0
10	-	-	-	-	-	+	-	+	-	0	-	-
11	-	-	-	-	-	+	-	-	-	+	-	-
12	-	-	-	-	-	+	-	+	-	+	-	-
13	-	-	-	-	-	-	-	+	-	-	-	-
14	-	-	-	-	-	-	-	0	-	+	-	-
15	-	-	-	0	-	-	-		-	0	-	-
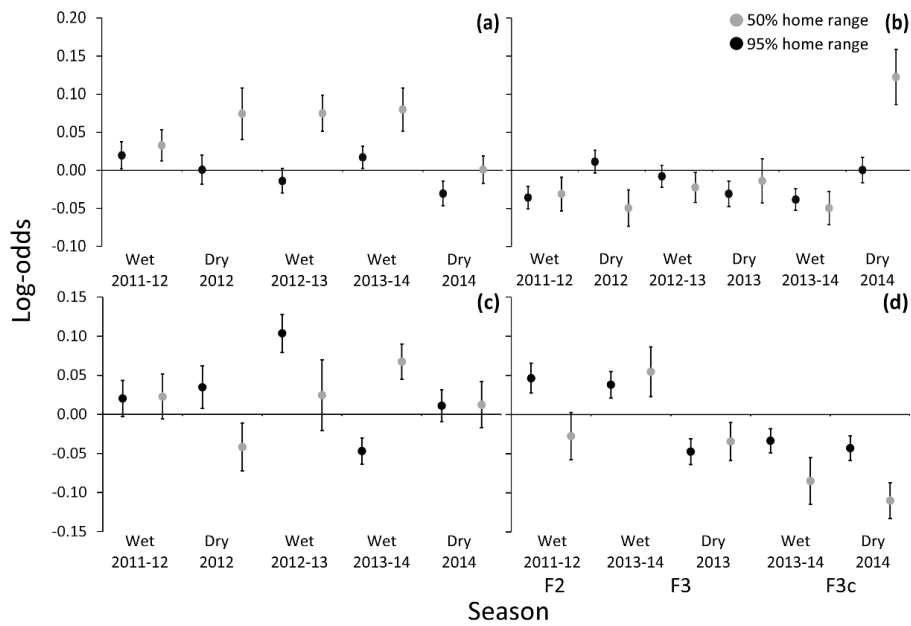
Fig. 5.4 Selection of road density within 50% and 95% home range by each lion group in Dinokeng Game Reserve, 2011-2014. Regression estimates and 95% confidence intervals from GLM model are presented. (a) M1, (b) F1, (c) M2, (d) F2, F3 and F3c.
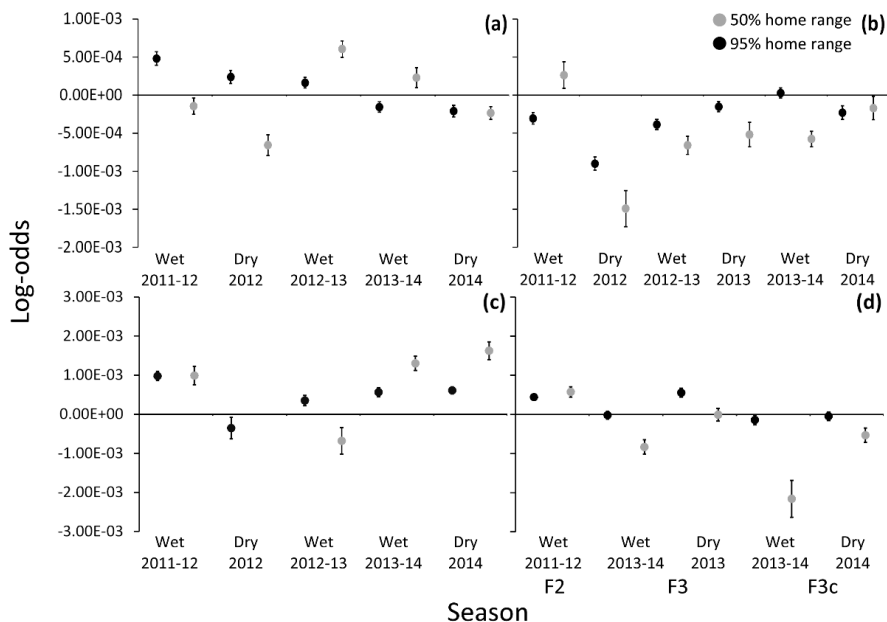
Fig. 5.5 Selection of distance to the nearest building within 50% and 95% home range by each lion group in Dinokeng Game Reserve, 2011-2014. Regression estimates and 95% confidence intervals from GLM model are presented. (a) M1, (b) F1, (c) M2, (d) F2, F3 and F3c.
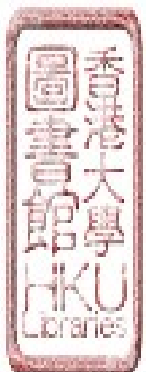
Effects of territorial conflicts and introduction of new individuals

The effects of the interactions between predicted probabilities of occurrence and time of events (before/after) were significant in the RSFs of all tested lion groups in response to territorial conflicts (death of M2b and F2) and introduction of new females ($Z < -1.929$ or > 2.814, $p < 0.01$; Table 5.5). M1 switched its selection from areas with lower probabilities to areas with higher probabilities of occurrence of M2 after the death of M2b (one of the group members in M2), i.e. M1 shifted selection to landscape features that had a higher probability of selection by M2 prior to the conflict. At the same time, M2 changed from selecting areas with higher probabilities to areas with lower probabilities of occurrence of M1 after M2b was killed, i.e. M2 was actively avoiding the landscape features selected by M1. M1 and F1 showed no selection or avoidance for areas with different probabilities of occurrence of F2 before the death of the latter. However, both groups selected areas with high predicted probability of F2 after the death, i.e. the lions were using the landscape features that were selected by F2 more frequently. M1 and F1 also changed from having no selection to avoiding areas with high predicted probability of occurrence of the females from the third release after they were introduced.

Table 5.5 Logistic regression results examining resource selection function (RSF) of lions in response to the predicted probability of occurrence of other groups, before and after territorial conflicts and introduction of new individuals in Dinokeng Game Reserve, 2011-2014.

Independent variable	Estimate	Standard error	z value	p value
Death of M2b				
M1				
P(M2)	-0.743	0.231	-3.213	0.001
Event (after)	-1.498	0.193	-7.757	<0.001
P(M2) X Event (after)	3.085	0.351	8.783	<0.001
M2				
P(M1)	9.695	0.922	10.516	<0.001
Event (after)	1.389	0.179	7.768	<0.001
P(M1) X Event (after)	-13.071	2.128	-6.143	<0.001
Death of F2				
M1				
P(F2)	0.540	0.418	1.293	0.196
Event (after)	-0.565	0.085	-6.66	<0.001
P(F2) X Event (after)	5.534	0.658	8.409	<0.001
F1				
P(F2)	-0.140	0.557	-0.252	0.801
Event (after)	-0.124	0.077	-1.615	0.106
P(F2) X Event (after)	2.480	0.881	2.814	<0.01
3rd reintroduction:				
M1	0.625	0.327	1.909	0.056
P(F3 + F3c)	0.295	0.084	3.528	<0.001
Event (after)	-3.208	0.586	-5.471	<0.001
P(F3 + F3c) X Event (after)				
F1				
P(F3 + F3c)	0.310	0.251	1.232	0.218
Event (after)	0.293	0.087	3.364	<0.001
P(F3 + F3c) X Event (after)	-2.550	0.484	-5.27	<0.001

Discussion

Features related to topographic roughness, prey availability and accessibility and human disturbances, all influenced the 3rd order habitat selection of the Dinokeng lions. Lions selected lower elevation and gentler slope either immediately after release or after initial exploration in the environment. Our results are in line with other studies on large carnivores (Dickson and Beier 2006; Sherpard and Whittington 2006; Abade et al. 2014), suggesting that lions selected landscape features that facilitate their movement in a new environment. However, the shift in selection by M2, from lower elevations in the dry season 2012 to higher elevations in the wet season 2012-13 after the territorial conflicts with M1 and translocation, suggests competitor avoidance, which might result in selection of less favourable resources (Winker et al. 1995; Vanak et al. 2013).

Lions showed an increasing tendency in selecting high tree cover over the course of the study. Previous studies on large felids suggest that high tree density improves prey ambushing success (i.e. prey catchability; Hopcraft et al. 2005; Loarie et al. 2013) and provides shelter from competitors and human disturbances (Spong 2002). However, after the third reintroduction, males reduced their selection for high tree cover while females chose to avoid high tree cover. Such behavioural changes may have been triggered by the needs for greater visibility to detect the newly introduced females; to avoid territorial conflicts among females and to increase mating opportunities of males (McComb et al. 1994; Mosser and Packer 2009). A similar response was also apparent in the pattern of home range utilization, with males expanding their home ranges to the home ranges of the newly introduced females, while the previously released females shifted their home ranges away (Chapter 4). Alternatively, as prey is known to adjust their movement and range use pattern in response to reintroduced predators (Creel et al. 2005; Kauffman et al. 2007), it is also possible that the prey had responded to the predation risk by avoiding dense tree cover over time, effecting a change in habitat selection of lions. However, this suggestion cannot be tested without further studies of the habitat selection of the prey species.

Lions selected areas further away from rivers but closer to dams. Water availability influences predator distribution indirectly by attracting prey (Spong

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2002; Valeix et al. 2010; Davidson et al. 2013). Although both rivers and dams are perennial water sources in DGR, most sections of the rivers are narrow with no conspicuous foot-slopes. On the contrary, all natural and artificial dams in the reserve are easily accessible to herbivores. Prey were therefore more likely to acquire water from and concentrate near dams rather than rivers (S-W Yiu, personal observation), likely contributing to the lions' preference for dams instead of rivers. Similar pattern is known from Hwange National Park, Zimbabwe, where lions prefer areas close to waterholes (Davidson et al. 2012). In DGR, the largest dam in the reserve (0.43 km^2) was located at the centre of the lions' home range and this has not changed throughout the study period (Chapter 4). The surrounding vegetation is comprised of reed beds (*Phragmites australis*) and was used by lions for hunting, resting and hiding of their cubs (S-W Yiu, personal observation), suggesting the importance of the dam in affecting their habitat selection. A change from avoiding to selecting distances closer to rivers in 50% home ranges was found after the dry season 2013, during which lion prides were formed and mating was seen. It might reflect a search for breeding sites by the lions because woody riparian vegetation provides ideal covers for the protection of cubs before weaning (Schaller 1972; Packer and Pusey 1983).

The floodplains and riparian vegetation were selected by the lions over other types of vegetation, except in their 50% HRs from the wet season 2012-13 to the wet season 2013-14. Similar types of vegetation were preferred by lions in numerous studies elsewhere with reasons ascribed to high prey abundance in these vegetation (Spong 2002; Cozzi et al. 2013). The moist nature of the floodplain and river substrate supports the growth of grass species with high palatability (e.g. *Panicum maximum*, *Cynodon dactylon* and *Setaria megaphylla*) in the study site (Contour Project Managers 2009), resulting in good grazing capacity that could attract a high number of herbivores (Bailey et al. 1996; van Oudtshoorn 2012) and thus the lions. The reduction in selection for floodplains and riparian vegetation from the wet season 2012-13 coincided with the expansion of home ranges by the animals to other parts of the reserve (Chapter 4), suggesting that the lions were exploring the vegetation in new areas. M2 restricted its vegetation use to *Tarchonanthus camphorates* and *Boschia albitrunca* veld and *Vachellia tortilis* and *Combretum apiculatum* veld within the dry season 2012 50% HR exclusively. Both

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are dense vegetation types that could provide refuge for the surviving individual, after the other member of the coalition was killed by M1. During that same period, M2 avoided the floodplains and riparian vegetation types within its 95% HR, which were selected by M1. This suggests that M2 was avoiding further territorial conflicts with M1 by changing its vegetation selection patterns, a behaviour commonly observed in sympatric competitors (Durant 1998; Fedriani et al. 2000; Vanak et al. 2013).

Resource selection of lions in response to human disturbances differed between sex, group, and spatial scale. Males were in general more tolerant to higher density of roads and distance closer to buildings than females, except for M2 which avoided the buildings increasingly over time. As males increase their fitness by maximising mating opportunities and females by maximising offspring survival (Clutton-Brock 1991, 2007; Møller and Thornhill 1998; Wade and Shuster 2002), female lions are more risk sensitive than males (McComb et al. 1994; Mosser and Packer 2009). They are likely to avoid human disturbances, often perceived as a form of predation risk (Frid and Dill 2002; Beale and Monaghan 2004), to a greater extent than males. Results also showed a scale dependent selection and individual differences. M1 selected higher road density within their 50% home range than within their 95% home range, while the opposite was true for M2. Individual behavioural characteristic is known to affect the responses of animals to the presence of humans (Martin and Réale 2008; Dingemanse et al. 2010). Habitat selection, including selection for roads, may also vary across spatial scales (Anderson et al. 2005; Boyce 2006; Jiang et al. 2009). Selection for low road density within the large scale 95% home range has likely allowed M1 to utilise higher road density within the 50% home range. On the contrary, M2 might have been more risk sensitive and therefore chose to stay in areas with low road density in the 50% HR where it spent most of the time.

Territorial conflicts and new introductions had a significant impact on the habitat selection of the DGR lions. F1 and M2 selected areas with low predicted probabilities of occurrence of their intrasexual competitors, after the competitors were introduced or had killed a group member. Also, all lions from the first release selected areas with high predicted probabilities of occurrence of lions from the second release after the latter were killed by M1. This selection indicates that lions

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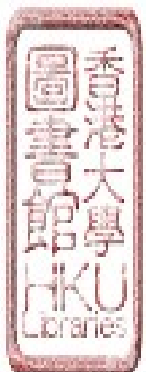
intensified the use of the areas that had previously been used by their intrasexual competitors after the latter was eliminated. The need for males to maximise mating opportunities and females to maximise survival of their young often leads to intense intrasexual competition (Clutton-Brock et al. 2006; Rosvall 2011). Competition between lions could be fatal due to their strong territoriality and aggressiveness towards intruders (McComb et al. 1994; Heinsohn and Packer 1995) and their intrasexual conflict in lions can lead to the expansion of the home range of the dominant individuals and avoidance behaviour by subordinates (Funston et al. 2003; Mosser and Packer 2009); a pattern well illustrated by our study. Contrary to our expectation, M1 selected areas with lower predicted probabilities of occurrence of females from the third release. The overlap of home ranges between this male and the females was large (Chapter 4), suggesting a scale dependent response to potential mates by the males.

Limited attempts have been made to understand the environmental determinants of the third order habitat selection of large carnivores (Davidson et al. 2012; Vanak et al. 2013), especially reintroduced animals. Our findings demonstrate that the third order habitat selection of reintroduced lions differ between home range scales and the pattern changes consistently through time, suggesting that the reintroduced animals were exploring and learning the landscape features as they were adapting to the new environment. Lions seemed to prefer areas with landscape features that facilitate movements and support high prey availability and accessibility. However, competition had large impacts on individual habitat selection, which could lead to subordinate individuals selecting suboptimal resources. There are considerable individual variations in resource selection patterns, including the response of lions to human disturbances. Our study suggests the importance of considering not only the spatial and temporal scales, but also individual differences and inter-group interactions when assessing animal habitat selection.
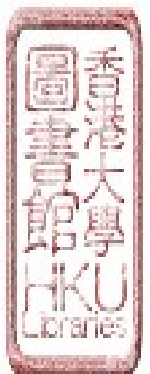
Chapter 6

Vigilance behaviour of blue wildebeest (*Connochaetes taurinus*) and Burchell's zebra (*Equus quagga burchellii*) in response to lion (*Panthera leo*) reintroductions

Introduction

Antipredator adaptation is a critical component that shapes predator-prey dynamics (Abrams and Matsuda 1997; Abrams 2000). Antipredator behaviour can be reactive: when prey responds to a predator encounter (Courbin et al. 2015; Martin and Owen-Smith 2016), or proactive: when prey responds to perceived predation risk (Creel et al. 2005; Creel et al. 2014). Predator creates a 'landscape of fear', where prey assess and adjust their behavioural responses to the level of predation risk (i.e. fear) in different areas (Laundré et al. 2001; Laundré et al. 2010). The levels of fear and thus the behavioural responses of prey are influenced by the topographies of the landscape of fear including predator encounter rate, predator lethality, effectiveness of antipredator strategies, survivor's fitness and marginal value of energy, which in turn, are affected by environmental factors (Brown 1999; Laundré et al. 2001). Behavioural changes of prey resulting from the fear of predation are energetically costly and typically represent a trade-off in fitness (Lind and Cresswell 2005). Elk (*Cervus elaphus*) was found to have shifted their habitat use and increased group size and vigilance in response to the landscape of fear created by wolves (*Canis lupus*) in Yellowstone National Park, which has resulted in a reduction in diet quality of elk (Laundré et al. 2001; Fortin et al. 2005; White et al. 2012). An understanding of antipredator behaviour is therefore critical for assessing non-lethal impacts of predator on prey fitness.

Behavioural strategies against predators are broad and diverse. The most readily studied and documented proactive strategies, in both marine and terrestrial ecosystems, are resource selection, group formation and vigilance (Krause and Godin 1994; Treves 2000). Vigilance behaviour increases the chance of prey to detect predators (Bednekoff and Lima 1998; Beauchamp 2015). It is therefore a commonly used behavioural indicator for predation risk impact assessment (Brown and Kotler 2004; Creel et al. 2014). Vigilance behaviour is assumed to be performed
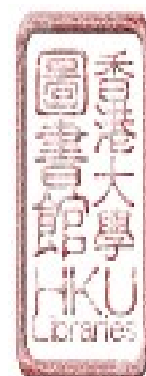
at the expense of foraging time and thus implies a trade-off in food intake rate (Houston et al. 1993; Illius and Fitzgibbon 1994). However, Fortin et al. (2004b) suggest that animals should be able to maintain their food intake rate because of their abilities to chew while being vigilant, something which has been rarely addressed in vigilance studies. Food intake rate is limited by the time required to search and handle (chewing, cropping and swallowing) food (Spalinger and Hobbs 1992). When food intake is handling-limited, i.e. the next bite can only be taken after the current bite is chewed, the chewing time can be used for other activities including vigilance, with minimal foraging cost (Fortin et al. 2004a, b). It is therefore possible to distinguish between two types of vigilance behaviour: routine vigilance, when an animal monitors the environment while chewing during their spare time; and induced (intense) vigilance, when it ceases feeding and responds to external stimuli (Blanchard and Fritz 2007). Routine vigilance is used for both social monitoring and threats detection while intense vigilance serves solely for the latter purpose (Beauchamp 2015). One study that applied this definition has found differences in the response between routine and intense vigilance of impala (*Aepyceros melampus*) and zebra (*Equus quagga*) to the presence of lions (*Panthera leo*) (Périquet et al. 2012). It shows the importance of distinguishing vigilance types when assessing the impacts of predation risks, which is rarely addressed in previous studies.

Various physiological and environmental factors have been identified which affect prey vigilance behaviour, e.g. reproductive status, group size, distance to group members, vegetation density and structure (Burger and Gochfeld 1994; Frid 1997; Burger et al. 2000; Whittingham et al. 2004; Li et al. 2009); yet, limited studies have related the factors to the landscape of fear topographies and tested their relative importance in influencing prey vigilance behaviour under actual and perceived (predicted) predation risk (Whittingham and Evans 2004; Heithaus and Dill 2006). Previous studies have shown contrasting influences of the two types of predation risk on the movement and habitat use of prey (Frair et al. 2005; Kittle et al. 2008), but few studies have examined this effect on vigilance behaviour.

There has been an increase in large carnivore reintroductions in small (< 1000 km^2) wildlife reserves in South Africa due to the fast growing tourism industry in the country (Hayward et al. 2007a, b; Di Minin et al. 2013). Large carnivores are

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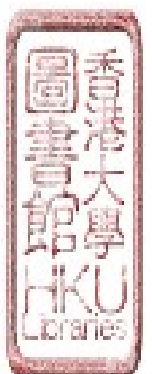
often extirpated before their introductions in these reserves, including the site of this study, resulting in a naïve prey population (Berger et al. 2001; Gittleman and Gompper 2001). The impacts of predator reintroductions on prey population could therefore be severe the prey are inexperienced in predator avoidance and assessment of predation risks (Berger et al. 2001). In Scandinavia, moose (*Alces alces*) have shown no behavioural adjustments after wolves have recolonized the area for more than 20 years (Sand et al. 2006), resulting in a high predation rate. On the contrary, a significant increase in vigilance of impala and blue wildebeest (*Connochaetes taurinus*) was observed in a South African reserve within one year of lions and cheetahs (*Acinonyx jubatus*) introductions (Hunter and Skinner 1998). Since the reserves in South Africa are entirely fenced, prey are unable to avoid predation by moving outside the reserve and might therefore rely more heavily on vigilance behaviour as an antipredator strategy (Tambling and Du Toit 2005; Hayward and Kerley 2009); it makes vigilance behaviour a suitable indicator for assessing the potential adverse effects of predator reintroductions on prey.

In this chapter, I examined the impacts of reintroduced lions on the vigilance response of blue wildebeest and Burchell's zebra (*Equus quagga burchelli*). I focus on wildebeest and zebra because these two species are important prey species for lions (Hayward and Kerley 2005). I quantified the landscape of fear by defining 1) two types of predator encounter rates using lions home range utilisation (actual rate) and resource selection functions (predicted rate); 2) predator lethality using parenthood, tree density, distance to cover and nearest-neighbour and position in the herd; 3) effectiveness of vigilance using grass height and herd size; and 4) marginal value of energy using season. The effects of these topographic features on the percentage of time spent on routine and intense vigilance by the two prey species were tested using a priori modelling approach. I also tested the interactive effects between actual and predicted predator encounter rates and that between actual predator encounter rate and season and herd size, because an animal might respond to a particular environmental cue in a lesser degree when other factors have already provided safety or when an animal is under nutritional stress (Frid 1997). I expected vigilance to increase when 1) predator encounter rates were high, i.e. the animal was within the home range of the lions or in areas with high predicted probabilities of lion occurrence; 2) predator lethality was high as indicated by the presence of

calf, high tree density, or when the animal was closer to cover, further away from herd member or at the edge of the herd; 3) effectiveness of vigilance was low with an increase in grass height or decrease in herd size; and 4) marginal value of energy decrease during dry season when forage quality was low.

Material and methods

Data collection

The study in this chapter was conducted from July 2012 to September 2013. Random transects were driven in the reserve at 20-30 km/h within three hours of sunrise and sunset, when predators were still mostly active (Hayward and Hayward 2006; see also Chapter 3). When feeding herds of wildebeest and zebra were located, I switched off and parked the vehicle at a spot which provided a view of most of the herd members. Wildebeests or zebras that have a nearest-neighbour distance of less than 100 m were defined as in the same herd. To eliminate any possible effects of the presence of other species (Schmitt et al. 2016), data was collected from single species herds only. To allow for the animals to habituate to the presence of the research vehicle, five minutes were used for habituation time before I started collecting data. I used focal animal sampling to collect behavioural data on randomly selected females in each herd. Each focal sample lasted five minutes, or until the focal animal was no longer visible. Observations less than four minutes were discarded. Five minutes were decided as habituation time and observation duration because it was the average amount of time needed to minimizing vigilance directed towards the research vehicle, and maximum amount of time allowed for observation before the herd moved off. During each focal observation, I recorded the duration and type of each vigilant bout. An animal was defined as being vigilant when the head was kept above its shoulder while standing still (Hunter and Skinner 1998) and I distinguished between two types of vigilance: intense vigilance, when the animal was exclusively scanning the environment without any chewing, and routine vigilance, when the animal was chewing while being vigilant (Periquet et al. 2012; Beauchamp 2015). I also recorded the reproductive status of the focal animal (with or without a calf following within 5 m), its distance to the nearest cover (0-5, 6-10, 11-50, 51-100 or 101-500 m), position in the herd (centre or edge), distance to the nearest neighbour (0, 1, 2-5, 6-10 or >10 body length) and grass
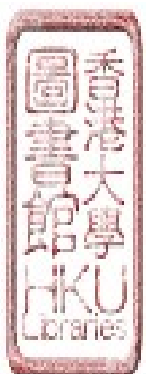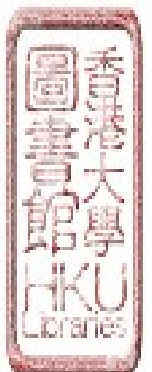
height (below ankle, below belly or below shoulder) (Table 6.1). In addition, I collected variables related to the herd observed: date, time, GPS location of the research vehicle, compass bearing of the herd from the vehicle, distance from the vehicle, herd size (calves, juveniles and adults of both sexes included) and tree density in the area (0-20, 21-40, 41-60, 61-80, 81-100%) (Table 6.1). To prevent pseudo-replication, transects were driven in different parts of the reserve for sunrise and sunset survey sessions in the same day, and data was collected from each individual only once within each session (Li et al. 2008). I picked focal animals until individual identifications were no longer possible due to herd movement, or when the herd moved away. In total I collected 105 observation samples from wildebeests and 106 from zebras.

Data analyses

For each focal observation I calculated the proportion of time the animal spent on intense and routine vigilance behaviour. To examine the effects of the landscape of fear on the vigilance behaviour of wildebeest and zebra, I categorized 10 variables into the four landscape of fear topographies according to Brown (1999): predator encounter rate, predator lethality, effectiveness of vigilance and marginal value of energy (Table 6.1). Actual predator encounter rate ('risk' from now on) was defined from the seasonal home ranges of lions that I constructed in another study using T-Local Convex Hull method (see Chapter 4; Lyons et al. 2013): areas within 95% home ranges were defined as high risk areas while areas outside the home ranges were defined as low risk areas. Predicted predator encounter rate (continuous variable, 'RSF' from now on) was derived from probability of occurrence maps predicted from the resource selection functions (GLMM) used to model lions space use (see Chapter 5; Manly et al. 2007). Maps were predicted for the dry season 2012, wet season 2012-13 and dry season 2013 using the raster calculator in ArcGIS 10.2 and the equation (Manly et al. 2002):

$$P = \frac{e^{a+bx_1+bx_2+\cdots+bx_\infty}}{1 + e^{a+bx_1+bx_2+\cdots+bx_\infty}}$$

Where *P* is the predicted probability of the lions, *a* is the intercept and *b* is the coefficient of each independent variable x extracted from the seasonal RSF built for the lions (Appendix C, Fig. C-1). To associate each observation to a level of

predator encounter rates, I calculated the GPS location of the focal herd using the observer GPS locations and compass bearing collected from the field, and overlaid these locations on the actual and predicted predator encounter rate maps of the corresponding season in ArcGIS 10.2 (ESRI, Redlands, Calif.). The other variables were all collected in the field during focal observations.

Using an information-theoretic approach (Burnham and Anderson 2002), I built a set of 14 a priori beta regression models (generalized linear model) with logit links in R3.2.3 using R package "betareg" (Cribari-Neto and Zeileis 2009). Beta regression was used because the independent variable, vigilance proportion, has a beta distribution with continuous values in the standard unit interval (0, 1) (Cribari-Neto and Zeileis 2009). All of the models included at least one variable from each of the landscape of fear topography category (Table 6.1). Variables that described similar ecological effects were not included in the same model (e.g. position in herd and distance to nearest-neighbour; table 6.1), except for the global model which included all independent variables (Creel et al. 2014). I also included the interactions between actual and predicted predator encounter rate, actual predator encounter rate and season, and actual predator encounter rate and herd size when building the models (Frid 1997). Multi-collinearity between independent variables was tested using the variance inflation factor (VIF) with a cut-off value of 10 (O'Brien 2007). The corrected Akaike information criterion (AICc), delta AICc (ΔAICc) and Akaike weight (ω) for each model were computed and compared. I employed the multi-model inference approach to obtain the final model, by selecting the models with a summed $\omega \geq 0.95$ and computing the average model parameters weighted by the Akaike weights of the selected models (Burnham et al. 2011). R^2 values were used to assess the goodness of fit of the models (Burnham and Anderson 2002; Grueber et al. 2011).

Table 6.1 Independent variables and levels of the variables used in vigilance behaviour modelling for blue wildebeest and Burchell's zebra in Dinokeng Game Reserve.

"Landscape of Fear" topography	Variable
Predator encounter rate	Actual rate - Risk: low (reference level), high; Predicted rate - RSF: continuous
Predator lethality	Parenthood (presence of calf): yes, no; Tree density (%): 0-20 (reference level), 21-40, 41-60, 61-80, 81-100; Distance to cover (m): 0-5 (reference level), 6-10, 11-50, 51-100, 101-500; Position in herd: centre (reference level), edge; Distance to nearest-neighbour (body length): 0 (reference level), 1, 2-5, 6-10, >10
Effectiveness of vigilance	Grass height: below ankle, below belly, below shoulder; Herd size: continuous variable
Marginal value of energy	Season: dry (reference level), wet

Results

Wildebeest

Model selection uncertainty was substantial for both intense and routine vigilance. In both cases, the value of Akaike weight for the best model was < 0.50, and the final averaged model involved six models that had a summed weight ≥ 0.95 (Table 6.2 and 6.3). The highest weighted intense vigilance model included both actual and predicted predator encounter rate. Models that included interactions between actual and predicted predator encounter rate and that between actual predator encounter rate and season were also selected for the final averaged model,
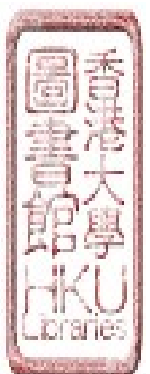
but they received <0.05 weight (Table 6.2). However, the 95% CIs of the log-odds for both risk and RSF included zero (Table 6.4), i.e. intense vigilance of wildebeest was not sensitive to either actual or predicted predator encounter rate although models that include both variables explained intense vigilance better than those including only one of the scales. Parenthood (with/without calf), tree density and position in the herd from the predator lethality category were included in the final model (Table 6.2). Intense vigilance was higher for animals that have a calf, and lower when tree density was at 21-40% than 0-20%, while the coefficient for position in the herd was insignificant (Table 6.4). Although herd size and grass height were both included in the final model (Table 6.2), wildebeest was sensitive to grass height only and have a higher intense vigilance when grass was below their belly than when it was below their knee (Table 6.4).

The six models averaged in the final routine vigilance model included similar variables to those in the intense vigilance model, but the animals responded differently to the variables. The final model included both actual and predicted predator encounter rate (Table 6.3), but response was significant for actual predator encounter rate only and routine vigilance was higher in low risk areas (Table 6.5 and Fig. 6.1d). Routine vigilance was also sensitive to grass height in the effectiveness of vigilance category in which vigilance was found to decrease with an increase in grass height (Table 6.5 and Fig. 6.1b), and to season in the marginal value of energy category in which vigilance was significantly higher in dry season than in wet season (Table 6.5 and Fig. 6.1d).

Table 6.2 A priori model set for modelling intense vigilance response of wildebeest to features of landscape of fear topography in Dinokeng Game Reserve and the model fit showing ΔAICc scores, Akaike weights (ωi) and R-squared (R^2) values. * indicates the model was selected for model averaging.

Model	df	ΔAICc	ωi	R^2
*Vigilance ~ Risk + RSF + TreeDensity + GrassHeight + Season	11	0.000	0.447	0.213
*Vigilance ~ RSF + Calf + Position + GrassHeight + HerdSize + Season	9	1.149	0.251	0.129
*Vigilance ~ Risk + RSF + Calf + Position + HerdSize + Season	8	2.068	0.159	0.089
*Vigilance ~ Risk + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	13	4.589	0.045	0.196
*Vigilance ~ Risk x Season + RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize	15	5.770	0.025	0.240
*Vigilance ~ Risk x RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	15	5.922	0.023	0.246
Vigilance ~ Risk x HerdSize + RSF + Calf + TreeDensity + Position + GrassHeight + Season	15	6.062	0.022	0.237
Vigilance ~ RSF + Calf + NN + GrassHeight + HerdSize + Season	12	6.942	0.014	0.143
Vigilance ~ Risk + RSF + Calf + NN + HerdSize + Season	11	7.315	0.012	0.110
Vigilance ~ Risk + RSF + Cover + GrassHeight + Season	12	9.870	<0.01	0.123
Vigilance ~ Risk + RSF + Calf + TreeDensity + Cover + Position + NN + GrassHeight + HerdSize + Season	23	16.971	<0.01	0.310
Vigilance ~ Risk x RSF + Calf + Cover + NN + Grassheight + HerdSize + Season	19	19.293	<0.01	0.214
Vigilance ~ Risk x HerdSize + RSF + Calf + Cover + NN + GrassHeight + Season	19	21.287	<0.01	0.188
Vigilance ~ Risk x Season + RSF + Calf + Cover + NN + GrassHeight + HerdSize	19	21.300	<0.01	0.187

Table 6.3 A priori model set for modelling routine vigilance response of wildebeest to features of landscape of fear topography in Dinokeng Game Reserve and the model fit showing ΔAICc scores, Akaike weights (ωi) and R-squared (R^2) values. * indicates the model was selected for model averaging.

Model	df	ΔAICc	ωi	R^2
*Vigilance ~ Risk + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	13	0.000	0.438	0.311
*Vigilance ~ Risk + RSF + Calf + Position + HerdSize + Season	8	1.595	0.197	0.230
*Vigilance ~ Risk + RSF + TreeDensity + GrassHeight + Season	11	2.153	0.149	0.261
*Vigilance ~ Risk x RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	15	3.468	0.077	0.318
*Vigilance ~ Risk + RSF + Calf + NN + HerdSize + Season	11	4.308	0.051	0.268
*Vigilance ~ Risk x HerdSize + RSF + Calf + TreeDensity + Position + GrassHeight + Season	15	5.098	0.034	0.313
Vigilance ~ Risk x Season + RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize	15	5.388	0.030	0.312
Vigilance ~ RSF + Calf + Position + GrassHeight + HerdSize + Season	9	6.525	0.017	0.185
Vigilance ~ Risk + RSF + Cover + GrassHeight + Season	12	9.782	0.003	0.241
Vigilance ~ RSF + Calf + NN + GrassHeight + HerdSize + Season	12	11.076	0.002	0.195
Vigilance ~ Risk x RSF + Calf + Cover + NN + Grassheight + HerdSize + Season	19	12.450	0.001	0.320
Vigilance ~ Risk x Season + RSF + Calf + Cover + NN + GrassHeight + HerdSize	19	14.932	0.000	0.323
Vigilance ~ Risk x HerdSize + RSF + Calf + Cover + NN + GrassHeight + Season	19	15.037	0.000	0.320
Vigilance ~ Risk + RSF + Calf + TreeDensity + Cover + Position + NN + GrassHeight + HerdSize + Season	23	22.544	0.000	0.321

Table 6.4 Averaged model coefficients for the intense vigilance response of wildebeest to features of landscape of fear topography in Dinokeng Game Reserve. Coefficients (β) are resented as log-odds, with associated standard errors (SE), confidence intervals, Z-values and p-values for each independent variable. * p < 0.05; ** p < 0.01.

Variable	β	SE	Confidence intervals	Z-value	p-value
Risk: high	0.024	0.237	-0.441, 0.489	0.102	0.918
RSF	1.022	0.581	-0.116, 2.160	1.760	0.079
Tree density: 21-40 %	-0.591	0.290	-1.160, -0.022	2.036	0.042*
Tree density: 41-60 %	0.299	0.272	-0.233, 0.831	1.101	0.271
Tree density: 61-80%	-0.083	0.288	-0.647, 0.481	0.287	0.774
Tree density: 81-100%	0.050	0.273	-0.484, 0.584	0.184	0.854
Grass height: below belly	0.457	0.218	0.029, 0.885	2.093	0.036*
Grass height: below shoulder	0.508	0.334	-0.147, 1.163	1.519	0.129
Season: wet	-0.011	0.208	-0.418, 0.396	0.053	0.957
Calf: yes	0.419	0.200	0.028, 0.811	2.100	0.036*
Position: edge	0.172	0.180	-0.181, 0.525	0.954	0.340
Herd Size	-0.003	0.008	-0.019, 0.012	0.420	0.674
Risk x Season: high x wet	0.381	0.455	-0.510, 1.272	0.838	0.402
Risk: high x RSF	-0.898	1.221	-3.292, 1.495	0.736	0.462

Table 6.5 Averaged model coefficients for the routine vigilance response of wildebeest to features of landscape of fear topography in Dinokeng Game Reserve. Coefficients (β) are resented as log-odds, with associated standard errors (SE), confidence intervals, Z-values and p-values for each independent variable. * p < 0.05; ** p < 0.01.

Variable	β	SE	Confidence intervals	Z-value	p-value
Risk: high	-0.666	0.235	-1.126, -0.206	2.836	0.005**
Calf: yes	-0.197	0.193	-0.575, 0.182	1.017	0.309
Tree density: 21-40 %	-0.030	0.276	-0.570, 0.511	0.108	0.914
Tree density: 41-60 %	0.441	0.286	-0.119, 1.002	1.543	0.123
Tree density: 61-80%	-0.109	0.285	-0.667, 0.449	0.383	0.702
Tree density: 81-100%	0.017	0.284	-0.539, 0.574	0.061	0.951
Position: edge	0.167	0.166	-0.157, 0.492	1.010	0.313
Grass height: below belly	-0.497	0.179	-0.849, -0.145	2.770	0.006**
Grass height: below shoulder	-0.832	0.336	-1.491, -0.174	2.477	0.013*
Herd size	-0.015	0.008	-0.030, 0.001	1.833	0.067
Season: wet	-0.502	0.234	-0.961, -0.043	2.143	0.032*
RSF	0.127	0.816	-1.473, 1.726	0.155	0.877
Risk: high x RSF	-1.488	1.077	-3.599, 0.622	1.382	0.167
NN: 1	0.150	0.249	-0.338, 0.637	0.602	0.547
NN: 2-5	-0.022	0.228	-0.469, 0.425	0.097	0.923
NN: 6-10	-0.197	0.282	-0.750, 0.356	0.698	0.485
NN: >10	0.619	0.319	-0.007, 1.245	1.939	0.053
Herd size x Risk: high	-0.008	0.015	-0.038, 0.021	0.560	0.575
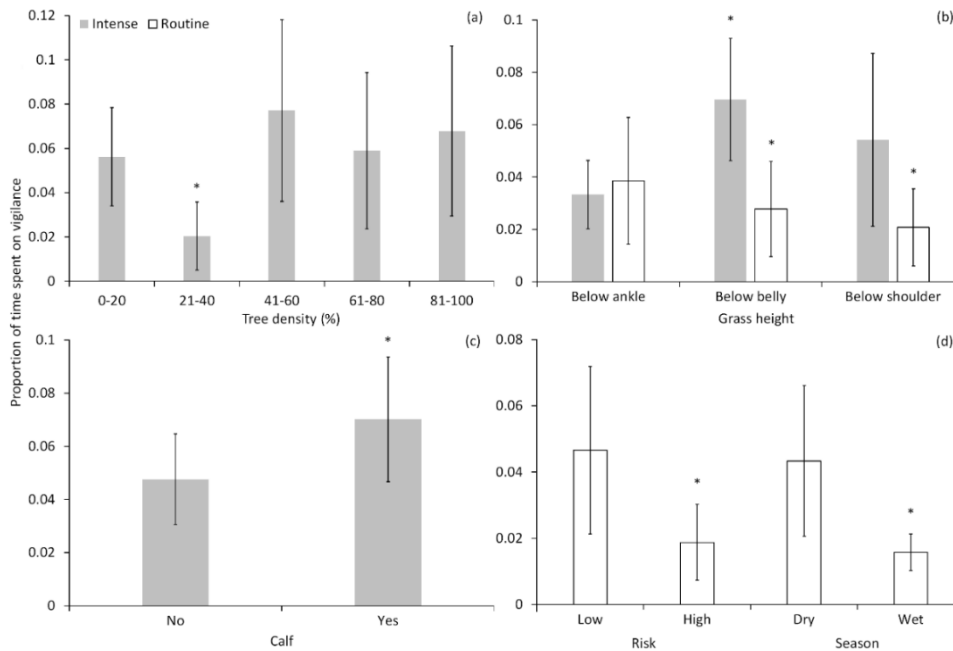
Fig. 6.1 Vigilance proportion (%) of wildebeest in Dinokeng Game Reserve, under the influence of (a) tree density, (b) grass height, (c) calf, and (d) risk and season, when the effects of other variables were controlled. Simple means and 95% confidence interval are presented in the graph. * indicates significant differences.

Burchell's zebra

For intense vigilance, two models have summed Akaike weight ≥ 0.95 (best model received > 0.93 weight) and were selected and averaged (Table 6.6). Both models include actual and predicted predator encounter rate without interaction terms. Intense vigilance was significantly different between levels of actual predator encounter rate, with higher vigilance in high risk areas compared to low risk areas (Table 6.7 and Fig. 6.2a). Parenthood (with/without calf), position in the herd and distance to nearest-neighbour from predator lethality category and herd size from effectiveness of vigilance category were included in the final model. However, zebra was sensitive to distance to nearest-neighbour only and had higher intense vigilance at 1 body length than at < 1 body length to the nearest herd member, but vigilance at distance greater than 1 body length was not significantly different than at < 1 body length (Table 6.7 and Fig. 6.2b).

Model selection for routine vigilance had higher uncertainty. The best model received < 0.50 weight and three models with summed Akaike weight ≥ 0.95 were

included in the final averaged model (Table 6.8). The final routine vigilance model included all variables that were included in the final intense vigilance model and one additional variable: distance to cover (Table 6.8). In contrast to intense vigilance, zebra has a higher routine vigilance in low risk areas compared to high risk areas (Table 6.9 and Fig. 6.2a). The animals were also found to have a significant increase in routine vigilance when distance to nearest cover increased from 0-5 m to 6-10 m (Table 6.9). However, results showed a trend of decrease in routine vigilance with an increase in distance to cover once the distance exceeded 10 m (Fig. 6.2c). Same as that of wildebeest, routine vigilance of zebra was higher in the dry season than in wet season (Table 6.9 and Fig. 6.2d).
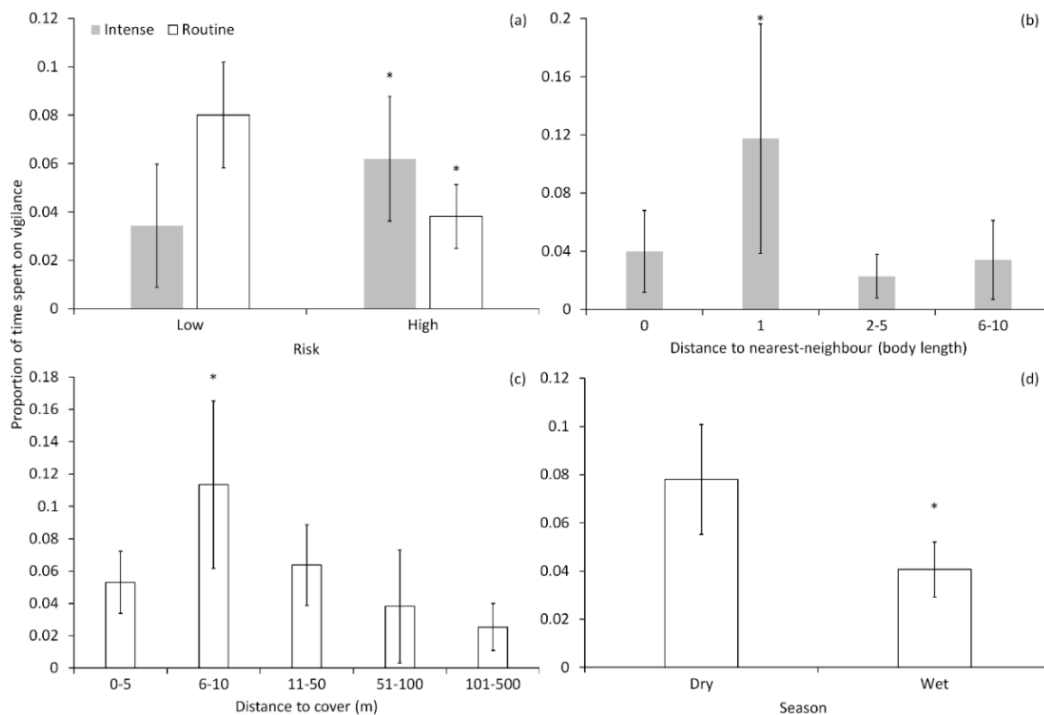
Fig. 6.2 Vigilance proportion (%) of zebra in Dinokeng Game Reserve, under the influence of (a) risk, (b) distance to nearest-neighbour, (c) distance to cover, and (d) season, when the effects of other variables were controlled. Simple means and 95% confidence interval are presented in the graph. * indicates significant differences.
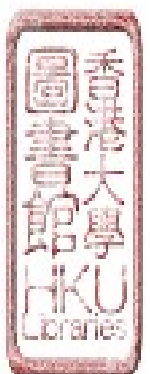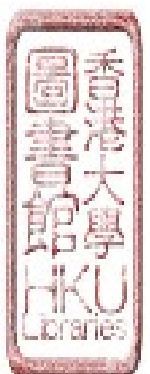
Table 6.6 A priori model set for modelling intense vigilance response of zebra to features of landscape of fear topography in Dinokeng Game Reserve and the model fit showing ΔAICc scores, Akaike weights (ωi) and R-squared (R^2) values. * indicates the model was selected for model averaging.

Model	df	ΔAICc	ωi	R^2
*Vigilance ~ Risk + RSF + Calf + NN + HerdSize + Season	10	0.000	0.929	0.217
*Vigilance ~ Risk + RSF + Calf + Position + HerdSize + Season	8	5.621	0.056	0.090
Vigilance ~ RSF + Calf + NN + GrassHeight + HerdSize + Season	12	8.910	0.011	0.160
Vigilance ~ Risk + RSF + Cover + GrassHeight + Season	12	12.563	<0.01	0.134
Vigilance ~ Risk + RSF + TreeDensity + GrassHeight + Season	12	13.899	<0.01	0.117
Vigilance ~ RSF + Calf + Position + GrassHeight + HerdSize + Season	10	14.015	<0.01	0.023
Vigilance ~ Risk x HerdSize + RSF + Calf + Cover + NN + GrassHeight + Season	18	14.866	<0.01	0.299
Vigilance ~ Risk x HerdSize + RSF + Calf + TreeDensity + Position + GrassHeight + Season	16	18.433	<0.01	0.215
Vigilance ~ Risk + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	14	19.200	<0.01	0.114
Vigilance ~ Risk x Season + RSF + Calf + Cover + NN + GrassHeight + HerdSize	18	19.489	<0.01	0.232
Vigilance ~ Risk x RSF + Calf + Cover + NN + Grassheight + HerdSize + Season	18	19.710	<0.01	0.238
Vigilance ~ Risk x RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	16	24.038	<0.01	0.125
Vigilance ~ Risk x Season + RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize	16	24.114	<0.01	0.120
Vigilance ~ Risk + RSF + Calf + TreeDensity + Cover + Position + NN + GrassHeight + HerdSize + Season	22	27.038	<0.01	0.247
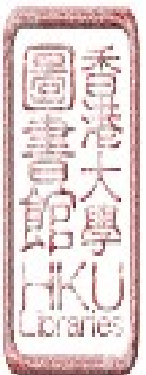
Table 6.7 Averaged model coefficients for the intense vigilance response of zebra to features of landscape of fear topography in Dinokeng Game Reserve. Coefficients (β) are resented as log-odds, with associated standard errors (SE), confidence intervals, Z-values and p-values for each independent variable. * $p < 0.05$; ** $p < 0.01$.

Variable	β	SE	Confidence intervals	Z-value	p-value
Risk: high	0.461	0.229	0.012, 0.909	2.013	0.044*
RSF	-0.344	0.446	-1.218, 0.530	0.771	0.441
Calf: yes	0.020	0.189	-0.350, 0.389	0.106	0.916
NN: 1	0.862	0.288	0.298, 1.426	2.996	0.003**
NN: 2-5	0.060	0.264	-0.458, 0.579	0.228	0.820
NN: 6-10	0.132	0.305	-0.467, 0.730	0.431	0.666
Herd size	0.005	0.014	-0.023, 0.033	0.360	0.719
Season: wet	-0.130	0.198	-0.519, 0.259	0.655	0.512
Position: edge	0.051	0.203	-0.347, 0.448	0.250	0.803

Table 6.8 A priori model set for modelling routine vigilance response of zebra to features of landscape of fear topography in Dinokeng Game Reserve and the model fit showing ΔAICc scores, Akaike weights (ωi) and R-squared (R^2) values. * indicates the model was selected for model averaging.

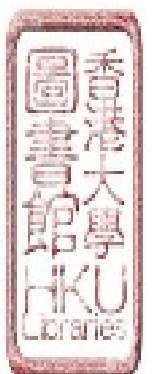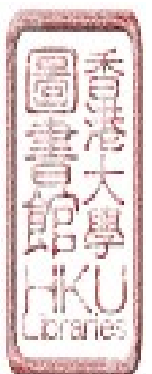| Model	df	ΔAICc	ωi	R^2
*Vigilance ~ Risk + RSF + Cover + GrassHeight + Season	11	0.000	0.460	0.202
*Vigilance ~ Risk + RSF + Calf + Position + HerdSize + Season	8	0.523	0.354	0.149
*Vigilance ~ Risk + RSF + Calf + NN + HerdSize + Season	10	2.214	0.152	0.184
Vigilance ~ Risk + RSF + TreeDensity + GrassHeight + Season	11	6.842	0.015	0.156
Vigilance ~ Risk x Season + RSF + Calf + Cover + NN + GrassHeight + HerdSize	17	8.718	0.006	0.258
Vigilance ~ Risk x HerdSize + RSF + Calf + Cover + NN + GrassHeight + Season	17	9.478	0.004	0.261
Vigilance ~ Risk + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	13	10.557	0.002	0.164
Vigilance ~ RSF + Calf + Position + GrassHeight + HerdSize + Season	9	10.782	0.002	0.080
Vigilance ~ RSF + Calf + NN + GrassHeight + HerdSize + Season	11	11.469	0.001	0.128
Vigilance ~ Risk x RSF + Calf + Cover + NN + Grassheight + HerdSize + Season	17	11.834	0.001	0.236
Vigilance ~ Risk x HerdSize + RSF + Calf + TreeDensity + Position + GrassHeight + Season	15	11.903	0.001	0.214
Vigilance ~ Risk x Season + RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize	15	14.029	0.000	0.179
Vigilance ~ Risk + RSF + Calf + TreeDensity + Cover + Position + NN + GrassHeight + HerdSize + Season	21	14.966	0.000	0.278
Vigilance ~ Risk x RSF + Calf + TreeDensity + Position + GrassHeight + HerdSize + Season	15	15.654	0.000	0.166
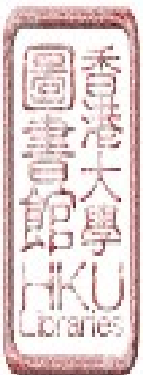
Table 6.9 Averaged model coefficients for the routine vigilance response of zebra to features of landscape of fear topography in Dinokeng Game Reserve. Coefficients (β) are resented as log-odds, with associated standard errors (SE), confidence intervals, Z-values and p-values for each independent variable. * p < 0.05; ** p < 0.01.

Variable	β	SE	Confidence intervals	Z-value	p-value
Risk: high	-0.556	0.192	-0.932, -0.180	2.899	0.004**
RSF	-0.053	0.405	-0.848, 0.741	0.132	0.895
Calf: yes	-0.174	0.158	-0.484, 0.135	1.104	0.269
Position: edge	0.173	0.172	-0.163, 0.510	1.011	0.312
Herd size	-0.003	0.012	-0.027, 0.021	0.272	0.786
Season: wet	-0.353	0.172	-0.691, -0.015	2.048	0.041*
NN: 1	-0.494	0.255	-0.993, 0.006	1.938	0.053
NN: 2-5	-0.200	0.213	-0.618, 0.217	0.940	0.347
NN: 6-10	-0.311	0.246	-0.793, 0.172	1.262	0.207
Cover: 6-10	0.715	0.219	0.287, 1.144	3.271	0.001**
Cover: 11-50	0.067	0.174	-0.274, 0.409	0.385	0.700
Cover: 51-100	0.453	0.473	-0.474, 1.380	0.957	0.339
Cover: 101-500	0.116	0.445	-0.755, 0.988	0.262	0.793
Grass height: below belly	0.028	0.170	-0.305, 0.362	0.165	0.869
Grass height: below shoulder	0.027	0.260	-0.483, 0.537	0.104	0.917
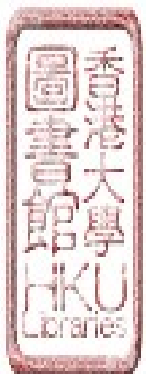
Discussion

Actual predator encounter rate influenced the intense vigilance of zebra but not wildebeest, with zebra increasing their intense vigilance in high risk areas. Species-specific results agree with Périquet et al. (2012) who found no effect of predation risk on the intense vigilance of impala but an increase in intense vigilance of zebra under a higher predation risk, and with Creel (2014) who showed varied vigilance response of five herbivore species to lion presence with wildebeest being the least responsive species. However, results were inconsistent with Wirsing et al. (2010)'s suggestion that prey species which have lower chances of surviving a predator encounter should have stronger proactive anti-predatory responses; wildebeest were expected to have greater response to predation risk due to their sedentary nature and smaller body size than zebra thus lower handling difficulties for predators (Woodward et al. 2005; Martin and Owen-Smith 2016). The lower intense vigilance response of wildebeest (similar to Creel et al. 2014 observations) might be explained by the use of other anti-predatory behaviour, such as aggregation (Fryxell et al. 2007). Herd size of wildebeest in DGR averaged 21 ± 14 (mean $\pm$ SD) compared to 11 ± 8 (mean $\pm$ SD) for zebra. Larger group size enhances dilution effect (lower probability of being predated upon per individual) and many-eyes effect (higher predator detection effectiveness with more vigilant group members), therefore lowering predation risk and the needs for individual vigilance (Lima 1995; Shi et al. 2011). Differences in vigilance response between wildebeest and zebra could also have resulted from a difference in prey naivety to a long extirpated predator (Sih et al. 2010; Mella et al. 2014; Carthey and Banks 2014), or prey preferences of lions, therefore, differences in predation pressure (Hunter and Skinner 1998; Hayward and Kerley 2005).

Routine vigilance of both species was higher in low risk areas compared to high risk areas. This is opposite to the effects of the actual predator encounter rates on intense vigilance. Routine vigilance differs from intense vigilance by incurring lower foraging costs, because the behaviour is performed during the spare time when the individual must finish chewing the current bite before the next bite can be taken, i.e. when animals forage in high quality patches and food intake rate is handling-limited (Fortin et al. 2004b; Blanchard and Fritz 2007). Predator is known to constrain habitat selection of prey and effect a reduction in their use of optimal

habitat (Ripple and Beschta 2004; Creel et al. 2005; Verdolin 2006). Being in a low risk area might have allowed the wildebeest and zebra to optimize foraging by selecting for and staying in high quality food patches, therefore, to have greater amount of spare time for routine vigilance. The decrease in intense vigilance by zebra in low risk area might also have contributed to an increase in spare time for chewing and routine vigilance. On the other hand, routine and intense vigilance are suggested to serve different purposes: routine vigilance functions for both predator detections and social monitoring while intense vigilance functions solely for threats detections (Périquet et al. 2012; Beauchamp 2015). The foraging cost of using intense vigilance for predator detection in low predation risk areas is high. Zebra and wildebeest might therefore be more likely to employ multifunctional routine vigilance in low risk areas for optimal foraging efficiency.
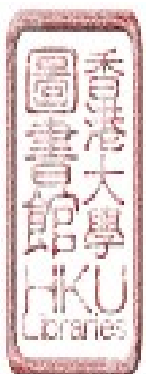
The lack in response to the predicted predator encounter rate for both species suggests a difference in prey perception of the two types of predation encounter rate. Studies in Ontario, Canada, have shown that direct predation risk from wolves (derived from GPS locations of wolves) had greater influence on resource selection of elk, white-tailed deer and moose than indirect predation risk (derived from landscape features associated with the presence of wolves) (Kittle et al. 2008). In Africa, browser species were found responding to both long-term (prediction of lion occurrence) and short-term (presence of lion in vicinity) predation risks by changing their space use patterns (Valeix et al. 2009). My findings provide evidence that actual predation risk is more important than predicted predation risk in influencing vigilance behaviour of prey. The learning and perception of predation risk by prey shape the predator-prey dynamics (Luttbeg and Schmitz 2000; Lima and Steury 2005). It is possible that wildebeest and zebra perceived the actual predator encounter rate, directly reflecting the frequencies of occurrence of lions, as a bigger threat than the predicted predator encounter rate, reflecting only the predicted probabilities of occurrence of lions, and therefore were sensitive only to the actual risk.

Wildebeest and zebra responded to different factors representing the predator lethality topography. In general, vigilance responses supported the hypothesis in Brown (1999): vigilance increased when the changes in environment indicate higher levels of predator lethality. Wildebeests with calves have higher intense

vigilance than those without. Females with calves are more vulnerable to predation, i.e. have higher predator lethality, and are observed to have higher vigilance across large mammalian herbivore species (Burger and Gochfeld 1994; Li et al. 2009). Wildebeest also show a reduction in intense vigilance with an increase in tree density from 0-20% to 21-40%, but vigilance increased again at tree densities above 40%. Zebra showed similar behavioural pattern in which more time was spent on routine vigilance when distance to cover increased from 0-5 m to 6-10 m, but vigilance decreased when distance exceeded 10 m. An increase in tree density and decrease in distance to cover both imply higher predator lethality as tree cover enhances lion ambushing success (Hopcraft et al. 2005; Loarie et al. 2013). This might explain the higher intense vigilance of wildebeest at tree density above 40%, but the reason for lower vigilance at tree density 21-40% is unclear. The same could explain the decrease in routine vigilance of zebra when distance to cover increased, in accordance with other studies (Burger et al. 2000; Beauchamp 2010). Also, zebra increased their intense vigilance when the distance to the nearest neighbour increased from zero to one. The stripped pattern on zebra coat provides motion camouflage for the animals when they move together as a herd during predator encounters (How and Zanker 2014; Hughes et al. 2014). An increase in distance from herd members likely reduces the effects of camouflage and increases predator lethality, therefore resulting in higher vigilance.

The effectiveness of vigilance influenced the behaviour of wildebeest only. Intense vigilance of wildebeest increased with grass height, but an opposite trend was observed for routine vigilance. Tall vegetation obstructs the view of the animals and reduces the effectiveness of vigilance (Valeix et al. 2009; Pay et al. 2012), which has likely led to the increase in intense vigilance to maximize predator detection. Similar behavioural patterns have been reported on other species of antelope, birds, and even rodents (Martella et al. 1995; Burger et al. 2000; Ebensperger and Hurtado 2005). However, an increase in intense vigilance could result in a reduction in foraging time and spare time for other behavioural activities including routine vigilance (Fortin et al. 2004b; Blanchard and Fritz 2007). This might explain the decrease in routine vigilance by wildebeest when grass height and intense vigilance increased. Also, wildebeest is known to prefer open areas with short grasses, or "grazing lawn", where grass species are of high palatability

(Cromsigt and Olff 2008; Martin and Owen-Smith 2016). In DGR, these grazing lawns are usually predominated by the highly nutritious species *Cynodon dactylon* where wildebeest were often observed to forage (Contour Project Managers 2009). High food quality in these areas with short grass height has likely resulted in handling-limited foraging (Farnsworth and Illius 1998), and therefore a greater amount of spare time for the wildebeest to perform routine vigilance. At the same time, high food quality increases intra-specific food competition and therefore might result in the increase in routine vigilance for monitoring of herd members (Beauchamp 2008).

I failed to find any effects of herd size (representing the effectiveness of vigilance category) on the vigilance behaviour within each species. Effects of herd size on vigilance behaviour are inconsistent between studies. Creel et al. (2014) suggested a complimentary relationship between vigilance behaviour and group formation: bigger group size leads to low level of vigilance because of the many-eyes and dilution effects; which has been frequently reported and already discussed (Burger et al. 2000; Childress and Lung 2003; Djagoun et al. 2013). On the other hand, studies which found no herd size effects suggested that larger group attracts predators more easily and increases intra-group competition for food (Smith and Cain III 2008). This could increase the needs for the animals to be vigilant for predator detection and social monitoring, therefore diminishing the overall effect of group size on vigilance (Ale and Brown 2007; Beauchamp 2008; Dalerum et al. 2008).

Routine vigilance of both species was higher in the dry season than in the wet season. Similar seasonal effects were reported by Périquet et al. (2012) but on intense vigilance. Results were different from my expectation: lower routine vigilance was expected in the dry season because of the reduction in spare time resulting from a decrease in food quality and quantity (lower marginal value of energy; Brown 1999) thus search-limited foraging, i.e. time needed for searching the next bite is greater than time needed for chewing (Spalinger and Hobbs 1992; Illius and FitzGibbon 1994). In fact, a decline in bite rate or size in dry season has been found in different grazers, e.g. zebra, bighorn sheep (*Ovis canadensis*) and Thomson's gazelles (*Gazella thomsoni*) (Bradbury et al. 1996; Ruckstuhl et al. 2003; Havarua et al. 2014). According to optimal foraging theory, however, herbivores

should become less selective by increasing bite rate and bite size during non-growing season in order to maximize their ingestion rate and food intake (Barreto and Herrera 1998; Ego et al. 2003; Macandza et al. 2004). Fibre content of grasses is also higher in dry season than in wet season, which lowers the efficiency and lengthen the time of chewing (Georgiadis and McNaughton 1990; Knox et al. 2011). These would lead to an increase in spare time for routine vigilance and likely explains the results in the current study.

This study represents a first attempt to define and tested the effects of landscape of fear topographies on prey vigilance behaviour using related environmental factors. Findings suggest species-specific response to the landscape of fear established by a reintroduced predator. Wildebeest and zebra responded to different factors representing the topographies and their responses differed between vigilance types. Results in general agree with Brown (1999): vigilance increases when the level of perceived predation risk, i.e. fear, increases; and with Blanchard and Fritz (2007): intense vigilance responses are strongly related to the necessity in predator detection while routine vigilance is influenced by the underlying amount of time spared from foraging under different environmental conditions. It is therefore important for future studies to distinguish between the two vigilance types. An increase in intense vigilance behaviour of zebra in high predation risk areas indicates a trade-off between foraging and predator avoidance, and should be further investigated to identify potential cascading effects on prey fitness (Lima 1995; Shi et al. 2011).

Chapter 7

General discussion and management implications for carnivore reintroduction in small reserves

The spatial behaviour of reintroduced lions as shown in the current study highlights the importance of long-term post-release monitoring in carnivore reintroductions. Home range establishments of lions, as defined by a stabilization in home range expansions, could take more than 3 years after release (Chapter 4). During this process of establishment in a new environment, lions displayed diverse movement and habitat selection patterns despite continuous increases in home range sizes for all groups. The patterns also changed over time with clear evidence of exploratory movements during early stages of release, including post-release dispersal (Chapter 3), high rates of home range expansions with some of the areas visited only once by the lions (Chapter 4), and shifts in resource selection patterns over time (Chapter 5). The animals were likely learning the locations of resources during the stage of exploration, before deciding on their locations of settlement and preferences for resources. Time taken for the movement and habitat selection patterns to stabilize varied, with early post-release movements stabilizing within a season after introduction (Chapter 3) but the expansion of home ranges and resource selections stabilizing either after more than a season or not stabilizing over the entire study period (Chapter 4 & 5). It is therefore essential to monitor reintroduced carnivores for years in order to understand the processes of their establishment. This type of long-term post-release monitoring is usually lacking in carnivore reintroductions projects (Hayward et al. 2007a; Hunter et al. 2007). The study also supports the potential of using spatial behavioural patterns in assessing establishment success; as suggested by Berger-tal and Saltz (2014) in their review using movement patterns of reintroduced Persian fallow deer (*Dama mesopotamica*) and the Arabian oryx (*Oryx leucoryx*) in Israel as examples.

Intra-specific interaction has a crucial role in shaping the behavioural dynamics of lion populations, which are influenced by lion social structure (Funston et al. 2003; Mosser and Packer 2009). Interactions between groups in this study were in turn affected by management decisions, especially on the order of release and locations of release sites. In DGR, the lions from the first and second
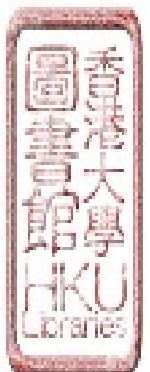
introductions were released at the same location one month apart. This practice had led to intense competition between different groups, resulting in the death of a male during territorial conflict within one season after its release (Chapter 3). Apart from direct confrontation, restriction of movement and habitat selection was also found in the lions released later. These lions had lower movement rates and dispersed further away from the release site than those from the earlier release (Chapter 3), and they avoided the home ranges of the latter (Chapter 4). The death of a group member had also resulted in the surviving member shifting its home range (Chapter 4), selecting for areas with lower predicted probabilities of occurrence of its competitors and avoiding the vegetation types selected by its competitors (Chapter 5). On the other hand, the lions from the first release had the largest home range sizes over the study period, and had taken over the home ranges of the lions that were killed in territorial conflicts and selected for a high predicted probability of occurrence of the latter (Chapter 4 & 5). Results suggest that the lions released later had been placed at a disadvantaged position in comparison with those released first, which could lead to sub-optimal movements and selection for sub-optimal resources, particularly during exploratory stage (Steffens et al. 2005; Roe et al. 2010; Bennett et al. 2012). Multiple releases of carnivores in reintroductions should be planned at different locations to minimise the intensity of competition during early stages of release, especially in small reserves, when it is the most critical time period for the animals to explore and learn the environment.

The significance of release locations was also shown by the locations of lion total home ranges over the entire study period. All of the animals had their core home ranges centred around the area of their release and frequently revisited those areas (Chapter 4), despite early post-release dispersal away from the release site for some of the groups (Chapter 3); other groups returned to their area of release even within early post-release period (Chapter 3). The male that was translocated to another part of the reserve during the study continued to utilise the home range it established at the area of release after the translocation (Chapter 4). On the other hand, the continuous increase in home range sizes of the lions indicate that the animals expanded their home ranges outwards from the locations of release, instead of relocating elsewhere (Chapter 4). Home range establishment and utilisation in relation to release locations were rarely addressed in previous studies (Preatoni et
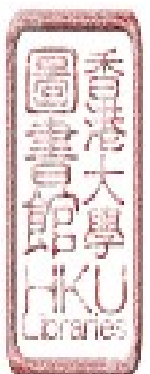
al. 2005; Hayward et al. 2009; Wauters et al. 2015). For future reintroductions, the location of release sites should be planned in areas with high quality and quantity of resources, such that the animals could gain quick access to resources critical for fitness and survival and could return to these areas after initial explorations.

In fact, the release sites in this study were located either next to the biggest dam in the reserve or close to river, which are surrounded by reed beds and riparian vegetation types. Results in Chapter 5 have proved that lions selected for these vegetation types, and the selection was likely due to the associated high prey availability and accessibility. Apart from access to prey, studies on resource selection of lions seldom address other landscape features (Hopcraft et al. 2005; Balme et al. 2007; Davidson et al. 2012). I found a selection for low topographic roughness (low elevation and gentle slope) and low human disturbances (low road density and distance away from buildings) by the lions with the latter further supported by their movements away from buildings during early stages of release (Chapter 3 & 5); these might potentially be used as guidelines for selecting appropriate release locations for lion reintroductions.

Another management intervention that had likely also influenced the behaviour of the lions is the application of contraceptives. This directly resulted in the death of 2 females, which were killed by the males possibly due to their unreceptivity and thus rejection of mating. It might have also contributed to the similar home range sizes between males and females (Chapter 4), disagreeing with most studies in which males have more extensive movement and space use in order to maximise mating opportunities (Loveridge et al. 2009; Mosser and Packer 2009). Sexual selection is a key driving force in animal behaviour and population dynamics (Cox and Le Boeuf 1977; Krebs and Davies 1997). The recent avocation of using contraceptives for reintroduced lion population control in small reserves should be carefully assessed and considered (Ferreira and Hofmeyr 2013; Miller et al. 2013), to prevent disruption of natural ecological and behavioural processes that could affect the fitness and survival of the animals and therefore reintroduction success.

The current study also addresses the importance of scales in understanding animal spatial behaviour. Ecological processes operate at different spatial scales,

therefore the behavioural responses of animals to environmental changes are scale-dependent (Anderson et al. 2005; Davidson et al. 2012). As mentioned already, even though all lions expanded their home ranges (Chapter 4), their movement and habitat selection patterns differed (Chapter 3 & 5). Individual habitat selection also differed between spatial levels, e.g. the male lions expanded their home ranges to cover the ranges of the females from the third release (seond order habitat selection) but did not selected for areas with high predicted probabilities of the females within the home ranges (third order habitat selection) (Chapter 4 & 5). On the contrary, the females and the surviving male from the group with one of the members killed did not only avoid the home ranges of their same-sex competitors, but also selected for areas with low probability of occurrence of their competitors (Chapter 4 & 5). Differences were found even within the third order habitat selection; the males selected for different levels of human disturbances in their 50% and 95% home ranges (Chapter 5).

One of the biggest challenges in large carnivore reintroductions in South Africa is the fencing of reserves. Fencing prevents human-wildlife conflicts, however, fences can also interfere with natural ecological processes by restricting animal movement (Hayward and Kerley 2009). Particularly for small reserves, fencing could intensify intra-specific competitions in long-range animals including lions and increase predation pressure on their prey (Miller et al. 2013; Miller and Funston 2014). Interestingly, the home ranges of the lions in this study remained small (<50 % of the reserve area; Chapter 4), even though the animals were continuously expanding their home ranges. It was likely due to the general high prey abundance in the reserve, but unfortunately prey density data in relation to lion home ranges were not available in this study to support the speculation. Also, some areas of the reserve (southwest) remained unused over the whole study period. Together with the stabilisation in resource selection patterns within home ranges (Chapter 5), results indicate that fencing did not restrict the movement and space use of the lions. In fact, if the release site for the second reintroductions had been planned in the unused area, the inter-group territorial conflicts and the death of the 3 lions might have been avoided.

In Chapter 6, the vigilance behaviour of prey suggests that the reintroduction of lions had created a landscape of fear (Brown 1999; Laundré et al. 2010).
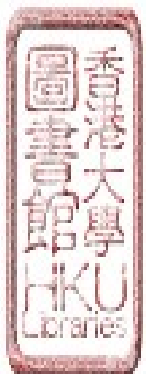
Wildebeest and zebra responded to the landscape of fear topographies relating to high levels of perceived predation risks, i.e. fear, by increasing their intense vigilance. However, vigilance responses were species-specific, with wildebeest and zebra responding to different landscape of fear topographic features. Zebra were more sensitive than wildebeest to predator encounter rates, as defined by the location of the lion home ranges, and had high intense vigilance when they were within these home ranges. Since intense vigilance implies trade-offs in foraging time (Fortin et al. 2004b; Blanchard & Fritz 2007), further studies should be conducted on zebra to assess the consistency of their vigilance response and the associated foraging and fitness costs. On the other hand, both species were not sensitive to predicted probability of lion occurrence, estimated from the resource selection of lions, indicating that the prey were more reactive to actual frequencies of lion occurrence than to indirect predation risk (Chapter 5). Therefore, continuous assessment of home range utilisation by reintroduced carnivores is essential to identify areas where potential adverse effects on prey might be severe. The impacts of the landscape of fear topographies differed also between routine and intense vigilance behaviour, which highlights the importance of distinguishing between the two that is not often done in vigilance studies; because only the intense vigilance implies foraging cost (Fortin et al. 2004b; Blanchard & Fritz 2007). The zebra and wildebeest in this study had not been exposed to lions for over a century; their behavioural responses to predator existence within a year from lion reintroductions addresses the importance of predator-prey dynamics monitoring in carnivores reintroductions, and the usefulness of prey vigilance behaviour as an indicator for reintroduced predator impact assessment.

A limitation of this study is the absence of prey density estimates. Prey density is an important factor in influencing the habitat selections of carnivores and is often reported as negatively correlated with home range sizes (Hayward et al. 2009). Although there were no significant seasonal or sexual differences in home range sizes, likely due to a high general abundance of prey across the whole study area (unpublished DGR aerial census data 2012) and unreceptivity of females as discussed in Chapter 4, individual variation did exist. Prey density estimates might allow for better understanding of the possible reasons behind this individual variation; it might also provide additional support for explaining the resource
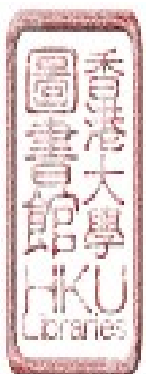
selection by lions (Chapter 5). Also, an increase in intense vigilance of zebra suggests potential trade-off in their foraging time thus fitness (Chapter 6), but further study on the foraging behaviour is required to confirm this relationship. An investigation into prey foraging behaviour would also provide better explanations for prey routine vigilance responses that are greatly influenced by the amount of time spared from food handling processes (Chapter 6).

To conclude, this study provides insights into the reintroduction ecology and management of large carnivores in small areas. Although sample size of lions was small, this is the common situation in carnivore reintroductions in South Africa and will likely be more common in the near future with an increase in the establishment of small reserves. The detailed investigation on the behaviour of individual lion groups therefore provides a typical scenario for these reserves to consider in reintroducing large carnivores. Careful planning is required in small areas to minimise intra-specific competitions at early stage of release, so as to maximise reintroduction success. This could potentially be achieved by distant release locations for multiple introductions. Release sites should also be selected in areas with high prey abundance and with vegetation types preferred by lions in general, to ensure both short-term and long-term resource access for lions. For post-release monitoring, movement and habitat selection patterns could be used for assessing establishment success of the reintroduced animals, and prey vigilance behaviour for assessing the impacts of the reintroductions on the local species.
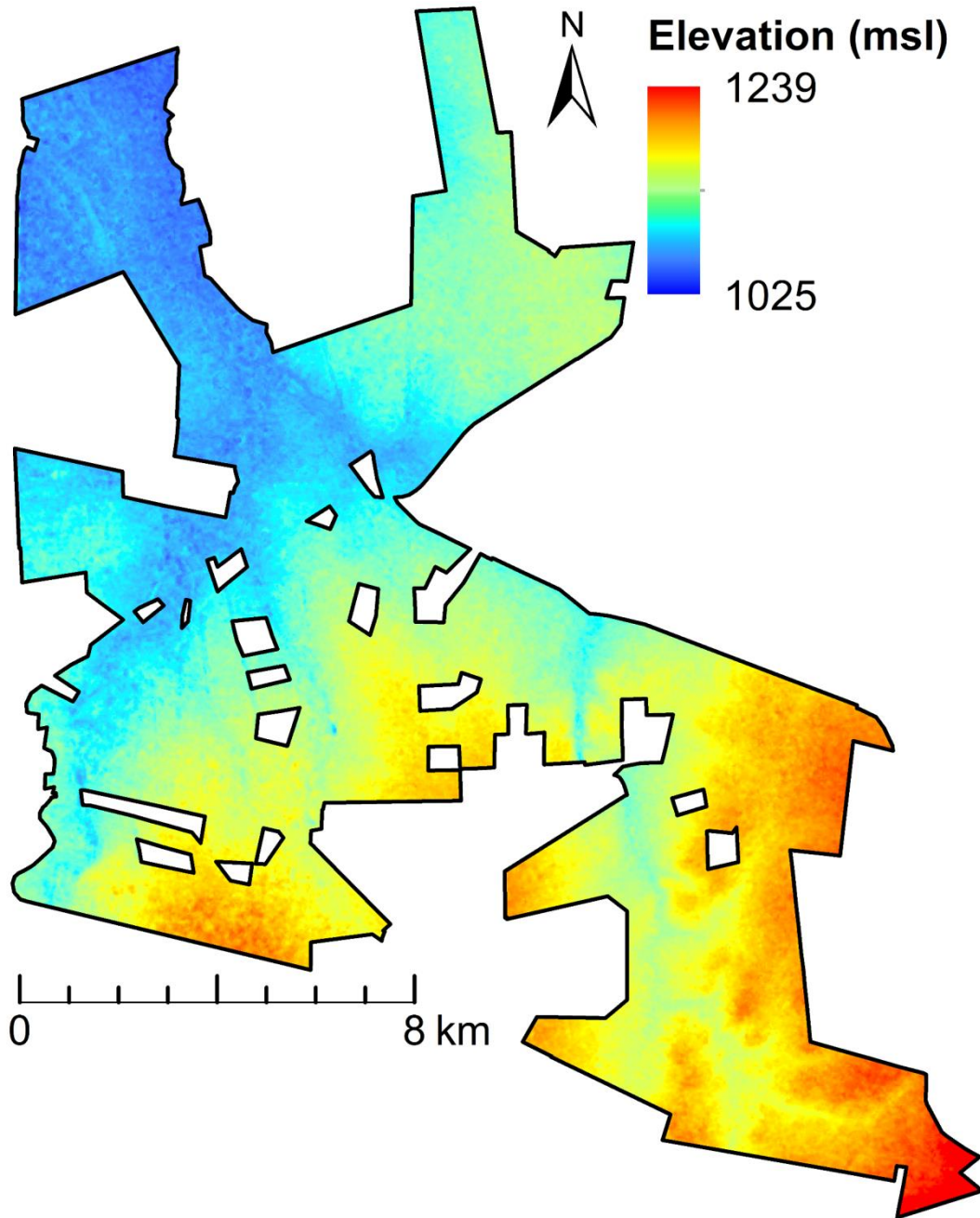
Fig. A-1 Map of elevation (msl) in Dinokeng Game Reserve, South Africa, derived from the ASTER Global Digital Elevation Model (GDEM) at 30 m resolution.
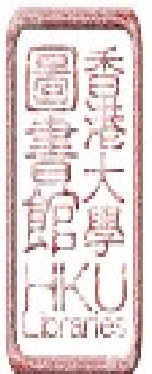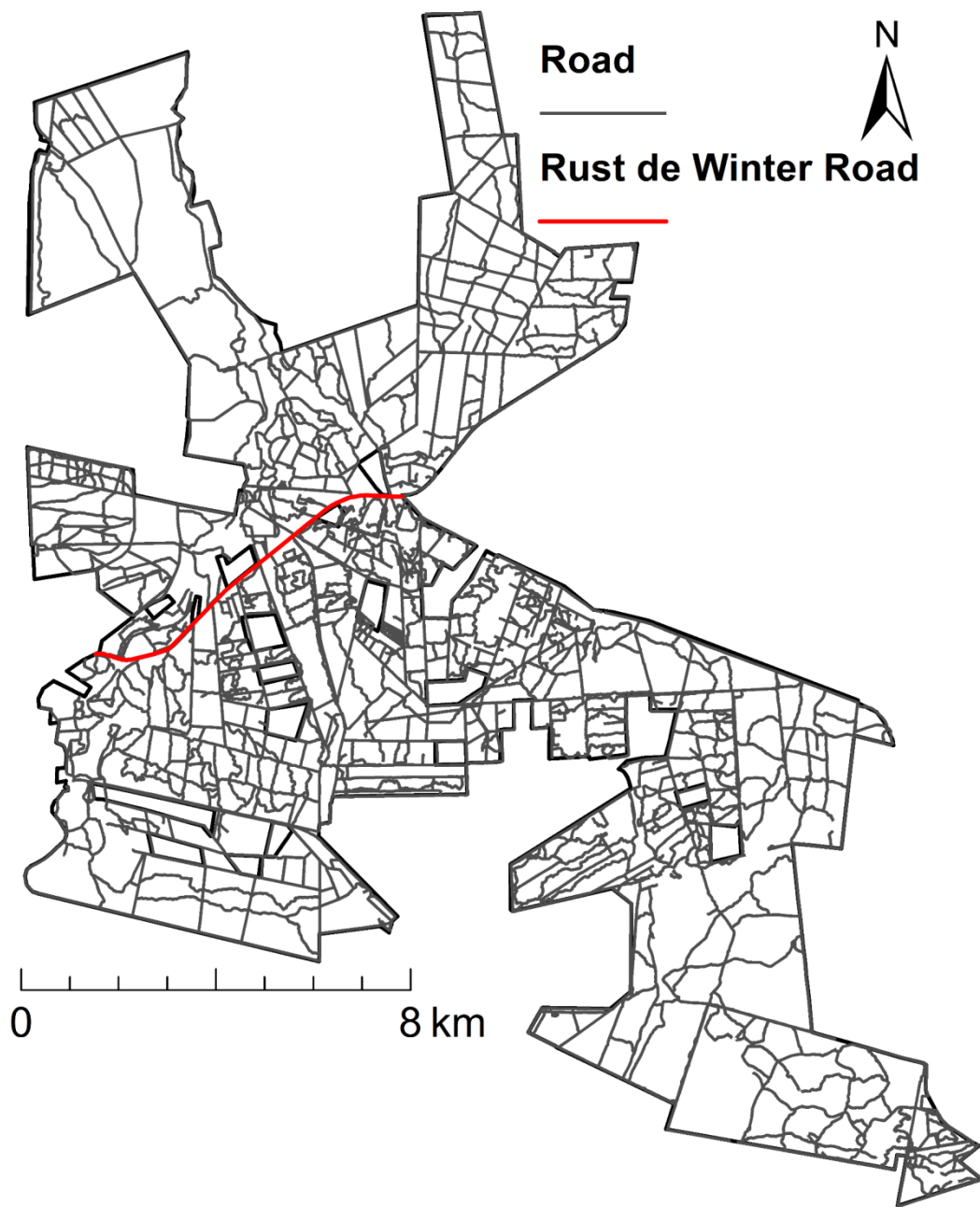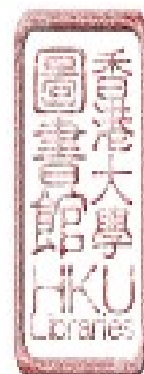
Fig. A-2 Map of road in Dinokeng Game Reserve, South Africa.
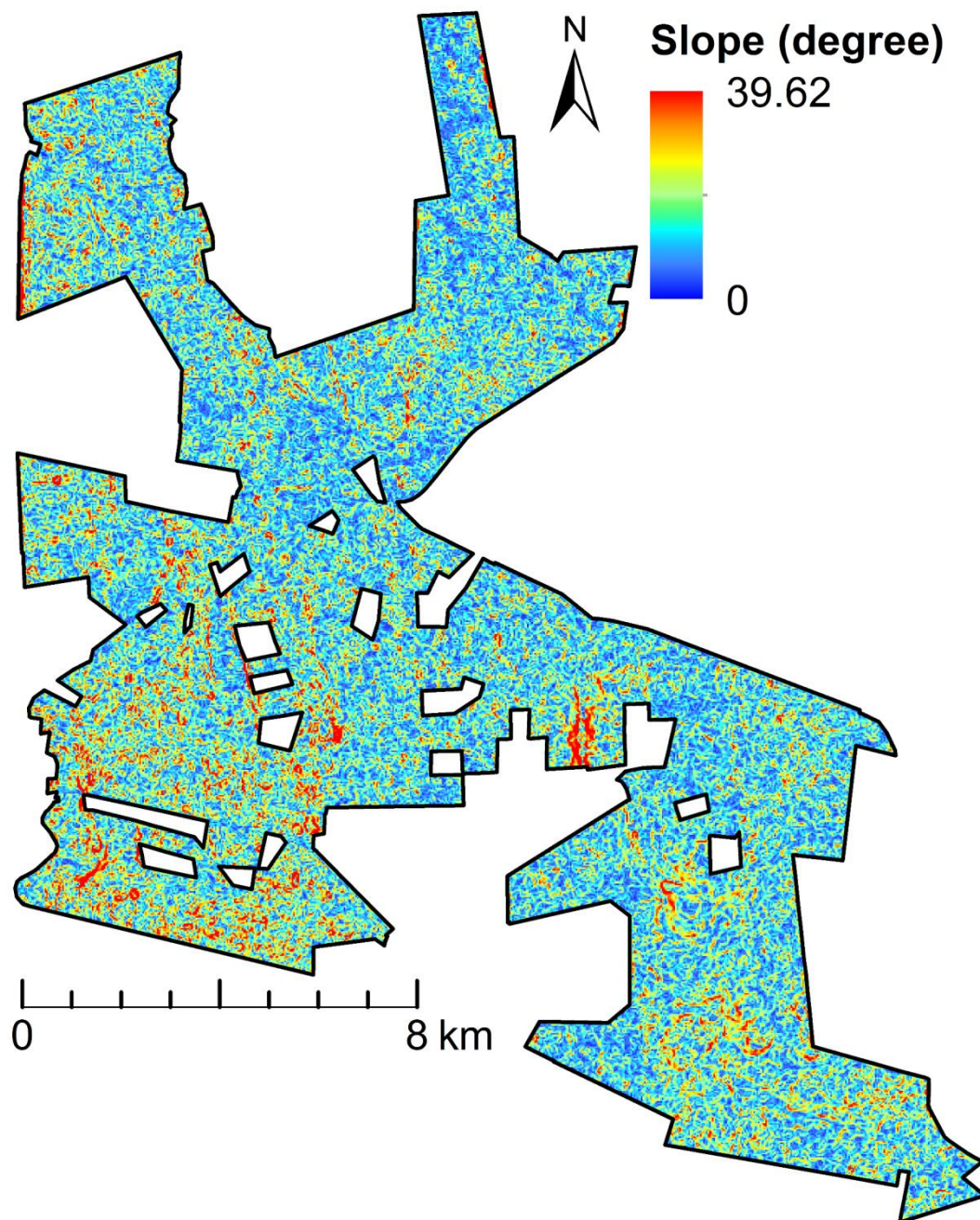
Fig. A-3 Map of slope (degree) in Dinokeng Game Reserve, South Africa, at 30 m resolution.
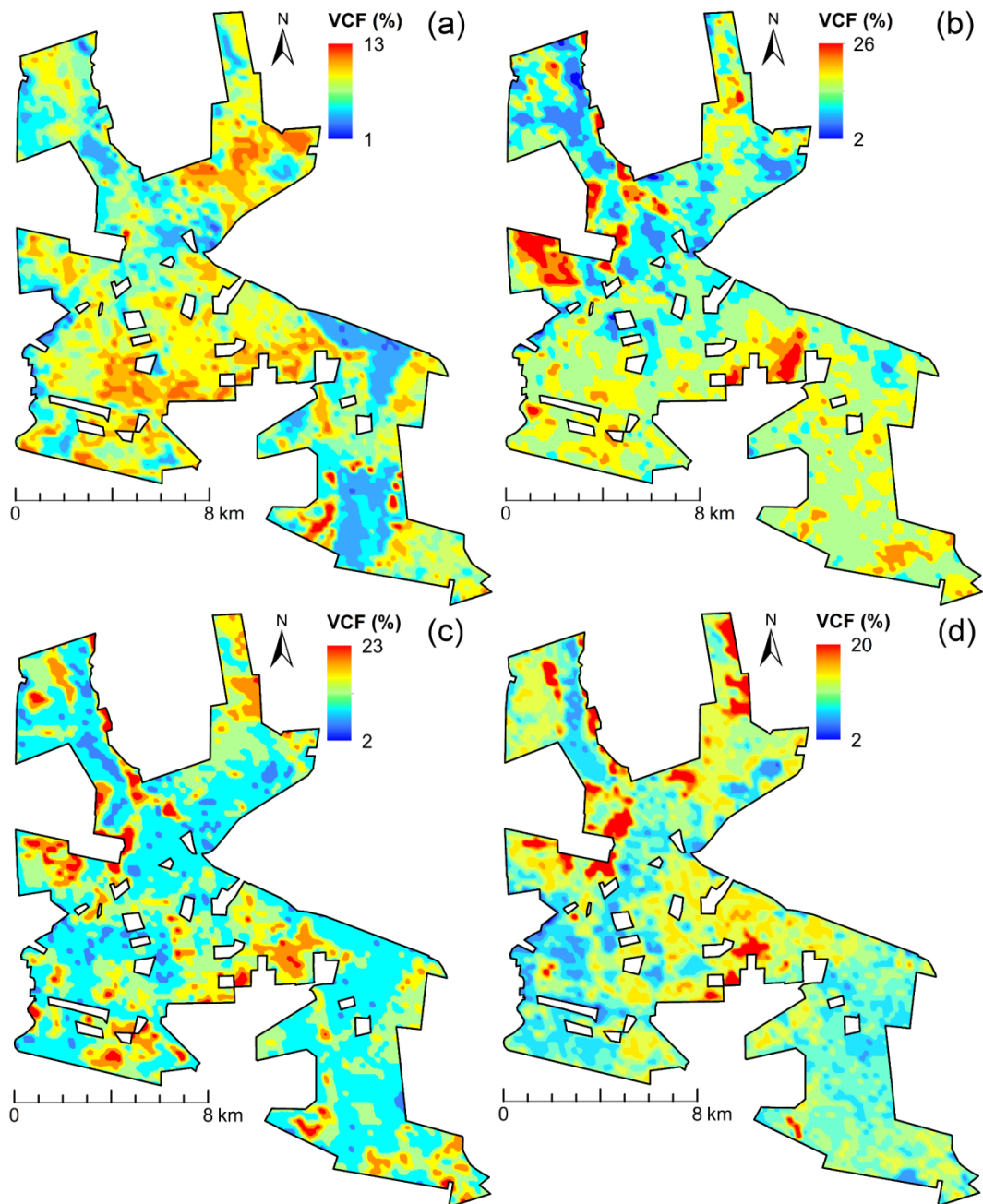
Fig. A-4 Maps of the percentage of tree cover (%) in Dinokeng Game Reserve, South Africa from 2011-2014, derived from Terra MODIS Vegetation Continuous Fields (VCF) imagery, resampled to 30 m resolution. (a) 2011-12, (b) 2012-13, (c) 2013-14, (d) 2014-15.
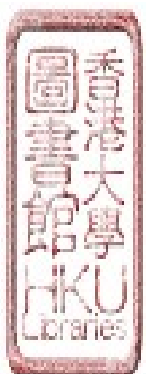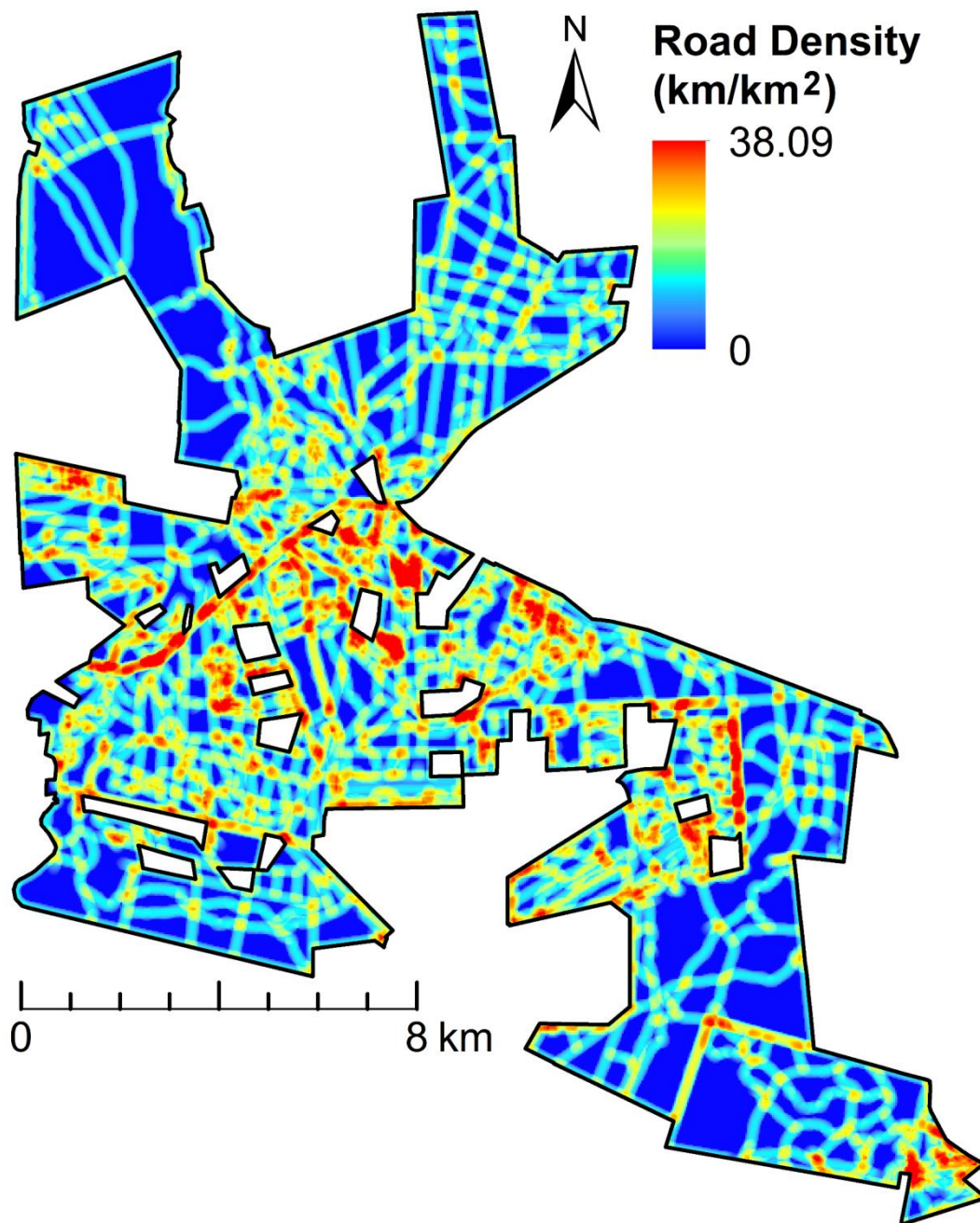
Fig. A-5 Map of road density (km/km^2) in Dinokeng Game Reserve, South Africa, at 30 m resolution.

Selection of vegetation types by lions

Table B-1 Selection of vegetation types by each lion group in Dinokeng Game Reserve, October 2011-September 2014. - indicates avoidance, 0 indicates no significant selection, + indicates preference. ref. = reference level.

Season	Wet 2011-12		Dry 2012		Wet 2012-13		Dry 2013		Wet 2013-14		Dry 2014	
Home range	95%	50%	95%	50%	95%	50%	95%	50%	95%	50%	95%	50%
M1												
1					−	0			−	0	+	+
2					−	0			−	0	+	+
3					−	0			−	0	+	+
4					+	0			+	0	+	+
6	0	0	−	−	−	−			−	−	−	−
7	−	−	−	0	−	−			−		−	−
8	−	−	−	−	−	−			−	−	0	−
9	ref.	ref.	ref.	ref.	ref.	ref.			ref.	ref.	ref.	ref.
10	−	−	−	−	−	0			−	0	−	−
11	−	−	−	−	0	−			−	0	−	−
12	−	−	−	−	−	−			−	−	−	−
13			−		−	0			−	−	0	−
14	0	0	−	0	+	0			−	0	−	−
15	0	0	−	0	+	−			−	0	−	+
M2												
1	0				−	−			−	−	−	−
2					−	−			−	−	−	−
3					−	−			−	−	−	−
4					ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.

5	0											
6	−		+		0				0		−	0
7	0		0		0				0		−	0
8	−	0	0		0				0		−	
9	ref.	ref.	ref.		−				0		−	−
10	−	−	+	+	0	0			−	0	−	−
11	−	−	−		−	0			−		−	−
12	−	−	0	ref.	−	0			0		−	−
13	0				0				−	0	−	0
14	0	0	0								0	0
15	−		0								0	0

F1												
1			0		−	0	+	+	−		−	0
2			0		−	0	+	+	−	0	+	0
3					−	0	−	0				
4					0	0	+	+	−	0	+	0
5			0		−	0						
6	−	−	−	−	−	−	−	+	−	−	−	0
7	−	0	−	−	−	−	−	+	−		−	0
8	−	−	−	−	−	−	−	+	−	−	−	−
9	ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.
10	0		+	0	0		−	+	−	0	−	+
11	−	0	−	−	−	−	−	0	−	−	−	−
12	−	−	−	−	−	−	−	0	−	−	−	−
13	−	−	−	−	−	−	−	+	−	−	0	0
14	−	−	−	−	−	−	−	0	−	−	0	0
15	−	−	−	0	−		−	0	−	0	−	
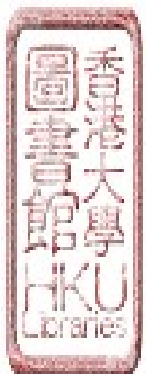
Group id	F2		F3				F3c			
Season	Wet		Wet		Dry		Wet		Dry	
	2011-12		2013-14		2014		2013-14		2014	
Home range	95 %	50 %	95 %	50 %	95 %	50 %	95 %	50 %	95 %	50 %
1			–	–	–	–	–	–	–	–
2			–	–	–	–	–	0	–	–
3			–	–	–	–	–	–	0	0
4			ref.	ref.	ref.	ref.	ref.	ref.	ref.	ref.
5	0				–				0	
6	–	–			–	0			–	0
7	–	+								
8	–	–								
9	ref.	ref.			0					
10	–	–								
11	–	–								
12	–	–								
13	–	0	–	0	–	–	–		–	
14	0									
15	0									
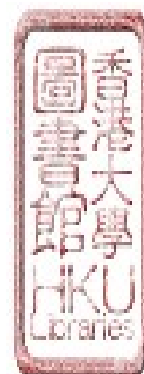
Appendix C

Predicted probabilities of occurrence of lions
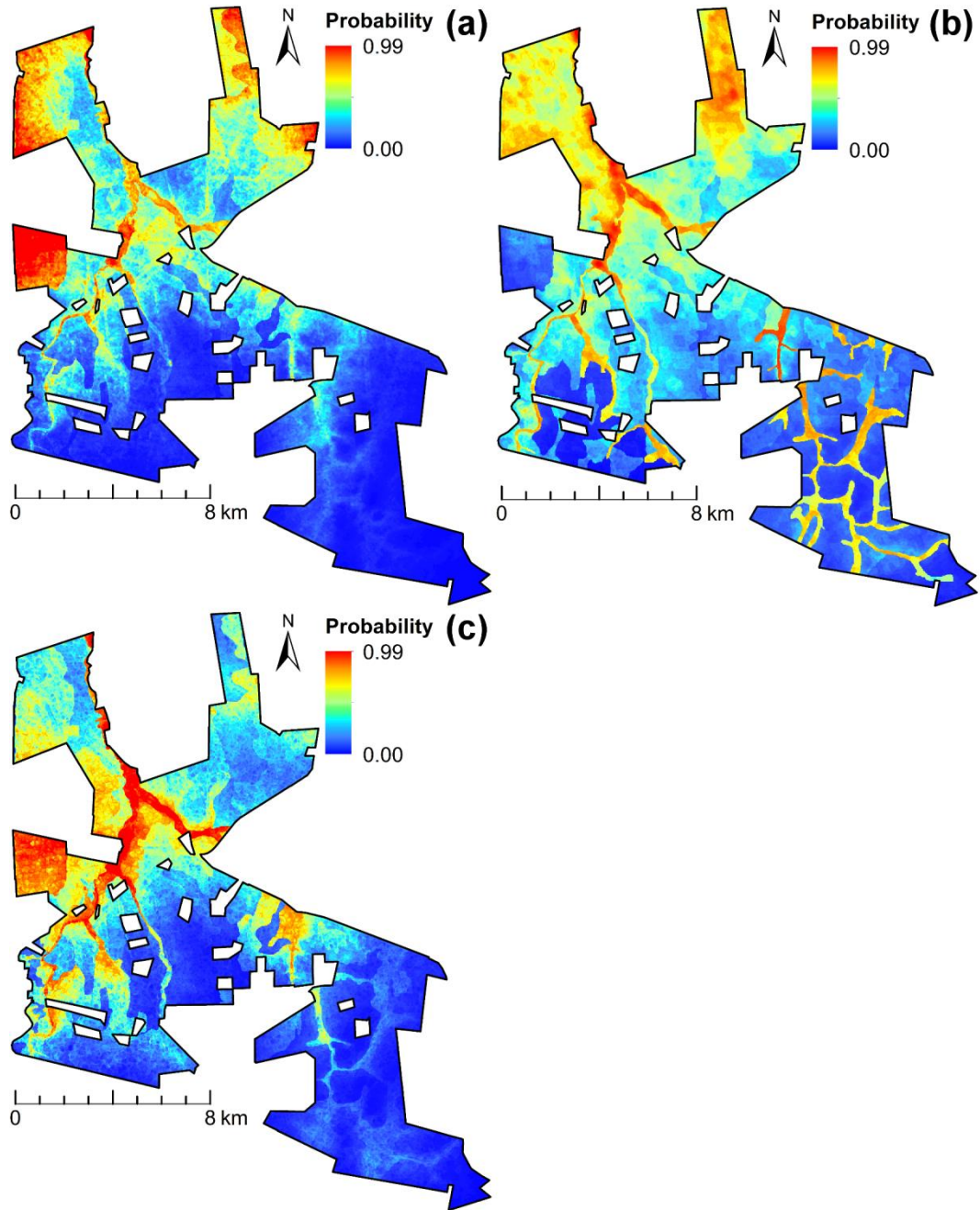
Fig. C-1 Maps of the predicted probabilities of occurrence of lions in Dinokeng Game Reserve. (a) dry season 2012, (b) wet season 2012-13, (c) dry season 2013.
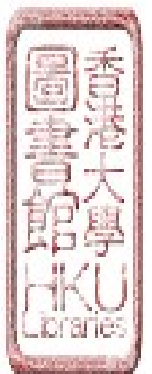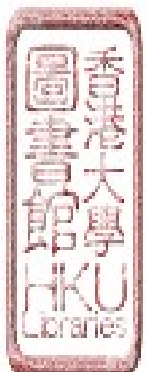
Reference list

Abade L., Macdonald D.W., & Dickman A.J., 2014. Using landscape and bioclimatic features to predict the distribution of lions, leopards and spotted hyaenas in Tanzania's ruaha landscape. *PloS ONE, 9*, e96261.

Abrams, P. A., 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics, 31*, 79-105.

Abrams, P. A., & Matsuda, H., 1997. Prey adaptation as a cause of predator-prey cycles. *Evolution, 51*, 1742-1750.

Ale, S. B., & Brown, J. S., 2007. The contingencies of group size and vigilance. *Evolutionary Ecology Research, 9*, 1263-1276.

Anderson, D. P., Turner, M. G., Forester, J. D., Zhu, J., Boyce, M. S., Beyer, H., & Stowell, L., 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management, 69*, 298-310.

Armstrong, D. P., Davidson, R. S., Dimond, W. J., Perrott, J. K., Castro, I., Ewen, J. G., Griffiths, R., & Taylor, J., 2002. Population dynamics of reintroduced forest birds on New Zealand islands. *Journal of Biogeography, 29*, 609-621.

Armstrong, D. P., & Seddon, P. J., 2008. Directions in reintroduction biology. *Trends in Ecology & Evolution, 23*, 20-25.

Ash, R. B. 2008. Basic probability theory. Mineola, USA: Dover Publications.

Aunapuu, M., & Oksanen, T. 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evolutionary Ecology, 17*, 371-392

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L., 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management, 49*, 386-400.
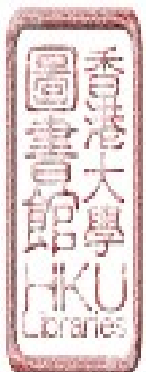
Balme, G., Hunter, L., & Slotow, R., 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour, 74*, 589-598.

Barreto, G. R., & Herrera, E. A., 1998. Foraging patterns of capybaras in a seasonally flooded savanna of Venezuela. *Journal of Tropical Ecology, 14*, 87-98.

Bartumeus, F., & Levin, S. A., 2008. Fractal reorientation clocks: linking animal behavior to statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 19072-19077.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C., 2014. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*, 1-48.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T., Macdonald, D.W., & Packer, C., 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences, 112*, 14894-14899.

Beale, C. M., & Monaghan, P., 2004. Human disturbance: people as predation-free predators? *Journal of Applied Ecology, 41*, 335-343.

Beauchamp, G., 2008. What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology, 19*, 1361-1368.

Beauchamp, G., 2010. Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. *Ethology, 116*, 645-652.

Beauchamp, G., 2015. Animal vigilance: monitoring predators and competitors. London, U.K.: Academic Press.

Bednekoff, P. A., & Lima, S. L., 1998. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology & Evolution, 13*, 284-287.

Bélichon, S., Clobert, J., & Massot, M., 1996. Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologica, 17*, 503-517.
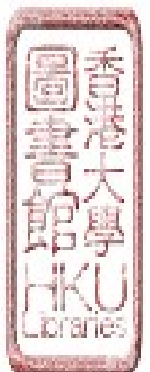
Bélisle, M., 2005. Measuring landscape connectivity: the challenge of behavioural landscape ecology. *Ecology, 86*,1988-1995.

Benard, M. F., & McCauley, S. J., 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. *American Naturalist, 171*, 553-567.

Benhamou, S., & Riotte-Lambert, L., 2012. Beyond the utilisation distribution: identifying home range areas that are intensively exploited or repeatedly visited. *Ecological Modelling, 227*, 112-116.

Bennett, V. A., Doerr, V. A. J., Doerr, E. D., Manning, A. D., Lindenmayer, D. B., & Yoon, H. J., 2013. Habitat Selection and Behaviour of a Reintroduced Passerine: linking Experimental Restoration, Behaviour and Habitat Ecology. *PLoS ONE, 8*, e54539.

Benson, J. F., & Chamberlain, M. J., 2007. Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *The Journal of wildlife management, 71*, 117-126.

Berger, J., Swenson, J. E., & Persson, I. L., 2001. Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science, 291*, 1036-1039.

Berger-Tal, O., Nathan, J., Meron, E., & Saltz, D., 2014. The Exploration-Exploitation Dilemma: A Multidisciplinary Framework. *PLoS ONE, 10*, e0119116.

Berger-Tal, O., & Saltz, D., 2014 Using the movement patterns of reintroduced animals to improve reintroduction success. *Current Zoology, 60*, 515-526.

Bernardo, C. S. S., Lloyd, H., Olmos, F., Cancian, L. F., & Galetti, M., 2011. Using post-release monitoring data to optimize avian reintroduction programs: a 2-year case study from the Brazilian Atlantic Rainforest. *Animal Conservation, 14*, 676-686.

Beyer, H. L., 2004. Hawth's Analysis Tools for ArcGIS. Version 3.27. http://www.spatialecology.com/htools/ Accessed Jul 2011.
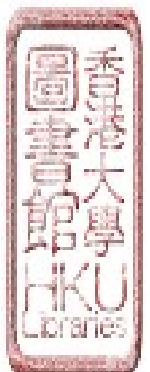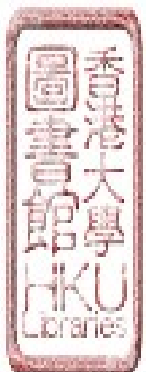
Biggins, D. E., Godbey, J. L., Matchett, M. R., & Livieri, T. M., 2004. Habitat Preferences and Intraspecific Competition in Black-footed Ferrets. In: Roelle, J. E., Miller, B. J., Godbey, J. L., & Biggins, D. E. (eds) Recovery of the black-footed ferret: progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005–5293, pp 129-140.

Biggs, R. & Scholes, R. J., 2002. Land-cover changes in South Africa 1911–1993. *South African Journal of Science, 98*, 420–424.

Bjornlie, D. D., Van Manen, F. T., Edinger, M. R., Haroldson, M. A., Thompson, D. J., & Costello, C. M., 2014. Whitebark Pine, population density, and home-range size of grizzly bears in the greater Yellowstone ecosystem. *PLoS One, 9*, e88160.

Blanchard, P., & Fritz, H., 2007. Induced or routine vigilance while foraging. *Oikos, 116*, 1603-1608.

de Boer, W. F., Marc, J. P. Vis., de Knegt, H. J., Rowles, C., Kohi, E. M., van Langevelde, F., Peel, M., Pretorius Y., et al., 2010. Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy, 91*, 1280-1286

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., et al., 2012. Costs of dispersal. *Biological Reviews, 87*, 290-312.

Bose, M., & Sarrazin, F., 2007. Competitive behaviour and feeding rate in a reintroduced population of Griffon Vultures *Gyps fulvus*. *Ibis, 149*, 490-501.

Bowler, D. E., & Benton, T. G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews, 80*, 205-225.

Boyce, M. S., 2006. Scale for resource selection functions. *Diversity and Distribution, 12*, 269-276.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmieglow, F. K. A., 2002. Evaluating resource selection functions. *Ecological Modelling, 157*, 281-300.

Boyd, L., & Bandi, N., 2002. Reintroduction of takhi, *Equus ferus przewalskii*, to Hustai National Park, Mongolia: time budget and synchrony of activity pre- and post-release. *Applied Animal Behaviour Science, 78*, 87-102.

Bradbury, J. W., Vehrencamp, S. L., Clifton, K. E., & Clifton, L. M., 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. *Ecology, 77*, 2237-2255.

Brown, J. S., 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research, 1*, 49-71.

Brown, J. S., & Kotler, B. P., 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters, 7*, 999-1014.

Burger, J., & Gochfeld, M., 1994. Vigilance in African mammals: differences among mothers, other females, and males. *Behaviour, 131*, 153-169.

Burger, J., Safina, C., & Gochfeld, M., 2000. Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethologica, 2*, 97-104.

Burnham, K. P., & Anderson, D. R., 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed.). New York, U.S.: Springer-Verlag.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*, 23-35.

Burt, W. H., 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy, 24*, 346–352.

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*, 516-519

Cardillo, M., 2003. Biological determinants of extinction risk: why are smaller species less vulnerable?. *Animal Conservation, 6*, 63-69.
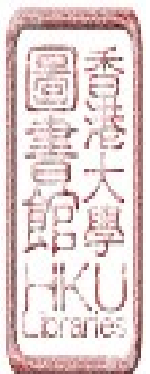
Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M., 2004. Human population density and extinction risk in the world's carnivores. *PLOS Biology, 2*, e197.

Carthey, A. J., & Banks, P. B., 2014. Naïveté in novel ecological interactions: lessons from theory and experimental evidence. *Biological Reviews, 89*, 932-949.

Ceballos, G. & Ehrlich, P. R., 2002. Mammal population losses and the extinction crisis. *Sciences, 296*, 904-907.

Childress, M. J., & Lung, M. A., 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour, 66*, 389-398.

Ciarniello, L. M., Boyce, M. S., Sep, D. R., & Heard, D. C., 2007. Grizzly bear habitat selection is scale dependent. *Ecological Application, 17*, 1424-1440.

Clark, J. D., Huber, D., & Servheen, C., 2002. Bear reintroductions: lessons and challenges. *Ursus, 13*, 335-34.

Clutton-Brock, T. H., 1991. The evolution of parental care. New Jersey, USA: Princeton University Press.

Clutton-Brock, T. H., Hodge, S. J., Sponge, G., Russell, F., Jordan, N. R., Bennett, N. C., Sharpe, L. L., & Manner, M. B., 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature, 444*, 1065-1068.

Contour Project Managers, 2009. Final draft consolidated report: comprehensive environmental management plan and specific species plans for Dinokeng Game Reserve.

Courbin, N., Loveridge, A. J., Macdonald, D. W., Fritz, H., Valeix, M., Makuwe, E. T., & Chamaillé-Jammes, S., 2015. Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos, 125*, 829-838.

Cox, C. R., & Le Boeuf, B. J., 1977. Female incitation of male competition: a mechanism in sexual selection. *The American Naturalist, 111*, 317-335.

Cozzi, G., Broekhuis, F., McNutt, J. W., & Schmidt, B., 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation, 22*, 2937-2956.

Craigie, I. D., Baillie, J. E., Balmford, A., Carbone, C., Collen, B., Green, R. E. & Hutton, J. M., 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation, 143*, 2221-2228.

Creel, S., Christianson, D., Liley, S., & Winnie, J. A. JR., 2007. Predation risk affects reproductive physiology and demography of elk. *Science*, *315*, 960.

Creel, S., & Christianson, D., 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, *23*, 194-201.

Creel, S., Schuette, P., & Christianson, D., 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology, 25*, 773-784.

Creel, S., & Winnie, J. A., 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour, 69*, 1181-1189.

Creel, S., Winnie, J. JR., Maxwell, B., Hamlin, K., & Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology, 86*, 3387-3397.

Cribari-Neto, F., & Zeileis, A., 2009. Beta regression in R. *Journal of Statistical Software, 34*, 1–24.

Cromsigt, J. P., & Olff, H., 2008. Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. *Oikos, 117*, 1444-1452.

Crooks, K. R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology, 16*, 488-502.

Dalerum, F., Lange, H., Skarpe, C., Rooke, T., Inga, B., & Bateman, P. W., 2008. Foraging competition, vigilance and group size in two species of gregarious antelope. *South African Journal of Wildlife Research, 38*, 138-145.
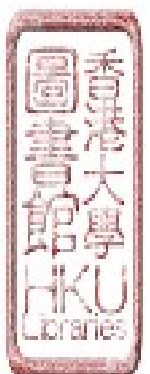
Davidson, Z., Valeix, M., Loveridge, A. J., Hunt, J. E., Johnson, P. J., Madzikanda, H., & MacDonald, D. W., 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy, 93*, 677-685.

Davidson, Z., Valeix, M., Van Kestrel, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & MacDonald, D., 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PloS ONE, 8*, e55182.

Debeffe, L., Moeller, N., Cargnelutti, B., Lourdes, B., Coulson, A., Gaillard, J. M., Bon, R., & Hewison, A. J. M., 2013. Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. *Animal Behaviour, 86*, 143-151.

Delgado, M. D. M., Penteriani, V., Names, V. O., & Campioni L, 2009. Changes of movement patterns from early dispersal to settlement. *Behavioral Ecology and Sociobiology, 64*, 35-43.

Di Minin, E., Fraser, I., Slotow, R., & MacMillan, D. C., 2013. Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. *Animal Conservation, 16*, 249-258.

Dickson, B. G., & Beyer, P., 2007. Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. *Journal of Zoology, 271*, 270-277.

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J., 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution, 25*, 81-89.

Djagoun, C. A., Djossa, B. A., Mensah, G. A., & Sinsin, B. A., 2013. Vigilance efficiency and behaviour of Bohor reedbuck *Redunca redunca* (Pallas 1767) in a savanna environment of Pendjari Biosphere Reserve (Northern Benin). *Mammal Study, 38*, 81-89.

Dolev, A., Saltz, D., Bar-David, S., & Yom-Tov, Y., 2002. Impact of repeated releases on space-use patterns of Persian fallow deer. *The Journal of Wildlife management, 66*, 737-746.
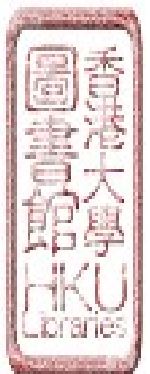
Druce, D., Genis, H., Braak, J., Greatwood, S., Delsink, A., Kettles, R., Hunter, L., & Slotow, R., 2004. Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Koedoe, 47*, 103-118.

Duffy, J. E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters, 6*, 680-687.

Dunham, K. M., 2001. Status of a reintroduced population of mountain gazelles *Gazella gazella* in central Arabia: management lessons from an aridland reintroduction. *Oryx, 35*, 111-118.

Durant, S. M., 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology, 67*, 370-386.

Ebensperger, L. A., & Hurtado, M. J., 2005. On the relationship between herbaceous cover and vigilance activity of degus (*Octodon degus*). *Ethology, 111*, 593-608.

Ego, W. K., Mbuvi, D. M., & Kibet, P. F. K., 2003. Dietary composition of wildebeest (*Connochaetes taurinus*) kongoni (*Alcephalus buselaphus*) and cattle (*Bos indicus*), grazing on a common ranch in south-central Kenya. *African Journal of Ecology, 41*, 83-92.

Elliott, J. P., & Cowan., I. M., 1978. Territoriality, density, and prey of the lion in Ngorongoro Crater, Tanzania. *Canadian Journal of Zoology, 56*, 1726-1734.

Emlen, S. T., & Oring., L. W., 1977. Ecology, sexual selection, and the evolution of mating systems. *Science, 197*, 215-223.

Ewen, J. G., Armstrong, D. P., Parker, K. A., & Seddon, P. J. (Eds.), 2012. Reintroduction biology: integrating science and management. West Sussex, UK: Blackwell Publishing.

Farnsworth, K. D., & Illius, A. W., 1998. Optimal diet choice for large herbivores: an extended contingency model. *Functional Ecology, 12*, 74-81.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M., & York, E. C., 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia, 125*, 258-270.
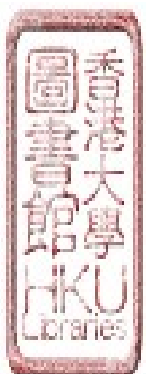
Ferreira, S. M., & Hofmeyr, M., 2014. Managing charismatic carnivores in small areas: large felids in South Africa. *South African Journal of Wildlife Research, 44*, 32-42.

Forsyth, D.M. 2000. Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Southern Alps. *New Zealand Journal of Zoology, 252*, 215-225.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology, 86*, 1320-1330.

Fortin, D., Boyce, M. S., & Merrill, E. H., 2004a. Multi-tasking by mammalian herbivores: overlapping processes during foraging. *Ecology, 85*, 2312-2322.

Fortin, D., Boyce, M. S., Merrill, E. H., & Fryxell, J. M., 2004b. Foraging costs of vigilance in large mammalian herbivores. *Oikos, 107*, 172-180.

Frair, J. L., Merrill, E. H., Visscher, D. R., Fortin, D., Beyer, H. L., & Morales, J. M., 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology, 20*, 273-287.

Fred, A., & Dill, L. M., 2002. Human-caused disturbance stimuli as a form of predation risk. *Ecology and Society, 6*, 11.

Frid, A., 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour, 53*, 799-808.

Fritts, S. H., Paul, W. J. & Mech, L. D., 1984. Movements of translocated wolves in Minnesota. *The Journal of Wildlife Management, 48*, 709-721.

Fryxell, J. M., Mosser, A., Sinclair, A. R. & Packer, C., 2007. Group formation stabilizes predator–prey dynamics. *Nature, 449*, 1041-1043.

Funston, P. J., Mills, M. G. L., Richardson, P. R. K., & van Jaarsveld, A. S., 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology, 259*, 131-142.

Georgiadis, N. J., & McNaughton, S. J., 1990. Elemental and fibre contents of savanna grasses: variation with grazing, soil type, season and species. *Journal of Applied Ecology, 27*, 623-634.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmer, C. C., 2007. LoCoH: Nonparametric kernel methods for constructing home ranges and utilisation distributions. *PloS One, 2*, e207.

Getz, W. M., & Wilmers, C. C., 2004. A local nearest-neighbor convex-hull construction of home ranges and utilisation distributions. *Ecography, 27*, 489-505

Gibbs, J. P., Marquez, C. & Sterling, E. J., 2008. The role of endangered species reintroduction in ecosystem restoration: tortoise–cactus interactions on Española Island, Galápagos. *Restoration Ecology, 16*, 88-93.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Fair, J. L., Sather, D. J., Stevens, C. E., et al., 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology, 75*, 887-898.

Gittleman, J. L., & Gompper, M. E., 2001. The risk of extinction: what you don't know will hurt you. *Science, 291*, 997-999.

Godvik, I. M. R., Loeb, L. E., Vik, J. O., Veiberg, V., Langvatn, R., & Mastered, A., 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology, 90*, 699-710.

Google Earth 6.0 (April 21, 2005). Accessed Jul 2013.

Grinnell, J., & K. McComb., 2001. Roaring and social communication in African lions: the limitations imposed by listeners. *Animal Behaviour, 62*, 93-98.

Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology, 24*, 699-711.

Gusset, M., Stewart, G. B., Bowler, D. E. & Pullin, A. S., 2010. Wild dog reintroductions in South Africa: a systematic review and cross-validation of

an endangered species recovery programme. *Journal for Nature Conservation, 18*, 230-234.

Happold, D. C. D. 1995. The interactions between humans and mammals in Africa in relation to conservation: a review. *Biodiversity and Conservation, 4*, 395-414.

Havarua, Z., Turner, W. C., & Mfune, J. K., 2014. Seasonal variation in foraging behaviour of plains zebra (*Equus quagga*) may alter contact with the anthrax bacterium (*Bacillus anthracis*). *Canadian Journal of Zoology, 92*, 331-337.

Hawkes, C., 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? *Journal of Animal Ecology, 78*, 894-906.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L. C., Bean, P., Fogarty, A., et al., 2007a. 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*, 1-11.

Hayward, M. W., & Hayward, G. J., 2006. Activity patterns of reintroduced lion *Panthera leo* and spotted *hyaena Crocuta crocuta* in the Addo Elephant National Pak, South Africa. African Journal of Ecology, 45, 135-141.

Hayward, M. W., Hayward, G. J., Druce, D. J., & Kelley, G. I. H., 2009. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity and Conservation, 18*, 887-904.

Hayward, M. W., & Kerley, G. I., 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology, 267*, 309-322.

Hayward, M. W., & Kerley, G. I., 2009. Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation, 142*, 1-13.

Hayward, M. W., Kerley, G. I., Adendorff, J., Moolman, L. C., O'brien, J., Sholto-Douglas, A, Bissett, C., Moorman, L. C., et al., 2007b. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx, 41*, 205-214.

Hayward, M. W., O'Brien, J., & Kelley, G. I. H., 2007c. Carrying capacity of large African predators: predictions and tests. *Biological Conservation, 139*, 219-229.

Hayward, M. W., & Slotow, R., 2009. Temporal partitioning of activity in large African carnivores, tests of multiple hypotheses. *South African Journal of Wildlife Research, 39*, 109-125.

Hayward, M. W., & Somers, M. J., (Eds), 2009. Reintroduction of top-order predators. West Sussex, U.K.: Blackwell Publishing.

Hebblewhite, M., Merrill, E. H., & McDonald, T. L., 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos, 111*, 101-111.

Hebblewhite, M., Miquelle, D. G., Murzin, A. A., Aramilev, V. V., & Pikunov, D. G., 2011. Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biological Conservation, 144*, 2403-2413.

Heinsohn, R., & Packer, C., 1995. Complex cooperative strategies in group-territorial African lions. *Science, 269*, 1260-1262.

Heithaus, M. R., & Dill, L. M., 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos, 114*, 257-264.

Herfindal, I., Linnell, J. D. C., Odden, J., Nilsen, E. B. & Andersen. R., 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology, 265*, 63-71.

Hoffman, M. T. & Rohde, R. F., 2007. From pastoralism to tourism: the historical impact of changing land use practices in Namaqualand. *Journal of arid environments, 70*, 641-658.

de Hoog, 2014. Habitat selection of African elephants (*Loxodonta africana*) after reintroduction in Dinokeng Game Reserve (MSc thesis). Johannesburg, South Africa: University of the Witwatersrand.

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C., 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology, 74*, 559-566.

Houston, A. I., McNamara, J. M., & Hutchinson, J. M., 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 341*, 375-397.

How, M. J., & Zanker, J. M., 2014. Motion camouflage induced by zebra stripes. *Zoology, 117*, 163-170.

Hughes, A. E., Troscianko, J., & Stevens, M., 2014. Motion dazzle and the effects of target patterning on capture success. *BMC Evolutionary Biology, 14*, 201.

Hunter, L. T. B., 1998. The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa (PhD thesis). Pretoria, South Africa: University of Pretoria.

Hunter, L. T. B., Pretorius, K., Carlisle, L. C., Rickelton, M., Walker, C., Slotow, R., & Skinners, J. D., 2007. Restoring lions *Panthera leo* to northen KwaZulu-Natal, South Africa: short-term biological and technical success but equivocal long-term conservation. *Oryx, 41*, 196-204.

Hunter, L. T. B., & Skinner, J. D., 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour, 135*, 195-211.

Illius, A. W., & Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates. *Animal Behaviour, 47*, 481-484.

IUCN, 1998. Guidelines for re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Jang, G., Ma, J., Zhang, M., & Stott, P., 2009. Multiple spatial-scale resource selection function models in relation to human disturbance for moose in northeastern China. *Ecological Research, 24*, 423-440.

Johnson, C. J., Sep, D. R., & Boyce, M. S., 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scale. *Journal of Applied Ecology, 41*, 238-251.

Johnson, D. H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology, 61*, 65-71.

Kauffman, M. J., Valley, N., Smith, D. W., Stapler, D. R., McNulty, D. R., & Boyce, M. S., 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letter, 10*, 690-700.

Kelley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B., & Hornocker, M. G., 2002. Effects of roads and human disturbances on Amur tigers. *Conservation Biology, 16*, 97-108.

Kettles, R., & Slotow, R., 2008. Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research, 39*, 23-33.

Killian, P. J., 2003. The ecology of reintroduced lions on the Welgeconden Private Game Reserve, Waterbury (MSc thesis). Pretoria, South Africa: University of Pretoria.

Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J., 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia, 157*, 163-175.

Knox, N. M., Skidmore, A. K., Prins, H. H., Asner, G. P., van der Werff, H. M., de Boer, W. F., van der Waala, C., de Knegt, H. J., et al., 2011. Dry season mapping of savanna forage quality, using the hyperspectral Carnegie Airborne Observatory sensor. *Remote Sensing of Environment, 115*, 1478-1488.
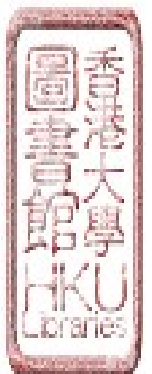
Koper, N., & Manseau, M., 2012. A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. *Rangifer, 20*, 195–203.

Krause, J., & Godin, J. G. J., 1994. Shoal choice in the banded killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae): effects of predation risk, fish size, species composition and size of shoals. *Ethology, 98*, 128-136.

Krebs, J. R., & N. B. Davies, (Eds), 1979. Behavioural ecology: an evolutionary approach. West Sussex, U.K.: Blackwell Publishing.

Kristal, W. H., & Wallis, W. A., 1952. Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association, 47*, 583-621.

Laundré, J. W., Hernández, L., & Altendorf, K. B., 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology, 79*, 1401-1409.

Laundré, J. W., Hernández, L., & Ripple, W. J., 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal, 3*, 1-7.

Le Gouar, P., Mihoub, J. B., & Sarrazin, F., 2012. Dispersal and habitat selection: Behavioural and Spatial Constraints for Animal Translocation. In Ewan, J. G., Armstrong, D. P., Parker, K. A., & Seddon, P. J., (Eds.), Reintroduction biology: integrating science and management (pp. 138-164). West Sussex, U.K.: Blackwell Publishing.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R., 2008a. Feeding behaviour of lions (*Panthera leo*) on a small reserve. *South African Journal of Wildlife Research, 38*, 66-78.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R., 2008b. Home range utilisation and territorial behavior of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PloS One, 3*, e3998.

Lenore, F., 2007. Non-optimal animal movement in human-altered landscapes. *Functional Ecology, 21*, 1003-1015.

Li, Z., Jiang, Z., & Beauchamp, G., 2009. Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *Journal of Zoology, 277*, 302-308.

Lima, S. L., 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour, 49*, 11-20.

Lima, S. L., & Steury, T. D., 2005. Perception of predation risk: the foundation of nonlethal predator–prey interactions. In Barbosa, P., & Castellanos, I. (Eds.), Ecology of predator–prey interactions (pp. 166-188). Oxford, U.K.: Oxford University Press.

Lima, S. L., & Zollner, P. A., 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution, 11*, 131-135.

Lind, J., & Cresswell, W., 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology, 16*, 945-956.

Linnell, J. D. C., Odden, J., & Smith, M. E., 1997. Translocation of carnivores as a method for managing problem animals: a review. *Biodiversity Conservation, 6*, 1245-1257.

Loarie, S. R., Tambling, C. J., & Asner, G. P., 2013. Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour, 85*, 899-906.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W., 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savannah. *Ecography, 32*, 953-962.

LP DAAC, NASA, USGS. 2009. ASTER Global Digital Elevation Model (GDEM). from http://gdex.cr.usgs.gov/gdex/ Accessed 02/07/2015.

Lund, U., & Agostinelli, C., 2014. CircStats: Circular Statistics, from "Topics in circular Statistics" (2001). R package version 0.2-4. http://CRAN.R-project.org/package=CircStats

Luttbeg, B., & Schmitz, O. J., 2000. Predator and prey models with flexible individual behavior and imperfect information. *The American Naturalist, 155*, 669-683.

Lyons, A. J., Turner, W. C., & Getz, W. M., 2013. Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology, 1*, 1-14.
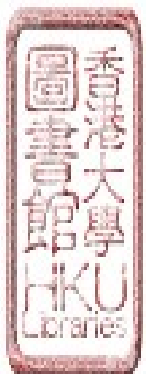
Macandza, V. A., Owen-Smith, N., & Cross, P. C., 2004. Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research, 34*, 113-121.

Manly, B. F. L., McDonald, L., Thomas, D., McDonald, T. L., & Erickson, W. P., 2002. Resource selection by animals: statistical design and analysis for field studies. New York, U.S.: Kluwer Academic Publishers.

Martella, M. B., Renison, D., & Navarro, J. L., 1995. Vigilance in the greater rhea: effects of vegetation height and group size (Vigilancia en el Ñandú: Effectos de la Altura de la Vegetación del Tamaño de Grupo). *Journal of Field Ornithology*, 66, 215-220.

Martin, J., & Owen-Smith, N., 2016. Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Animal Behaviour, 116*, 163-170.

Martin, J. G. A, & Réale D., 2008. Animal temperament and human disturbance: Implications for the response of wildlife to tourism. *Behavioural Processes, 77*, 66-72.

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P., 2009. Habitat selection at multiple scales. *Écoscience, 16*, 238-247.

McCarthy, M. A., Armstrong, D. P. & Runge, M.C., 2012. Adaptive management of reintroduction. In Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (Eds), Reintroduction biology: integrating science and management (pp. 256–289). Oxford, U.K.: Wiley-Blackwell.

McCarthy, M. A. & Possingham, H. P., 2007. Active adaptive management for conservation. *Conservation Biology, 21*, 956-963.

McCombs, K., Packer, C., & Pusey A., 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour, 47*, 379-387.

Mella, V. S., Cooper, C. E., & Davies, S. J., 2014. Behavioural responses of free-ranging western grey kangaroos (*Macropus fuliginosus*) to olfactory cues of historical and recently introduced predators. *Austral Ecology, 39*, 115-121.

Miller, B., Ralls, K., Reading, R. P., Scott, J. M., & Estes, J., 1999. Biological and technical considerations of carnivore translocation: a review. *Animal Conservation, 2*, 59-68.

Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., Ferreira, S., Funston, P. J., et al., 2013. Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research, 43*, 138-154.

Miller, S. M., & Funston, P. J., 2014. Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: a management dilemma. *South African Journal of Wildlife Research, 44*, 43-55.

MØller, A. P., & Thornhill, R., 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour, 55*, 1507-1515.

Moorcroft, P. R., M. A. Lewis, & R. L. Crabtree., 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories. *Proceedings of the Royal Society of London B, 273*, 1651-1659.

Moorhouse, T. P., Gelling, M. & Macdonald, D. W., 2009. Effects of habitat quality upon reintroduction success in water voles: evidence from a replicated experiment. *Biological Conservation, 142*, 53-60.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H. & Haydon, D. T., 2010. Building the bridge between animal movement and population dynamics. *Philisophical Transactions of the Royal Society, 365*, 2289-2301.

Moseby, K. E., Read, J. L., Paton, D. C., Copley, P., Hill, B.M., & Crisp, H. A., 2011. Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation, 144*, 2863-2872.

Mosser, A., & Packer, C., 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour, 78*, 359-370.

Mucina, L., & Rutherford, M. C. (Eds), 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria.

Nelson, E. H., Matthews, C. E. & Rosenheim, J. A., 2004. Predators reduce prey population growth by inducing changes in prey behavior. *Ecology, 85*, 1853-1858.

New, M., Lister, D., Hulme, M., & Makin, I., 2002. A high-resolution data set of surface climate over global land areas. *Climate Research, 21*, 1-25.

Ngoprasert, D., Lynam, A. J., & Gale, G. A., 2007 Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx, 41*, 343-351.

Nichols, J. D. & Armstrong, D. P., 2012. Monitoring for reintroductions. In Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (Eds), Reintroduction biology: integrating science and management (pp. 223–255). Oxford, U.K.: Wiley-Blackwell.

O'Brien, R. M., 2007. A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Quality & Quantity, 41*, 673-690.

Packer C., & Pusey, A. E., 1983. Adaptations of female lions to infanticide by incoming males. *The American Naturalist, 121*, 716-728.

Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., et al., 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia, 169*, 419-430.

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., et al., 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology, 23*, 970-976.

Powell, R. A. 2000. Animal home range and territories and home range estimators. In Boitani L., & Fuller, T. K. (Eds), Research techniques in animal ecology:

controversies and consequences (pp. 65-103). New York, USA: Columbia University Press.

Preatoni, D., Mustoni, A., Martinolia, A., Carlinib, E., Chiarenzib, B., Chiozzinib, S., van Dongenc, S., Wautersa, L. A., et al., 2005. Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. *Acta Oecologica, 28*, 189-197.

Preisser, E. L., Bolnick, D. I. & Benard, M. F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology, 86*, 501-509.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Recto, M. R., Mathieu, R., Virgós, E., & Seddon, P. J., 2014. Quantifying fine-scale resource selection by introduced feral cats to complement management decision-making in ecologically sensitive areas. *Biological Invasions, 16*, 1915-1927.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., et al., 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation, 22*, 17-35.

Ripley, B., 2015. boot: Bootstrap functions. R package version 1.3-17. http://CRAN.R-project.org/package=boot.

Ripple, W.J., & Beschta, R. L., 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management, 184*, 299-313.

Ripple, W. J., & Beschta, R. L., 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience, 54*, 755-766.

Roe, J. H., Frank, M. R., Gibson, S. E., Attum, O., & Kingsbury, B. A., 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. *Journal of Applied Ecology, 47*, 1253-1261.

Rogers, L. L., 1988. Homing tendencies of large mammals: a review. In Nielsen, L., & Brown, R. D. (Eds), Translocation of wild animals (pp 76-92). Wisconsin, USA: Wisconsin Humane Society.

Rosenbaum, D. A., Slotta, J. D., Vaughan, J., & Plamondon, R., 1991. Optimal movement selection. *Psychological Science, 2*, 86-91.

Rosier, D. A., Dorr, V. A. J, & Dorr, E. D., 2008. Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologica, 156*, 465-477.

Rosvall, K. A., 2011. Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology, 22*, 1131-1140.

Ruckstuhl, K. E., Festa-Bianchet, M., & Jorgenson, J. T., 2003. Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex and reproductive status. *Behavioral Ecology and Sociobiology, 54*, 167-173.

Rutherford, M. C., Mucina, L., & Powrie, L. W., 2006. Biomes and bioregions of southern Africa. *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia, 19*, 30-51.

Saltz, D., Rowen, M., & Rubenstein, D. I., 2000. The effect of space-use patterns of reintroduced Asiatic wild ass on effective population size. *Conservation biology, 14*, 1852-1861.

Samuel, M. D., Pierce, D. J., & Gorton, E. O., 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology, 54*, 711-719.

Sand, H., Wikenros, C., Wabakken, P., & Liberg, O., 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society of London B: Biological Sciences, 273,* 1421-1427.

Santana, L., Marco, M. D., Viscount, P., Baisero, D., Botanic, L., & Rondinini, C., 2013. Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix, 24*, 181-186.

Sarrazin, F., & Barbault, R., 1996. Reintroduction: challenges and lessons for basic ecology. *Tree, 11*, 474-478.

Schaller, G. B., 1972. The Serengeti lion. Chicago, USA: University of Chicago Press.

Scheepers, J. L., & Venzke, K. A. E., 1995. Attempts to reintroduce African wild dogs *Lycaon pictus* into Etosha National Park, Namibia. *South African Journal of Wildlife Research, 25*, 138-140.

Schmitt, M. H., Stears, K., & Shrader, A. M., 2016. Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behavioral Ecology*, doi: 10.1093/beheco/arw015.

Schradin, C., Schmohl, G., Rödel, H. G., Schoepf, I., Treffler, S. M., Brenner, J., Bleeker, M., Schubert, M., Königa, B., & Pillay, N., 2010. Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour, 79*, 195-203.

Schuett, W., Tregenza, T., & Dall, S. R. X., 2010. Sexual selection and animal personality. *Biological Reviews, 85*, 217-246.

Seddon, P. J., 1999. Persistence without intervention: assessing success in wildlife reintroductions. *Trends in Ecology & Evolution, 14*, 503.

Seddon, P. J., Armstrong, D. P., & Maloney, R. F., 2007. Developing the science of reintroduction biology. *Conservation Biology, 21*, 303-312.

Shepherd, B., & Whittington, J. 2006. Response of wolves to corridor restoration and human use management. *Ecology and Society, 11*, 1.

Shi, J., Li, D., & Xiao, W., 2011. Influences of sex, group size, and spatial position on vigilance behavior of Przewalski's gazelles. *Acta Theriologica, 56*, 73-79.

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., Preisser, E., Rehage, J. S., et al., 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos, 119*, 610-621.

Simcharoen, S., Barlow, A. C. D., Simcharoen, A., & Smith, J. L. D., 2008. Home range size and daytime habitat selection of leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Biological Conservation, 141*, 2242-2250.

Sitati, N. W., Walpole, M. J., Smith, R. J., & Leader-Wiliams, N., 2003. Predicting spatial aspects of human-elephant conflict. *Journal of Applied Ecology, 40*, 667-677.

Smith, S. M., & Cain III, J. W., 2009. Foraging efficiency and vigilance behaviour of impala: the influence of herd size and neighbour density. *African Journal of Ecology, 47*, 109-118.

Spalinger, D. E., & Hobbs, N. T., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist, 140*, 325-348.

Spinoza, R. M., Serfass, T. L., & Brooks, R. P., 2008. Survival and post-release movements of river otters translocated to western New York. *Northeast Naturalist, 15*, 13-24.

Sponge, G., 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioral Ecology and Sociobiology, 52*, 303-307.

Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., & Parks, S. A., 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation, 157*, 187-195.

Stamps, J. A., Krishnan, V. V., & Willits, N. H., 2009. How different types of natal experience affect habitat preferences. *American Naturalist, 174*, 623-630.

Stamps, J. A., & Swaisgood, R. R., 2007. Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science, 102*, 392-409.

Steffens, K. E., Seddon, P. J., Mathieu, R., & Jamieson, I. G., 2005. Habitat selection by South Island saddlebacks and Stewart Island robins reintroduced to Ulva Island. *New Zealand Journal of Ecology, 29*, 221-229.

Steury, T. D., & D. L. Murray, 2004. Modeling the reintroduction of lynx to the southern portion of its range. *Biological Conservation, 117*, 127-141.

Sutherland, W. J., 1998. The importance of behavioural studies in conservation biology. *Animal Behaviour, 56*, 801-809.

Tambling, C. J., Cameron, E. Z., Du Toit, J. T., & Getz, W. M., 2010. Methods for locating African lion kills using global positioning system movement data. *Journal of Wildlife Management, 73*, 549-556.

Tambling, C. J., & Du Toit, J. T., 2005. Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. Journal of Applied Ecology, 42, 431-441.

Thacker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Neumann, S. M., & Slotow, R., 2011. Minimising predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology, 92*, 398-407.

Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J. R. M., Midgley, G. F. & Corsi, F., 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology, 12*, 424-440.

Tillman, D., & Kareiva, P. (Eds), 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. New Jersey, USA: Princeton University Press.

Townshend, J. R. G., Carroll, M., Dimiceli, C., Solberg, R., Hansen, S. M., & DeFries, R., 2011. Vegetation Continuous Fields MOD44B, 2011-2014 Percentage Tree Cover, Collection 5.1, University of Maryland, College Park, Maryland, 2001. https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod44b. Accessed 09/09/2015.

Travis, J. M. J., Mustin, K., & Barton, K. A., 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behavior and the multiple costs involved. *Methods in Ecology and Evolution, 3*, 628-641.
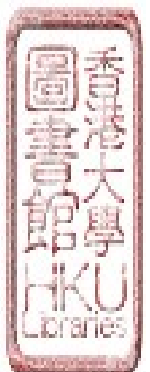
Treves, A., 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour, 60*, 711-722.

Tuqa, J. H., Funston, P., Musyokib, C., Ojwangh, G. O., Gichukid, N. N., Bauerc, H., Tamisa, W., Dolrenryi, S., et al., 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation, 2*, 1-10.

Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W., et al., 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology, 90*, 23-30.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & MacDonald, D. W., 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology, 25*, 337-351.

Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., & Mastered, A., 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology, 80*, 771-785.

Van Moorter, B. V., Rolandsen, C. M., Basille, M., & Gaillard. J. M., 2016. Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology, 85*, 21-30.

Van Oudtshoorn F., 2012. Guide to grasses of southern Africa. Pretoria, South Africa: Briza Publication.

Vanak, A. T., Fortin, D., Thacker, M., Ogden, M., Owen, C., Greatwood, S., & Slotow, R., 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology, 94*, 2619-2631.

Vander Wal, E., & Rodgers., A. R., 2012. An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling, 224*, 48-53.
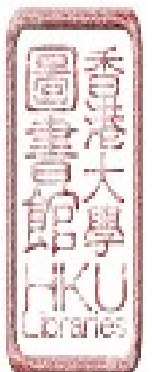
Vanthomme, H., Kozlowski, J., Korte, L., & Alonso, A., 2013. Distribution of a community of mammals in relation to roads and other human disturbances in Gabon, Central Africa. *Conservation Biology, 27*, 281-291.

Verdolin, J. L., 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology, 60*, 457-464.

Vickery, S. S., & Mason, G. J., 2003. Behavioural persistence in captive bears: implications for reintroduction. *Ursus, 14*, 35-43.

Wade, M. J., & Shuster, S. M., 2002. The evolution of parental care in the context of sexual selection: a critical reassessment of parental investment theory. *The American Naturalist, 160*, 285-292.

Wauters, L., Casale, P., & Fornasari, L., 2015. Post-release behavior, home range establishment and settlement success of reintroduced red squirrels. *Italian Journal of Zoology, 64*, 169-175.

Wear, B. J., Eastridge, R., & Clark, J. D., 2005. Factors affecting settling, survival, and viability of black bears reintroduced to Felsenthal National Wildlife Refuge, Arkansas. *Wildlife Society Bulletin, 33*, 1363-1374.

White, P. J., Proffitt, K. M., & Lemke, T. O., 2012. Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist, 167*, 174-187.

Whittingham, M. J., Butler, S. J., Quinn, J. L., & Cresswell, W., 2004. The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos, 106*, 377-385.

Whittingham, M. J. & Evans, K. L., 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis, 146*, 210-220.

Wilmer, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., Kermish-Wells, J., Yovovich, V., et al, 2013. Scale dependent behavioral responses to human development by a large predator, the puma. *PloS One, 8*, e60590
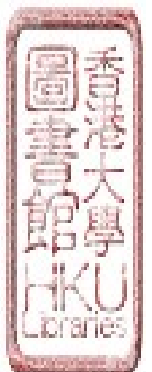
Winker, K., Rappole, J. H., & Ramos, M. A., 1995. The use of movement data as an assay of habitat quality. *Oecologia, 101*, 211-216.

Wirsing, A. J., Cameron, K. E., & Heithaus, M. R., 2010. Spatial responses to predators vary with prey escape mode. *Animal Behaviour, 79*, 531-537.

Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation, 3*, 165-173.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H., 2005. Body size in ecological networks. *Trends in Ecology & Evolution, 20*, 402-409.

Worton, B. J., 1987. A review of models of home ranges for animal movement. *Ecological Modelling, 38*, 277-298.

Zara, J. H., 1984. Biostatistical analysis. New Jersey, USA: Prentice-Hall.
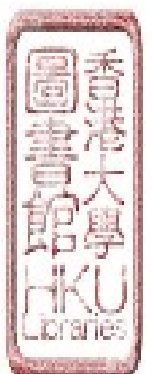
Publication

ORIGINAL ARTICLE

Early post-release movement of reintroduced lions (Panthera leo) in Dinokeng Game Reserve, Gauteng, South Africa

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Abstract Reintroductions have been increasingly used in carnivore conservation. Animal movement influences fitness and survival and is the first behavioural response of reintroduced animals to 'forced dispersal' in a new habitat. However, information available on early post-release movement of reintroduced carnivores remains limited. We studied movements of 11 reintroduced lions (Panthera leo) in Dinokeng Game Reserve, South Africa, in their first season of release and investigated changes in movements over time. Movement patterns of lions were more diverse than expected and varied between sexes and individual groups. Some lion groups returned to the area surrounding the release site after initial exploration and avoided human settlements, suggesting that vegetation and human disturbances influenced dispersal upon release. Cumulative home range size continued to increase for all lions despite individual differences in movement patterns. We highlight the importance of considering the variation in individual-specific behaviour and movement patterns to assess early establishment and reintroduction success.

Keywords Carnivore · Reintroduction · Dispersal · Exploration · Home range · Space use

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Introduction

Dispersal is a key process in animal movement ecology and can happen more than once at any stage in an animal's lifespan (Santini et al. 2013). It can be defined as an animal moving away from its natal or current home range to settle in another area (Bowler and Benton 2005). Dispersal behaviour allows animals to optimize their fitness and breeding opportunities with a trade-off between resource exploration and exploitation (Bonte et al. 2012). Before deciding to settle in a new area, animals typically perform exploratory movements that allow them to learn and compare habitat quality and distribution of competitors and predators (Delgado et al. 2009; Debeffe et al. 2013). However, exploration cost could be high because of the unfamiliarity with the environment, which leads to fitness reduction and high mortality risk due to misadventures (Bonte et al. 2012). Animals therefore need to balance the time and energy spent between exploration and exploitation to maximise benefits gained in dispersal.

While natural dispersal occurs in wild populations, early post-release movement of reintroduced animals can be viewed as 'forced dispersal' (Stamps and Swaisgood 2007). Reintroduction has been increasingly used to reestablish species in their former ranges in which they have been extirpated (Seddon et al. 2007; Armstrong and Seddon 2008). During reintroduction, an animal bred in captivity or captured from a wild population is translocated to a new area (IUCN ...). The process resembles natural dispersal as the animals have to balance the trade-off between exploration and exploitation in both situations, but forced dispersal implies bigger challenges and risks for reintroduced animals because they are forced to learn as efficiently and as quickly as possible, the landscape, environmental conditions and resource distributions that are completely new to them (Berger-Tal and Saltz 2014). ... the lack of knowledge in landscape features, predators ...

competitors, mortality risk during exploration is even higher than in natural dispersals (Spinola et al. 2008), particularly for territorial species like lions (Panthera leo) which defend against intruders aggressively. In addition, homing behaviour is a common occurrence in reintroductions, when animals tend to travel towards the direction of their capture sites upon release (Rogers 1988). Such behaviour has been interpreted as a rejection to the forced dispersal and typically results in lowsite fidelity, i.e. animals are unwilling to settle in the new area (Miller et al. 1999). Understanding movement patterns in the early post-release period is thus critical for the survival and reestablishment of reintroduced animals (Preatoni et al. 2005; Berger-Tal and Saltz 2014).

Large carnivores are frequent subjects of reintroductions due to their predisposed risk of extirpation because of high ecological demands, sensitivity to habitat loss and high potential for human conflicts (Woodroffe 2000; Cardillo et al. 2004; Hayward and Somers 2009). In South Africa, there has been an increase in establishment of small reserves and demand for reintroducing flagship carnivores including lions, leopards (Panthera pardus), cheetahs (Acinonyx jubatus), wild dogs (Lycaon pictus) and spotted hyaenas (Crocuta crocuta) in recent years (Hayward et al. 2007a, b). Most studies on reintroduced carnivores have focused mainly on population control, inbreeding, diseases and human-wildlife conflicts (Ferreira and Hofmeyr 2013; Miller and Funston 2014), while information on post-release movement behaviour is limited (Hayward et al. 2007b; Hunter et al. 2007). Post-release movement pattern allows us to understand the exploration-exploitation trade-off of reintroduced animals during establishment stage and individual variation in movement strategies in adapting to a new environment, which can be used as a tool to assess establishment success (Berger-tal and Saltz 2014). On the other hand, individual movement decisions do not only affect individual fitness but also the behaviour and the interactions of conspecifics and sympatric species (Fortin et al. 2005), which could ultimately have important implications on community structure and population dynamics (Hawkes 2009; Morales et al. 2010). Studying individual animal movement, particularly of large mammalian species that are able to undertake long-distance movement and have large home ranges, is therefore crucial in understanding their spatial dynamics and broader population processes (Tilman and Kareiva 1997).

Our study investigated space use and movement patterns of reintroduced lions subjected to forced dispersal during their early post-release period and to assess the potential of using movement patterns to identify successful reintroductions. Directions of movements, daily movement rates and distances from release sites were compared over time, as well as animal locations in relation to human settlements. We expected movement rates to be highest upon release, decrease over the study period and eventually stabilize, together with an initial increase in distances from the release site during exploration and stabilization or reduction when the animals had settled. An increase in distances from buildings over time was expected in avoidance to human disturbances, a factor found to influence carnivore behaviours in various studies (Kerley et al. 2002; Ngoprasert et al. 2007). We also compared movements at different times of the day to test if forced dispersal increases diurnal activities of lions due to the need to explore the environment and avoid previously released conspecifics. Lastly, we constructed utilisation distributions, a statistical representation of home ranges, and expected a positive relationship between movement rates and cumulative home range sizes for as long as the lions still display exploratory behaviours.

Materials and methods

Study area

The study was undertaken in the entirely fenced 185-km^2 Dinokeng Game Reserve (DGR), situated in the Gauteng and Limpopo Province in South Africa (25.370634° S, 28.379726° E, Fig. 1). DGR is located within the savannah biome, with mixed Bushveld, Kalahari thornveld, and sourish mixed Bushveld representing major vegetation units (Mucina and Rutherford 2006). Altitude of the reserve varies from 1100 m in the southeast to 1200 m in the northwest. Average annual rainfall is 674 mm with distinct wet (October–April) and dry (May–September) seasons (New et al. 2002). The Pienaars River in the west of DGR is joined by the Kaallaagte Spruit and the Boekenhout Spruit, providing perennial source of water in the reserve together with more than 40 natural and artificial dams (Fig. 1; unpublished report, Contour Project Managers CC 2009).

DGR was officially opened in 2011 with the main aim of promoting eco-tourism. It is the first initiative in South Africa to involve provincial government and over 250 private landowners in removing fences and incorporating their land into a larger reserve. DGR is still at a stage of expansion and is expected to span an area of 1200 km^2 after completion (unpublished report, Contour Project Managers CC 2009). More than 15 species of antelopes can be found in DGR; the abundant are blue wildebeest (Connochaetes tau 1635), impala (Aepyceros melampus; 1239), Burc zebra (Equus quagga burchelli; 818) and ble (Damaliscus dorcas phillipsi; 686) (unpublished aerial census data 2012). Prior to the reintroduction leopard and brown hyaena (Hyaena brunnea) were th large carnivores confirmed to exist, but sightin leopards were less than once per year (unpublished Contour Project Managers CC 2009).
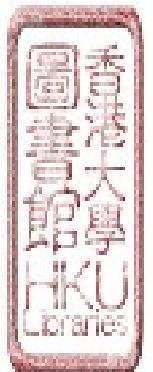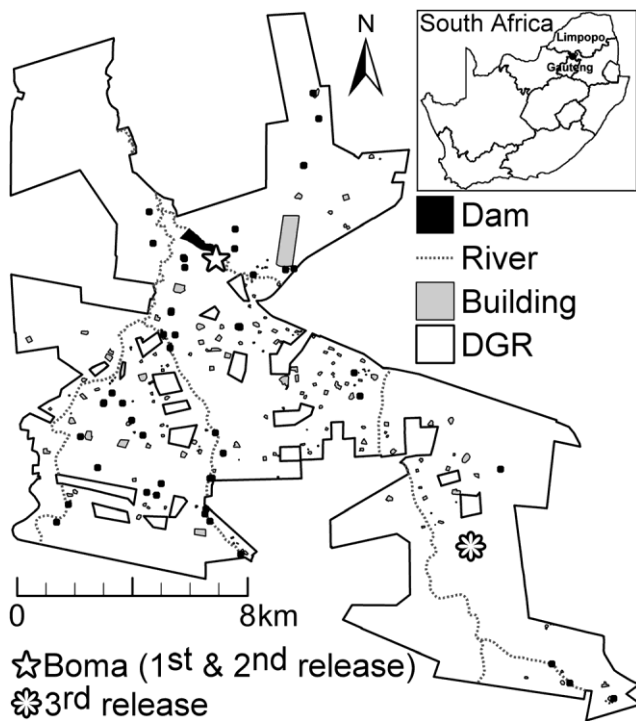
Fig. 1 Study area, the Dinokeng Game Reserve (DGR), with indicated locations of boma and release sites. Location of DGR in South Africa (inset map)

Lion reintroductions and data collection

Eleven lions, four males and seven females of different ages and genetic relatedness, were introduced in three different release events between 2011 and 2013 (Table 1). All information on the reintroductions was collected from Dinokeng Game Reserve Management Association (DGRMA), the official management company of DGR. Lions were captured and translocated from Welgevonden Game Reserve, Pilanesberg Game Reserve, Madikwe Game Reserve and Tembe Elephant Park. Individuals released together were kept in a 45×85 m boma (Fig. 1) for 1 month prior to the release. Keeping the animals in captivity before release is a procedure widely recommended in carnivore reintroduction to facilitate recovery from the shock of capture and translocation and to allow for

acclimation to a new environment and enhance bonding formation between unrelated individuals (Miller et al. 2013). Lions in the first and second reintroduction were released directly from the boma, while animals in the third reintroduction were first translocated from the boma to the southeast of the reserve and released (Fig. 1). The boma was situated next to the biggest dam in the reserve surrounded by dense reed beds (Phragmites australis) and floodplain and riparian vegetation complex that is also the major vegetation type at the release site of the third reintroduction located closely to the river. Females in the first and second releases were injected with contraceptives as a management decision by DGRMA.

All lions were fitted with satellite collars manufactured by Africa Wildlife Tracking (Pretoria, South Africa) that recorded GPS locations at regular intervals (first and second release every 4 h; third release every 5 h). The locations were sent via satellite to an online centralized database and downloaded from there. To document group structure and interactions between groups that could affect their movements, sightings information were obtained from ranger and landowner reports and, where possible, direct observation in the field. We obtained ArcGIS shapefiles of the rivers from unpublished report, Contour Project Managers CC (2009) and created shapefiles of dams and buildings using satellite image from Google Earth (2005). All shapefiles were projected as UTM WGS1984 35S coordinate system in ESRI® ArcMap™ 9.3.1.

Data analyses

We defined early post-release period as the first wet season (October–April; first and second release 2011–2012; third release 2013–2014) after release to control for potential seasonal effects on lion movements due to seasonal distribution of prey (Hunter 1998; Hayward et al. 2009). Movement was analysed as the movements of groups, based on association of animals after release (Table 1). GPS locations of the group member that had the most regular fixes were used, and movements were compared between each 30-day period. Six time periods were included for all groups except lions in the second release that had five time periods only, as they were released in mid-November 2011.

Table 1 Details of the lions reintroduced into Dinokeng Game Reserve during three reintroduction events between 2011 and 2013

Date of release	Group structure after release (group id: lion id)	Age in years at release	Genetic relationship	Capture site
19/10/2011	Males-release 1: M1*, M2	2.5	Brothers	Welgevonden Game R
	Females-release 1: F1*, F2	2	Sisters	
14/11/2011	Males-release 2: M3*, M4	2	Brothers	Pilanesberg Game Re
	Females-release 2: F3*, F4	2	Sisters	Madikwe Game Rese
02/11/2013	Females-release 3: F5*, F6	5	Sisters	Tembe Elephant Park
	Lone female-release 3: F7*	2	Daughter of F5	

Asterisk indicates individual group members with GPS locations data used to representing the group
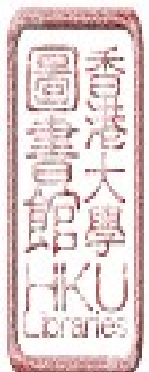
Distance and bearing between consecutive locations, bearing between release and capture site of each group and distance between each location and the release site and nearest buildings were calculated using Hawth's Analysis Tools 3.27 (Beyer 2004) and ESRI® ArcMap™ 9.3.1. Distances between locations were separated into six different time slots and defined as 0400–0800 hours (sunrise), 0800–1200 hours (morning), 1200–1600 hours (afternoon), 1600–2000 hours (sunset), 2000–0000 hours (night) and 0000–0400 hours (midnight) for the lions in first and second release. Because of the 5-h recording interval, locations for lions in the third release were taken at different time in each day, and we defined 0400–0900 hours as sunrise, 0800–1300 hours as morning, 1200–1700 hours as afternoon, 1500–2000 hours as sunset, 1900–0000 hours as night and 2300–0400 hours as midnight. Daily distances travelled were calculated by summing up the distances between locations in each day. Distances to release sites and buildings were averaged across each day, using only the first location when animals remained stationary for more than one location (when distance to the next location was <100 m, a distance used to identify GPS clusters of potential feeding sites of carnivores; Tambling et al. 2010; Wilmers et al. 2013) to prevent pseudo-replication.

Rayleigh test of uniformity (one-sample test for mean angles, Zar 1984) was performed to test the bearings of movement against random distribution separately for each 30-day period using R 3.1.1 (R Core Team 2015) and the R package 'CircStats' (Lund and Agostinelli 2014). Homing behaviour was assumed to be present if the direction from release to capture site fell within the confidence interval of significant direction of travel.

Daily distances travelled were square root transformed and compared between 30-day periods for each lion group using one-way analysis of variance (ANOVA) with post hoc Tukey's HSD test. Due to violation of model assumptions of normality and equal variances even after data transformation, comparison of distances travelled at different times of day and distances between locations and release site and nearest building were done using Kruskal-Wallis non-parametric ANOVA with post hoc Bonferroni-Dunn test. Apart from the 30-day periods, distances to buildings were also compared between weekdays (Monday to Thursday) and weekends (Friday to Sunday; Fridays were included into weekends because of local customary reasons) using Mann-Whitney U test, because human disturbances might be higher on weekends due to higher number of visitors. Kruskal-Wallis non-parametric ANOVA compares data by ranks; therefore, results were reported in box plots showing medians, minimum and maximum values and first and third quartile (Kruskal and Wallis 1952). All statistical tests were performed in R 3.1.1 (R Core Team 2015).

The k-LoCoH (local convex hull; Getz and Wilmers 2004) method was used to construct 50 % core and 95 % full home range utilisation distributions using R package 'adehabitat' in

R2.13.0 (Calenge 2006). Values for k were selected as $\sqrt{n/2}$, where n equals number of locations (Getz and Wilmers 2004). To investigate the process of expansion and stabilization of home ranges over time, we constructed cumulative utilisation distributions by adding the locations of the previous time period, i.e. number of locations was cumulated over time.

Results

Post-release group structure and survival

Lions kept in boma and released together showed varied post-release association (Table 1). In the first and second release, the animals split into pairs of brothers and sisters, and these pairs remained together throughout the early post-release period. In the third release, the youngest females roamed alone most of the time but occasionally joined the two adult females that remained associated. Movement analyses were therefore done separately for these six groups (males-release 1, females-release 1, males-release 2, females-release 2, females-release 3, lone female-release 3).

The females-release 2 and one of the males from males-release 2 were killed in their seventh and fourth month of release, respectively, by the males-release 1. Consequently, from the fifth time period, movement of males-release 2 represented only the one survived individual.

Direction of movements and homing behaviour

None of the lions were found to have movement directions different from random (Rayleigh test of uniformity, p≥0.15). Consequently, no lions were moving towards a specific direction, and no homing behaviour was detected.

Daily movement rate

Average daily distance travelled by lions ranged from 2.42 ± 0.44 to 6.64 ± 0.57 km (mean±SE, Fig. 2). Movements through time varied greatly between groups, with an increase in distance travelled observed in male pair-release 1 in fourth time period (one-way ANOVA, $F_{5,174}=5.49$, p<0.001; Tukey's HSD test, p<0.05) and females-release 1 in [   ] time period (one-way ANOVA, $F_{5,174}=4.01$, p<0.01; T[   ] HSD test, p<0.05). On the contrary, females-releas[   ] lone female-release 3 significantly reduced their distanc[   ] elled in third (one-way ANOVA, $F_{4,145}=2.68$, p[   ] Tukey's HSD test, p<0.05) and fourth time p[   ] (one-way ANOVA, $F_{5,173}=2.94$, p<0.05; Tukey's HS[   ] p<0.05), respectively. Movement of these four lion[   ] stabilized after the initial increases and decreases. A s[   ] cant increase in distance travelled was found in males-r[   ]
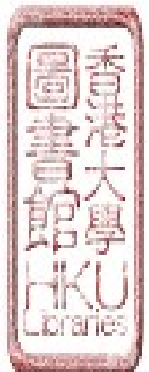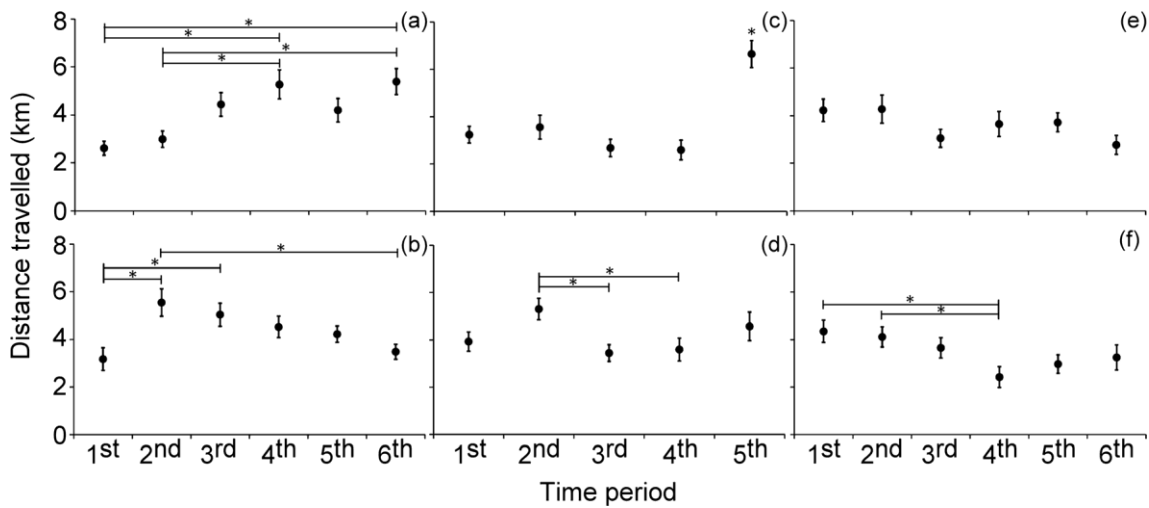
Fig. 2 Average daily distance travelled by lions (mean±SE) during early post-release period in 2011–2012 and 2013–2014 in the Dinokeng Game Reserve, South Africa. Asterisk indicates significant difference. a Males-release 1, b females-release 1, c males-release 2, d females-release 2, e females-release 3 and f lone female-release 3

2 in fifth time period after one member was killed (one-way ANOVA, $F_{4, 144} = 11.92$, $p < 0.001$; Tukey's HSD test, $p < 0.05$), while females-release 3 had similar travel distances throughout the early post-release period.

Movement rates at different times of the day

Lions moved different distances during different times of the day (Fig. 3) and in general moved more at sunrise, night and midnight. The least movements occurred in the morning and afternoon. The animals in the first and second release travelled significantly less in the morning and afternoon than in other times of the day (Kruskal-Wallis test, $\chi^2 > 46.73$, df=5, $p < 0.001$; Bonferroni-Dunn test, $p < 0.05$) during which individual variation was low throughout the entire early post-release period (Fig. 3).

In comparison, lions in the last release travelled significantly less in mornings and afternoons only in the first time period (Kruskal–Wallis test, $\chi^2 > 23.28$, df=5, $p < 0.001$; Bonferroni-Dunn test, $p < 0.05$). Their movement remained similar through the day from second time period onwards.

Distance from release site

Variation among lions in dispersal behaviour upon releases was large. Medians of distances from release site ranged from 1.50 to 7.18 km, first quartile from 0.81 to 6.68 km and third quartile from 1.68 to 8.18 km (Fig. 4), and in all cases but one (females-release 2), these distances differed between time periods (Kruskal-Wallis test, males- and females-release 1 and 3: $\chi^2 > 40.77$, df=5, $p < 0.001$; males-release 2: $\chi^2 = 90.06$, df=4, $p < 0.001$), but what varied was the pattern of these changes. Two lion groups (males-release 2, lone female-release 3) dispersed, resulting in an increase in distance from the sites

through time, while three groups (males-release 1, females-release 2 and females-release 3) travelled back to the area of release sites after initial dispersal, which led to a decrease in distances after an initial increase.

Distance to buildings

Distances to nearest buildings significantly differed between weekdays and weekends only in certain time periods (males-release 1: first time period, females-release 1 and males-release 2: third time period, females-release 2: first and third time period, females-release 3: fifth time period, lone female-release 3: sixth time period; Mann-Whitney U test, U>35, $p < 0.05$).

The effects of the presence of buildings on lion movements changed through time. The distance from buildings kept by males increased significantly over time in both weekdays and weekends (Kruskal-Wallis test, males-release 1: $\chi^2 > 44.32$, df=5, $p < 0.001$; males-release 2: $\chi^2 > 29.25$, df=4, $p < 0.001$; Bonferroni-Dunn Test, $p < 0.05$) (Fig. 5). Among females, some retained a similar distance to buildings during weekdays throughout the entire period (Kruskal-Wallis test, females-release 2: $\chi^2 = 6.68$, df=4, $p = 0.15$; lone female- and females-release 3: $\chi^2 < 8.11$, df=5, $p > 0.15$), while showed a more varied pattern, with their distance to bu decreased from the first to third time period but increase fourth time period onwards (Kruskal–Wallis test, fe release 1: $\chi^2 = 39.27$, df=5, $p < 0.001$). On weekend the exception of a significant decrease in distance fr fifth to sixth time period in lone female- and females-r 3 (Kruskal–Wallis test, $\chi^2 > 14.38$, df=5, $p \leq 0.01$; Bonfe Dunn Test, $p < 0.05$), no obvious difference was seen fro time period to the next. However, all females displ pattern of a gradual decrease in distances over time,
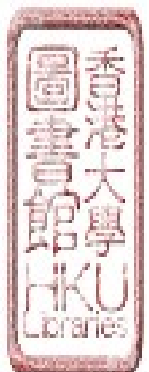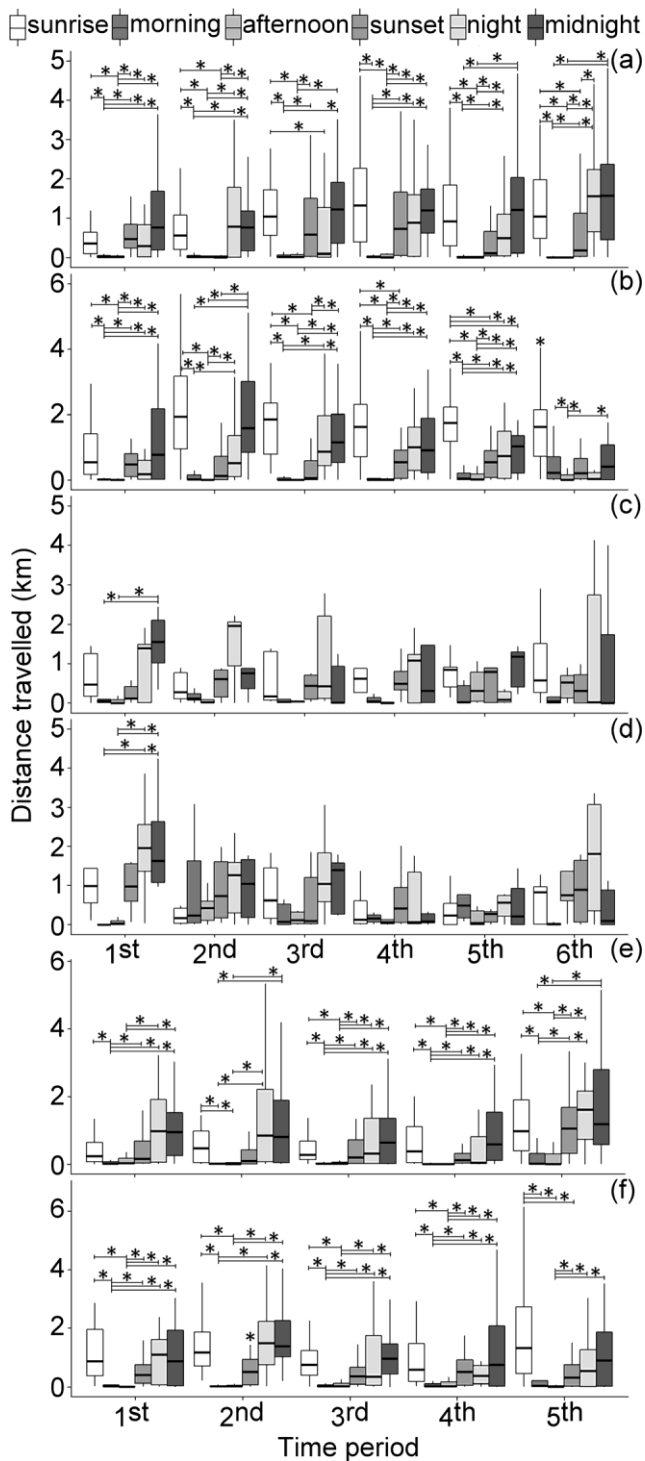
Fig. 3 Average distance travelled by lions in different time of a day during early post-release period in 2011–2012 and 2013–2014 in the Dinokeng Game Reserve, South Africa. Box plot shows median, minimum and maximum values, and first and third quartile. Asterisk indicates significant difference. a Males-release 1, b females-release 1, c females-release 3, d lone female-release 3, e males-release 2 and f females-release 2

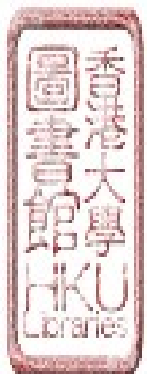though the differences were not statistically significant (Fig. 5).

Utilisation distribution and home range establishment

Cumulative area of 50 % core UD and 95 % full UD of all lions continued to increase through the early post-release period, indicating an expansion in home range (Fig. 6). However, the rates of increase from the first to last time period differed between groups, with females-release 1 having the largest increase of both 50 % core (from 0.06 to 2.71 km^2) and 95 % full UD (from 2.45 to 26.75 km^2), while males-release 2 and males-release 1 had the smallest increase of 50 % core (from 0.03 to 0.54 km^2) and 95 % full UD (1.82 to 13.38 km^2), respectively, in the entire early post-release period (Fig. 6). Although no sign of stabilization in cumulative area was detected, home range expansion appeared to slow down from fifth time period (Fig. 6).

Discussion

As our study shows, individual movement patterns can vary greatly between sexes and individual groups of lions. We found no evidence of homing behaviour, indicating that the animals did not reject the forced dispersal by attempting to break away from the reserve. However, the one dominant pattern in early post-release movement was that of an overwhelming variability. Even though all individuals displayed exploratory behaviour, they performed exploratory movements differently such that certain groups increased while other groups decreased their rates of movement upon release. However, changes in movement rates all occurred in either the second, third or fourth time period, and movements remained similar thereafter. Previous studies in Phinda (Hunter 1998) and Welgevonden Game Reserve (Kilian 2003) both found a general trend of increase in daily movements of reintroduced lions, but these studies were conducted only for the first 3 months of release. Results in DGR suggest that reintroduced lions might take up to 120 days in exploration before making decisions on the most cost-effective movement pattern, which then lead to stabilization of movement rates as we expected.

Increase in rates of movement was found only in lions in the first release. In later releases, the animals had in general lower movement rates than those in the first release, and these rates either decreased or remained relatively unchanged. These differences are likely due to the fact that lions re[...] first were at an advantage of being able to exp[...] competitor-free environment. As territorial carnivores, [...] ural populations, lions are less likely to disperse from [...] main close to their natal prides during dispersal wh[...] numbers of unrelated lions in the surrounding areas ar[...] as exploration in a landscape with high density of comp[...] could lead to territorial conflicts between groups and r[...] fatality (Funston et al. 2003). Without other lions to c[...] with, individuals released first had an opportunity to ex[...]
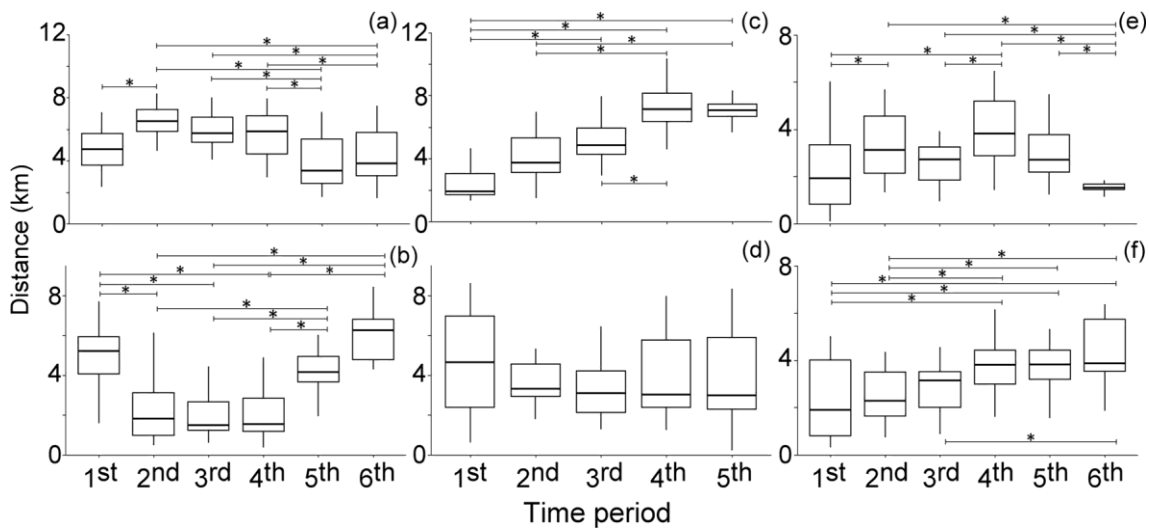
Fig. 4 Average daily distance of lions from release sites during early post-release period in 2011–2012 and 2013–2014 in the Dinokeng Game Reserve, South Africa. Box plot shows median, minimum and maximum values, and first and third quartile. Asterisk indicates significant difference. a Males-release 1, b females-release 1, c males-release 2, d females-release 2, e females-release 3 and f lone female-release 3

and establish territories with no intra-specific constraints. Low intra-specific competition also explains the general increase in movement found in Phinda Game Reserve (Hunter 1998) where lions were released in different areas and in Welgevonden Game Reserve (Kilian 2003) where there was only one release. In contrast, lions released later avoided the already released lions by having lower rates of movements and establishing home ranges that were non-overlapped with the animals released earlier (the authors, unpublished information).

After the death of one male in males-release 2, the remaining one male increased its movement during sunrise and sunset. This coincides with the behaviour observed previously in lions and other carnivores where nomadic individuals became more active diurnally to minimise interactions with dominant competitors (Hayward and Hayward 2006; Hayward and Slowtow 2009). The increase in movement might also result

from the animal relocating itself more frequently to minimise the chance of being detected, as highlighted by a shift in home range of the surviving male away from its original range taken by males-release 1 after the death of the coalition member (the authors, unpublished information). Avoidance of conspecifics could also explain why lions released in the last reintroduction had similar movement rates across different time of a day, compared to lions in the first release that had the lowest rate of movement during day time throughout the study period.

Dispersal from the release sites varied between lion groups and did not coincide with changes in movement rates. This differs from the increase in distance of released lions from boma reported by Hunter (1998) and Kilian (2003) but is similar to the diverse dispersal patterns found in other translocated or reintroduced carnivores (Linnell et al. 1997; Preatoni et al. 2005). Various factors including intra-specific

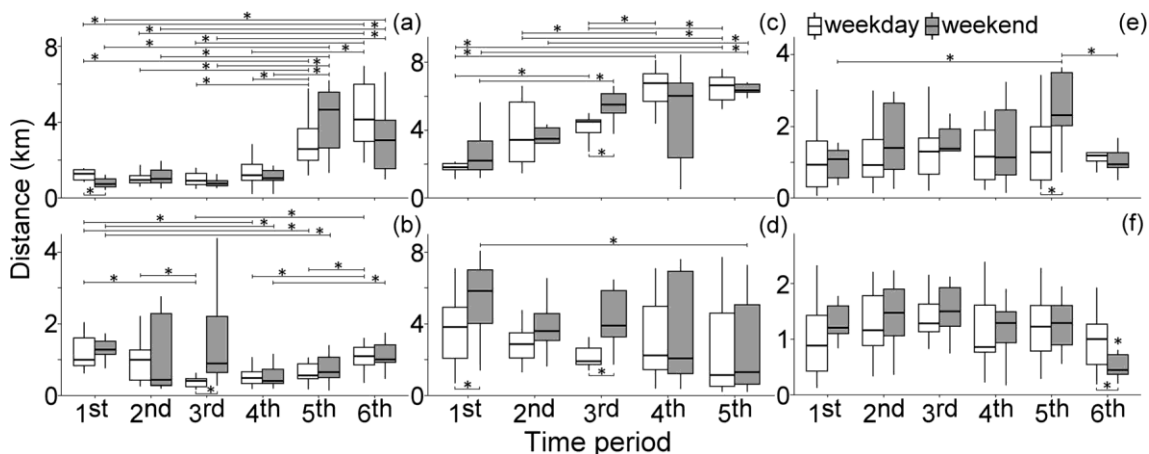Fig. 5 Average daily distance of lions from nearest building during early post-release period in 2011–2012 and 2013–2014 in the Dinokeng Game Reserve, South Africa. Box plot shows median, minimum and maximum values, and first and third quartile. Asterisk indicates significant difference. a Males-release 1, b females-release 1, c males-release 2, d females-release 2, e females-release 3 and f lone female-release 3
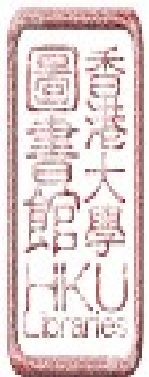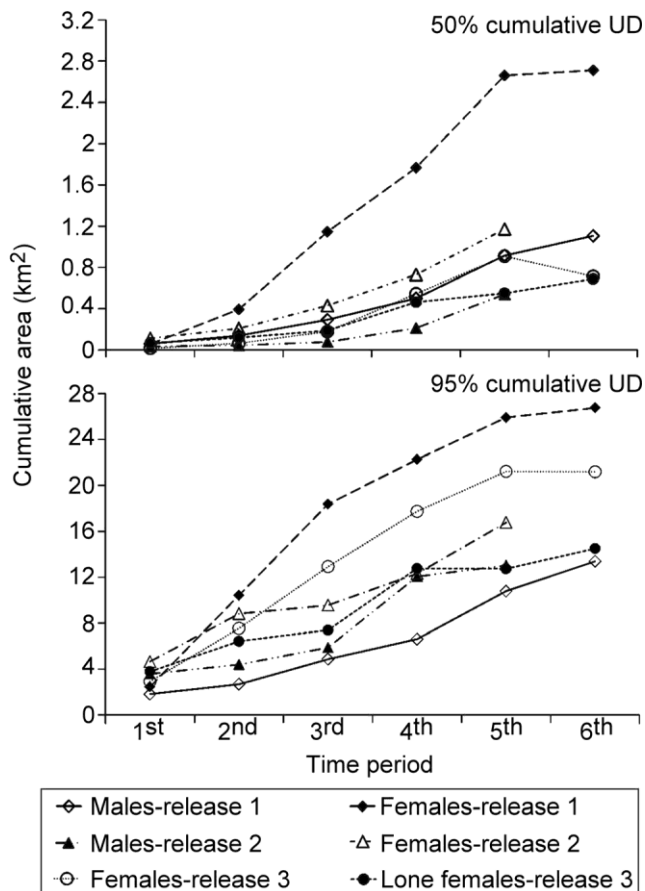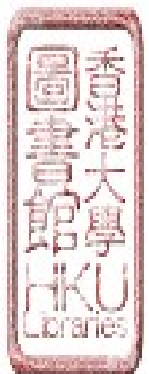
Fig. 6 Cumulative area of 50 % core and 95 % full utilisation distribution of lions during early post-release period in 2011–2012 and 2013–2014 in the Dinokeng Game Reserve, South Africa

interactions, internal states of individuals, habitat quality and experiences in natal habitats are suggested to influence dispersal and settlement decisions of animals (Benard and McCauley 2008; Stamps et al. 2009; Santini et al. 2013). The boma in DGR is situated next to the biggest dam in the reserve (Fig. 1) which attracts different herbivores, with vegetation in the area consisting mainly of dense reed beds and riparian vegetation that are ideal for lions to ambush their prey and rest (Spong 2002). During the first release, the behaviour of lions returning to and settling in the area around the boma after initial dispersals was likely because of a preference for the reed beds after initial exploration of the environs. In fact, the core home ranges with high frequencies of revisit of the animals were centred at the dam throughout their first 3 years of release, and they were observed to hunt and rest continuously and hide their cubs in the area (the authors, unpublished information). In contrast, males in the second release dispersed continuously, while females in the same release settled in an area at least 3 km away from the boma after initial dispersal. The differences in dispersal upon release indicate that lions released later did not only move differently as mentioned before but also used the space differently in order to

avoid conflicts with the lions released first. The lions released last were translocated and released in open Combretum molle vegetation in the south east side of the reserve. They then dispersed and settled 3–4 km away from the site close to rivers with floodplains and riparian vegetation, two vegetation types preferred by the lions in the study site (the authors, unpublished information) that are known to favour lions hunting (Spong 2002; De Boer et al. 2010).

The presence of buildings affected males and females differently. Upon release, males continued to move away from buildings, while females, after initial increase, generally decreased distance to building over time. Results coincide with the behaviour of reintroduced elephants in DGR that selected areas away from buildings (De Hoog 2014) and other species in several studies elsewhere that avoided human activities (Ngoprasert et al. 2007; Vanthomme et al. 2013), suggesting that human settlement was perceived as a disturbance by lions and elephants reintroduced to the reserve. While initial responses of females were to move away from buildings, the decrease in distance over time likely indicates their habituation to the disturbance which was not observed in males. Differences of distance to buildings between weekdays and weekends were found in certain time periods. DGR was still newly established with visitors and tourists consisting mainly of local people who came to visit during weekends (S-W Yiu, personal observation). Thus, higher disturbances during weekends could have contributed to the larger distances of lions to buildings in weekends than in weekdays. Differences in the number of weekend visitors staying in different lodges and residences during different times could have led to continuous changes in the intensity of disturbances and explained why lions behaved differently between time periods.

Despite the highly varied movement patterns, cumulative home ranges of all lion groups continued to increase in size over time. Space use is mostly driven by resource availability that determines the size of animal home ranges (Herfindal et al. 2005; Hayward et al. 2009). Previous studies of home ranges of reintroduced carnivores focused primarily on seasonal ranges (Hunter 1998; Druce et al. 2004), not the process of establishment and expansion of home ranges after release. Our investigation of cumulative home ranges suggests that reintroduced lions were continuously expanding their range of exploration, with different movement strategies u different groups. Although lions expanded both core an home ranges, their core home range remained below which indicate that they were able to acquire resour survival within small areas, and the presence of fence impose a constraint on their movement. Hayward et al suggested that fencing does not affect predator behav- ic home range sizes remained correlated with prey abu in fenced reserves. DGR has high prey abundance (ove herbivores excluding elephants Loxodonta

africana, white rhinoceros Ceratotherium simum and hippopotamus Hippopotamus amphibius; unpublished DGR aerial census data 2012); therefore, the lions did not have to establish large home ranges to secure food. The decline in home range expansion upon the fifth time period indicates that lions begun reducing their exploration and starting to settle in the established home ranges.

To summarize, the reintroduced lions displayed highly complex and diverse post-release movements, where rates of movement do not necessarily correlate with spatial exploration. Optimal movement decisions of animals are to a certain extent influenced by individual ability to learn and navigate through a landscape of heterogeneous resource patches (Bélisle 2005; Roshier et al. 2008), which in DGR was shown by the varied movement patterns of different lions. As this study demonstrates, behavioural responses of lions to forced dispersal of reintroduction, their subsequent ways in exploring and adapting to a new habitat and optimal movement decisions can differ greatly between individuals, depending on intra-specific interactions, habitat preferences, human disturbances and individual experiences that vary in spatial and temporal scales. The absence of homing behaviour, stabilization in movement rates, habituation to human disturbances and decline in rates of home range expansion all together suggest release site fidelity and successful establishment of reintroduced lions. An absence of homing behaviour and a sign of stabilization in movement patterns could potentially be used as criteria for assessing early establishment success in future reintroductions. However, we show how movements can be disrupted by inter-group interactions as evidenced by the changes in movement of a male after the coalition member was killed. The behavioural differences between lions in different releases show that the presence of competitors greatly affects the exploratory movement of reintroduced animals, with intra-specific competition being the most important driver of movement decisions for those released later. Therefore, the order and release site of lion reintroductions should be planned to minimise intra-specific competition and direct conflict between groups in early establishment stages which could otherwise lead to selection of suboptimal resources and reduction in fitness.

References

Armstrong DP, Seddon PJ (2008) Directions in reintroduction biology. Trends Ecol Evol 23(1):20–25

Bélisle M (2005) Measuring landscape connectivity: the challenge of behavioural landscape ecology. Ecology 86(8):1988–1995

Benard MF, McCauley SJ (2008) Integrating across life-history stages: consequences of natal habitat effects on dispersal. Am Nat 171(5): 553–567

Berger-Tal O, Saltz D (2014) Using the movement patterns of reintroduced animals to improve reintroduction success. Curr Zool 60(4):515–526

Beyer HL (2004) Hawth's analysis tools for ArcGIS. Version 3.27. http://www.spatialecology.com/htools/ Accessed Jul 2011

Bonte D, Dyck HV, Bullock JM et al (2012) Costs of dispersal. Biol Rev 87:290–312

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80(2):205–225

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197: 516–519

Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. PLoS Biol 2(7), e197. doi:10.1371/journal.pbio.0020197

de Boer WF, Vis MJP, De Knegt HJ et al (2010) Spatial distribution of lion kills determined by the water dependency of prey species. J Mammal 91(5):1280–1286

de Hoog (2014) Habitat selection of African elephants (Loxodonta africana) after reintroduction in Dinokeng Game Reserve. MSc thesis, University of the Witwatersrand, South Africa

Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Coulon A, Gaillard JM, Bon R, Hewison AJM (2013) Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. Anim Behav 86:143–151

Delgado MM, Penteriani V, Nams VO, Campioni L (2009) Changes of movement patterns from early dispersal to settlement. Behav Ecol Sociobiol 64:35–43

Druce D, Genis H, Braak J, Greatwood S, Delsink A, Kettles R, Hunter L, Slotow R (2004) Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. Koedoe 47(1):103–118

Ferreira SM, Hofmeyr M (2013) Managing charismatic carnivores in small areas: large felids in South Africa. S Afr J Wildl Res 44(1): 32–42

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330

Funston PJ, Mills MGL, Richardson PRK, van Jaarsveld AS (2003) Reduced dispersal and opportunistic territory acquisition in male lions (Panthera leo). J Zool 259:131–142

Getz WM, Wilmers CC (2004) A local nearest-neighbor conv[...] construction of home ranges and utilisation distrib[...] Ecography 27:489–505

Google Earth 6.0 (2005). Accessed Jul 2013

Hawkes C (2009) Linking movement behaviour, dispersal and po[...] processes: is individual variation a key? J Anim Ecol 78:89[...]

Hayward MW, Hayward GJ (2006) Activity patterns of reintrodu[...] Panthera leo and spotted hyaena Crocuta crocuta in th[...] Elephant National Pak, South Africa. Afr J Ecol 45(2):135–[...]

Hayward MW, Slowtow R (2009) Temporal partitioning of ac[...] large African carnivores, tests of multiple hypotheses. [...] Wildl Res 39(2):109–125
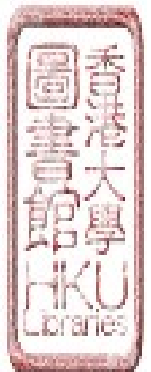
Hayward MW, Somers MJ (eds) (2009) Reintroduction of top-order predators. Blackwell Publishing, West Sussex

Hayward MW, Adendorff J, O'Brien J et al (2007a) The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. Oryx 41(2):205–214

Hayward MW, Adendorff J, O'Brien J et al (2007b) Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. Open Conserv Biol J 1:1–11. doi:10.2174/1874-8392/07

Hayward MW, Hayward GJ, Druce DJ, Kerley GIH (2009) Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. Biodivers Conserv 18:887–904

Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). J Zool 265(1):63–71

Hunter LTB (1998) The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa. PhD thesis, University of Pretoria, South Africa

Hunter LTB, Pretorius K, Carlisle LC, Rickelton M, Walker C, Slotow R, Skinner JD (2007) Restoring lions Panthera leo to northern KwaZulu-Natal, South Africa: short-term biological and technical success but equivocal long-term conservation. Oryx 41(2):196–204

IUCN (1998) Guidelines for re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group. IUCN, Gland

Kerley LL, Goodrich JM, Miquelle DG, Smirnov EN, Quigley HB, Hornocker MG (2002) Effects of roads and human disturbances on Amur tigers. Conserv Biol 16(1):97–108

Kilian PJ (2003) The ecology of reintroduced lions on the Welgeconden Private Game Reserve, Waterberg. MSc thesis, University of Pretoria, South Africa

Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. J Am Stat Assoc 47:583–621

Linnell JDC, Odden J, Smith ME (1997) Translocation of carnivores as a method for managing problem animals: a review. Biodivers Conserv 6:1245–1257

Lund U, Agostinelli C (2014) CircStats: Circular Statistics, from BTopics in circular Statistics^ (2001). R package version 0.2-4. http://CRAN.R-project.org/package=CircStats

Miller SM, Funston P (2014) Rapid growth rates of lion (Panthera leo) populations in small, fenced reserves in South Africa: a management dilemma. S Afr J Wildl Res 44(1):43–55

Miller B, Ralls K, Reading RP, Scott JM, Estes J (1999) Biological and technical considerations of carnivore translocation: a review. Anim Conserv 2(1):59–68

Miller SM, Blssett C, Burger A et al (2013) Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines. S Afr J Wildl Res 43(2):138–154

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. Philos Trans R Soc Lond B 365:2289–2301

Mucina L, Rutherford MC (eds) (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria

New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. Clim Res 21:1–25

Ngoprasert D, Lynam AJ, Gale GA (2007) Human disturbance affects habitat use and behaviour of Asiatic leopard Panthera pardus in Kaeng Krachan National Park, Thailand. Oryx 41(3):343–351

Preatoni D, Mustoni A, Martinoli A et al (2005) Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. Acta Oecol 28:189–197

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Rogers LL (1988) Homing tendencies of large mammals: a review. In: Nielsen L, Brown RD (eds) Translocation of wild animals. Wisconsin Humane Society, Wisconsin, pp 76–92

Roshier DA, Doerr VAJ, Doerr ED (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. Oecologia 156(2):465–477

Santini L, Marco MD, Visconti P, Baisero D, Boitani L, Rondinini C (2013) Ecological correlates of dispersal distance in terrestrial mammals. Hystrix 24(2):181–186

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conserv Biol 21(2):303–312

Spinola RM, Serfass TL, Brooks RP (2008) Survival and post-release movements of river otters translocated to western New York. Northeast Nat 15(1):13–24

Spong G (2002) Space use of lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. Behav Ecol Sociobiol 52:303–307

Stamps JA, Swaisgood RR (2007) Someplace like home: experience, habitat selection and conservation biology. Appl Anim Behav Sci 102:392–409

Stamps JA, Krishnan VV, Willits NH (2009) How different types of natal experience affect habitat preferences. Am Nat 174(5):623–630

Tambling CJ, Cameron EZ, Du Toit JT, Getz WM (2010) Methods for locating African lion kills using global positioning system movement data. J Wildl Manag 73(3):549–556

Tilman D, Kareiva P (eds) (1997) Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, New Jersey

Vanthomme H, Kolowski J, Korte L, Alonso A (2013) Distribution of a community of mammals in relation to roads and other human disturbances in Gabon, Central Africa. Conserv Biol 27(2):281–291

Wilmers CC, Wang Y, Nickel B, Houghtaling et al (2013) Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE 8(4), e60590

Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. Anim Conserv 3(2):165–173

Zar JH (1984) Biostatistical analysis. Prentice-Hall, New Jersey