UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

Prey and range use of lions on Tswalu Kalahari Reserve

by

David James Roxburgh

Submitted in partial fulfillment of the requirements for the degree of
Magister Scientiae in Wildlife Management

Centre for Wildlife Management
Department of Animal and Wildlife Sciences
Faculty of Natural and Agricultural Sciences
University of Pretoria
Pretoria
0002

Supervisor: Prof. J. du P. Bothma

November 2008

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

This dissertation is dedicated to my family and friends.

Thank you for all your love and support

Prey and range use of lions on Tswalu Kalahari Reserve

By

David James Roxburgh

Supervisor: Prof. J. du P. Bothma

Centre for Wildlife Management
Department of Animal and Wildlife Sciences
Faculty of Natural and Agricultural Sciences
University of Pretoria

Magister Scientiae (Wildlife Management)

ABSTRACT

The exact ecological and economic role of lion *Panthera leo* populations on small enclosed reserves is poorly understood. The management and monitoring of such populations is important to ensure their long-term survival. The prey use, range use and habitat selection of an isolated lion population were investigated. The study was conducted on a small (> 1000km^2), enclosed predator camp of Tswalu Kalahari Reserve, situated in the Northern Cape Province of the Republic of South Africa.

The prey selection, prey preferences and prey biomass removal were determined by using indirect and direct observations. Kill sites, carcasses and scats were located by spoor tracking and opportunistic observations and collated into a prey selection list. The prey selection was used to determine any prey preferences and the prey biomass removal by the lion population. The scats data was corrected for relative prey biomass and compared to the kill data and uncorrected scat data. 19 prey types were used, with the gemsbok *Oryx gazelle* and blue wildebeest *Connochaetes taurinus* being utilized most. The lion population had clear preferences for specific small and large mammals which concurred with other studies done on Kalahari lion behaviour. The prey biomass removal (9.9kg/Lion feeding Unit/day) was higher than several other studies done on lion consumption rates.

The range use and habitat selection were determined by using direct and indirect observations. The minimum convex polygon method and kernel density estimates were used to delineate the ranges of the lion population. The mean range size of the Tswalu lions (91 km^2) was similar to those found for lions in more mesic environments. The lions also had clear habitat preferences which depended on the habitat preferences of the prey and the prey density.

A population viability analysis, using VORTEX 9.72, was conducted. An Ecological capacity was determined and used to model various environmental scenarios. The population was found to be viable, but constant monitoring and updating are needed. Management recommendations for the conservation of lions and their prey are provided

Key words: Lions, Kalahari, small reserve, prey use, range use, habitat selection, population viability analysis.

DECLARATION

I hereby declare that this dissertation, which I hereby submit for the degree: Magister Scientiae (M.Sc) (Wildlife Management) at the University of Pretoria, is my own work and has not previously been submitted by me for degree purposes at this or any other tertiary institution.

Signature:………………………………………………

Date:……………………………………………………

ACKNOWLEDGEMENTS

Any project requires the generous assistance of many people. I would sincerely like to thank the following people and organizations:

First and foremost I would like to sincerely thank my family, Robbie, Giddy and John for all the loving support provided throughout my time at University and throughout my life. I really appreciate everything you have done for me and continue to do for me. They also provided financial assistance and assistance in the field, even if it meant throwing shoes at a charging lion.

My supervisor, Prof. J. du P. Bothma, for his encouragement and support. Prof, thank you for listening to me even if I did repeat painful questions. I was very honoured to have worked with such an expert in the field of carnivore biology. Thank you also for the numerous corrections and suggestions that were provided in the dissertation

Dr. Michael Somers, for comments on the management recommendations chapter (Chapter 7) and his positive attitude towards the study of wildlife.

The staff and students of the Centre for Wildlife Management at the University of Pretoria. Tannie Liset Swanepoel, affectionately known as ‘Ma’, provided hours of entertainment through stories, tea times and field trips. Tannie, I will never forget the support and help you have given me, thank you so much. Prof. Wouter van Hoven, Ben Orban, Dr Michael Somers and L.D van Essen are thanked for their help with my many questions on GIS, lion biology, stats and the best way to cook fresh springbok fillets. To my colleagues in the ‘Senior Nagraads Gebou’ Samuel Laurence, Marzanne Cromhout, Jason Turner, Jason Tarr, Jerome Gaugris, Kelly Marnewick, Haemish Melville, Danie van Eeden, Danie Venter and Lourens Swanepoel who all played a part in my research, either by answering questions or just providing high quality entertainment during the long days in the office. Marie Venter, Henda van Vuuren and Prof Ned Donkin always had a kind word and offered loads of support during my lengthy stay at University.

Craig Tambling was a rock when it came to statistical analysis and general comments regarding my masters. Samuel Laurence also deserves a special mention for pulling Craig back on track when we weren't having fun.

Dr Frans Kamfer and Rina Owen, Department of Statistics, University of Pretoria, provided initial assistance with the statistical analysis of the data set

Emily Lehman, who provided several days of field assistance, love and support throughout the many cold winter nights. Thank you so much for all your help

The various sponsors of the project: Tony and Mandy of Bridgestone-Firestone South Africa, Richard Gie of GPTech, SAB-Miller and Safari Centre Menlyn. This research would have been very difficult were it not for your kind and generous assistance.

To the staff of Tswalu Kalahari Reserve: Gus van Dyk, Mark Rutherford, Richard Sathekge, Murray Letcher, Keith Jenkinson, Andrew Stainthorpe, the late Johan Lensing, Zaccharia Assegaai, Nicolene Kotze and Francois Lombard. A special mention must go to Mark Rutherford, the Lekgaba section ranger, for all his assistance and spaghetti-on-toast dinners.

The Tswalu game scouts: Nonnas, Doctor, Andries and John. Your knowledge was an invaluable tool for me in getting to know the lions and spoor tracking techniques.

To Oom Marius and family. You were my family away from home. Thank you for all the meals and friendly conversation you provided. I will always be indebted to you for everything you did for me.

Oom Seun, who fixed my car many times and provided hours of entertainment

The Oppenheimer trust, especially Nicky and Strilli Oppenheimer, who allowed me to study on their beautiful reserve, the helicopter and airplane trips and the dinners at Motse. Duncan MacFadyen is sincerely thanked for co-coordinating the project and providing answers to my silly questions.

Finally, I would like to thank Kleintjie, Molelo, Mokgaladje, Marara, Bonolo, Kagisho, Bontle and the cubs for providing me with such good memories and fun times. I really enjoyed the time spent with the lion population of Tswalu Kalahari Reserve.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The future of large African predators, particularly the lion *Panthera leo* (Linnaeus, 1758), is uncertain in the wild. Nowell & Jackson (1996) estimated that a total African lion population of 30 000 to 100 000 individuals exist in sub-saharan Africa. However, this number has recently been placed at only 40 000 lions, in 36 sub-populations, existing in sub-saharan Africa today (Chardonnet 2002). The majority of these sub-populations occur in east and southern Africa (Chardonnet 2002), with the highest concentration of lions, half of the total African population, found in southern Africa. Lions are listed as vulnerable (east and southern African subspecies) by the World Conservation Union and are listed on Appendix II of CITES (Convention on International Trade in Endangered Species). The current human population explosion and increase in livestock densities have caused a drastic decline in the available habitat for lions (Chardonnet 2002). Few wild lion populations exist today (Killian 2003), with the majority of the lion populations occurring in conservation areas (Figure 1). Several diseases are one reason for the drastic decline in lion population numbers, such as feline immunodefiency virus (FIV), canine distemper virus (CDV) and feline parvovirus (Packer, Altizer, Appel, Brown, Martenson, O'Brien, Roelke-Parker, Hoffman-Lehmann & Lutz 1999; Chardonnet 2002).

Large carnivore management in Africa is a political and scientific challenge because of human conflict and related mortalities with large carnivores (Cotterill 1997; Caro, Pelkey, Borner, Campbell, Woodworth, Farm, Ole Kuwai, Huish & Severre 1998; Butler 2000; Treves & Karanth 2003; Graham, Beckerman & Thirgood 2005; Van Bommel; Bij de Vaate, de Boer & de Iongh 2007). The booming tourism industry in southern Africa has contributed to many lion relocations and breeding programmes (Chardonnet 2002; Killian 2003).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

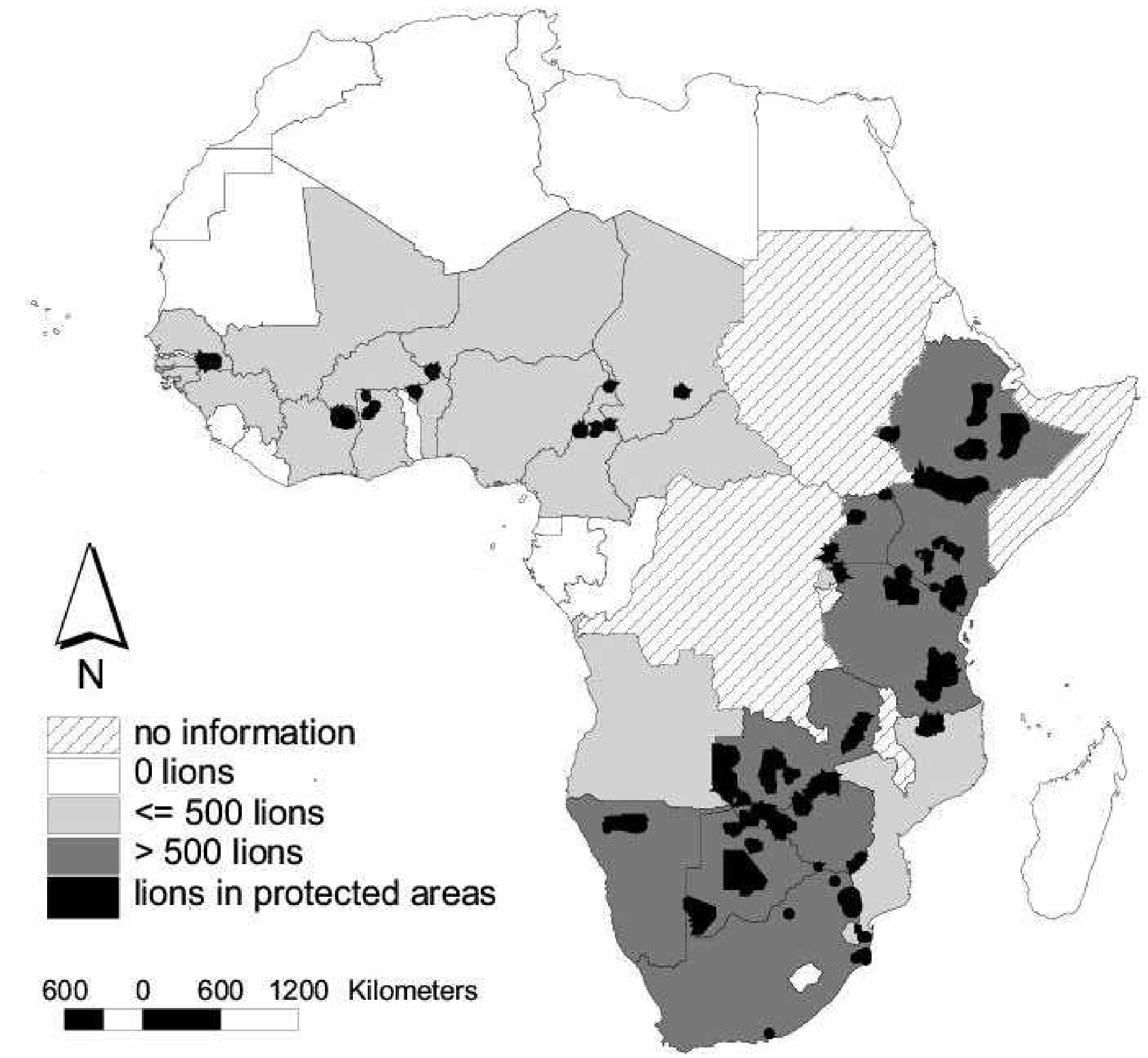

Figure 1: The distribution of the lion *Panthera leo* in Africa (Bauer & Van der Merwe 2002).

These lions have been established in almost every available type of habitat in southern Africa.

Lions are the only truly social felid species (Cooper 1991; Kays & Patterson 2002; Viljoen 2002) with groups of related and unrelated individuals living together within a pride (Grinnell & McComb 2001). A pride can consist of two to nine related females and their young, and a single male or a coalition of males that have entered the pride from another area (Bertram 1975; Caraco & Wolf 1975; Smuts 1982; Nowell and Jackson 1996; Packer, Gilbert, Pusey & O'Brien 1991; Heinsohn 1997; Sunquist & Sunquist 2002; West & Packer 2002). Cooperative hunting and cooperative parental care contribute to it being truly social (Bertram 1975; Packer & Rutton 1988; Packer, Pusey & Eberly 2001). A large proportion of every day is spent conserving energy (Estes 1997). This rest period can last as long as 20 hours in a day. Playing, grooming and offspring care also form important parts of lion behaviour (Heinsohn & Packer 1995).

The advantages of living in a group are protection from physical factors such as extreme cold by huddling together and conserving energy, protection against other predators in this case against other lion populations and invading lions, finding and obtaining food, taking down large prey, group defense of natural resources and a division of labour where males provide protection and the females provide food and care for the young (Davies & Dee Boersma 1984; Cooper 1991). There are, however, a few disadvantages of living in a group. An increased risk of the spread of disease (Smuts 1982; Atwood & Weeks 2003) and parasites is present in populations which live in close proximity. Intraspecific competition occurs within prides, causing injury or death to certain individuals and reproductive interference occurs which results in inbreeding and the killing of cubs (Packer & Pusey 1983; Feldhammer, Drickamer, Vessey & Merritt 1999; Sunquist & Sunquist 2002)

Lions are the top predator in Africa, being able to capture prey from as small as elephant shrews *Elephantulus* spp. to as large as immature elephants *Loxodonta africana* (Skinner & Smithers 1990; Estes 1997; Van Dyk 1997; Sunquist & Sunquist 2002; Joubert 2006), and have even been recorded to be able to kill and adult black rhinoceros *Diceros bicornis* (Brain, Forge & Erb 1999). Lions are mainly nocturnal hunters, but will hunt during the day when the need arises (Skinner & Smithers 1990). The prey preference of lions depends on the size of the pride, the terrain and the availability of a particular type of prey. Some prides seem to specialize in killing certain prey and develop strategies accordingly.

Many factors have to be taken into consideration when measuring the impact of predation on the prey items (Mills & Schenk 1992). They include:

- Prey selection
- Predator behaviour
- Frequency of kills
- Fecundity and survival rates of prey

The tourism and hunting industries have developed an economically driven need for the introduction of large predators on wildlife ranches or small commercial wildlife reserves (Van Schalkwyk 1994; Yamazaki 1996; Creel & Creel 1997; Van Dyk 1997; Power 2003; Loveridge, Searle, Murindagomo & Macdonald 2007). Smaller reserves require intense management of their lion populations (Power 2003), while larger reserves with more space and a larger prey base require less intensive management (Van Schalkwyk 1994). On enclosed reserves, it is essential to monitor the population parameters of the lions (Viljoen 2002) because the lions will have a negative effect on the prey within the reserve (Power 2003). Prey resources have to be replenished on an annual basis on small enclosed reserves (Power 2003). The highest natural population densities (4 lions per $10km^2$) occur in East Africa and it is suggested that these maximum densities are maintained in intensively managed enclosed reserves (Power 2003).

The predator section (Lekgaba) on Tswalu Kalahari Reserve is a self-sustaining natural predator-prey system of around 20 000 ha in a semi-arid environment in the eastern Kalahari region of South Africa. In June 2001, four problem lions were captured from the southern Kalahari (Kgalagadi Transfrontier Park) and were introduced onto the Lekgaba section of Tswalu. These 'fence-jumpers' prove a serious problem for neighbouring farmers and rather than be shot they are captured and moved to other areas (Van Vuuren, Herrmann & Funston 2005). The unique hunting patterns and behaviour of the Kalahari lion (Eloff 2002) necessitated the capture of lions from similar habitats to that of Tswalu. Two unrelated females and two unrelated males were introduced into holding bomas for approximately three months until they had acclimatized to the specific local conditions. Four litters have been produced since their release. All four litters were sired by the dominant male. The fourth litter, born to the younger female, did not survive due to infanticide and as such were not included in the study. The younger male was also not included in the study because he had escaped several times and was deemed a problem animal by the Tswalu management staff. This younger male was later transported to the Johannesburg Zoological Gardens and was then sold to a private institution.

Lekgaba currently has five main waterholes. This area is relatively large when compared with other reserves that accommodate lions (Killian 2003; Power 2003), but still requires management of the lion population. A confined prey base cannot escape from predation pressure (Killian 2003) and is subjected to constant utilization by predators (Power 2003). However, it is expected that Lekgaba will be able to sustain the lion population for an extended period of time because of the large prey base present. However, further growth of the lion population will depend on the continued abundance of prey (Smuts 1978). As the lion population increases it will exert increasing pressure on the prey (Mills & Schenk 1992) that may lead to a drastic decline in food quality and quantity for the lions. The size of the ranges that are currently being used by the lions within Lekgaba will determine whether or not the population can grow in the future. If it is found that the lions are not detrimental to the prey base, and are not utilizing the entire available habitat (20 000 ha) yet, then the potential for growth of the lion population can be estimated.

Knowledge of the impact of the lion population on their prey base and the other resources within Lekgaba will allow the management to determine the optimum size of the lion population. Introducing preferred prey items could influence prey use patterns in the future. This should ensure that the lion population remains healthy, while enhancing the numbers of other less-preferred prey. If prey numbers are declining, new prey can be introduced into Lekgaba. A constant prey base that does not migrate, as is the case on Lekgaba, has a positive influence on the numbers of cubs that survive during the dry season (Anderson 1981). This increased probability of survival of offspring will allow the lion population to increase in size at a fairly rapid rate. Furthermore captive populations show wider behavioural characteristics than wild ones of the same species (McPhee & Silverman 2004), necessitating the need for a study captive lion behaviour.

The present study tests two hypotheses. The first being that the lion population of Tswalu will not over utilize the current prey base that occurs in the enclosed Lekgaba predator section of Tswalu Kalahari Reserve and will be able to grow without a detrimental effect on the resource base subject to management actions based on known lion behaviour. The second hypothesis is that the lions utilize their habitats proportionally to the size of each habitat type available to them. To test these hypotheses, the following key questions will have to be addressed:

- Is Lekgaba large enough to sustain the lion population on Tswalu?
- Are there any clear prey preferences by the current lion population?
- Is there enough prey available for the lions to survive indefinitely?
- To what extent do the lions utilize the habitat?
- Is there an indication of a specific habitat preference?

The study is arranged broadly into two themes, Prey use, prey preference, range use and habitat selection are presented in Chapters 4 and 5 respectively. A population viability analysis is also presented in Chapter 6. Management recommendations for the effective management of the lion population in Tswalu Kalahari Reserve are presented in Chapter 7, and a final summary is provided in Chapter 8.

CHAPTER 2

STUDY AREA

Location

Tswalu Kalahari Reserve (hereafter referred to as Tswalu) is the largest privately owned wildlife reserve in South Africa. It lies in the Northern Cape Province, at the foot of the Korannaberg Mountains (Figure 1). The central geographical co-ordinates are S 27°13'30" and E 022°28'40". Kuruman, which is famous for being the starting point of Dr. Livingston's African expedition, is the closest town, some 140 km east of Tswalu.

Tswalu was started as a conservation area in 1994 by Stephen Boler, who re-introduced several types of wildlife species to the area. The area was previously reserved for cattle, goat and sheep farming, with some parts allocated to wildlife ranches. After Mr. Boler's death in 1998, Tswalu was bought by the Oppenheimer family who have continued Mr. Boler's vision. The Oppenheimer family have expressed their goal for Tswalu to be to 'restore the Kalahari to itself'.

Tswalu consists of three sections (Figure 2). The Korannaberg section in the north and west is ± 60 000 ha in size. It is regarded as the main section of Tswalu and houses the lodges, administration buildings and staff accommodation. The Tsamma section in the west and south is circa 20 000 ha in size and is not accessible to guests. The Lekgaba section (Fig. 2), where the present study took place, lies in the north and east of Tswalu and is separated from the other two sections by a fenced-off gravel road. Lekgaba is also circa 20 000 ha in size and is the only section to house lions and wild dogs *Lycaon pictus*. The fence surrounding Lekgaba is electrified to prevent predators escaping into the main reserve. A small section, north of Korannberg is used as a breeding camp for roan antelope *Hippotragus equinus equines* and sable antelope *Hippotragus niger niger*. This section is currently being added to on order to increase the size of the breeding camps.

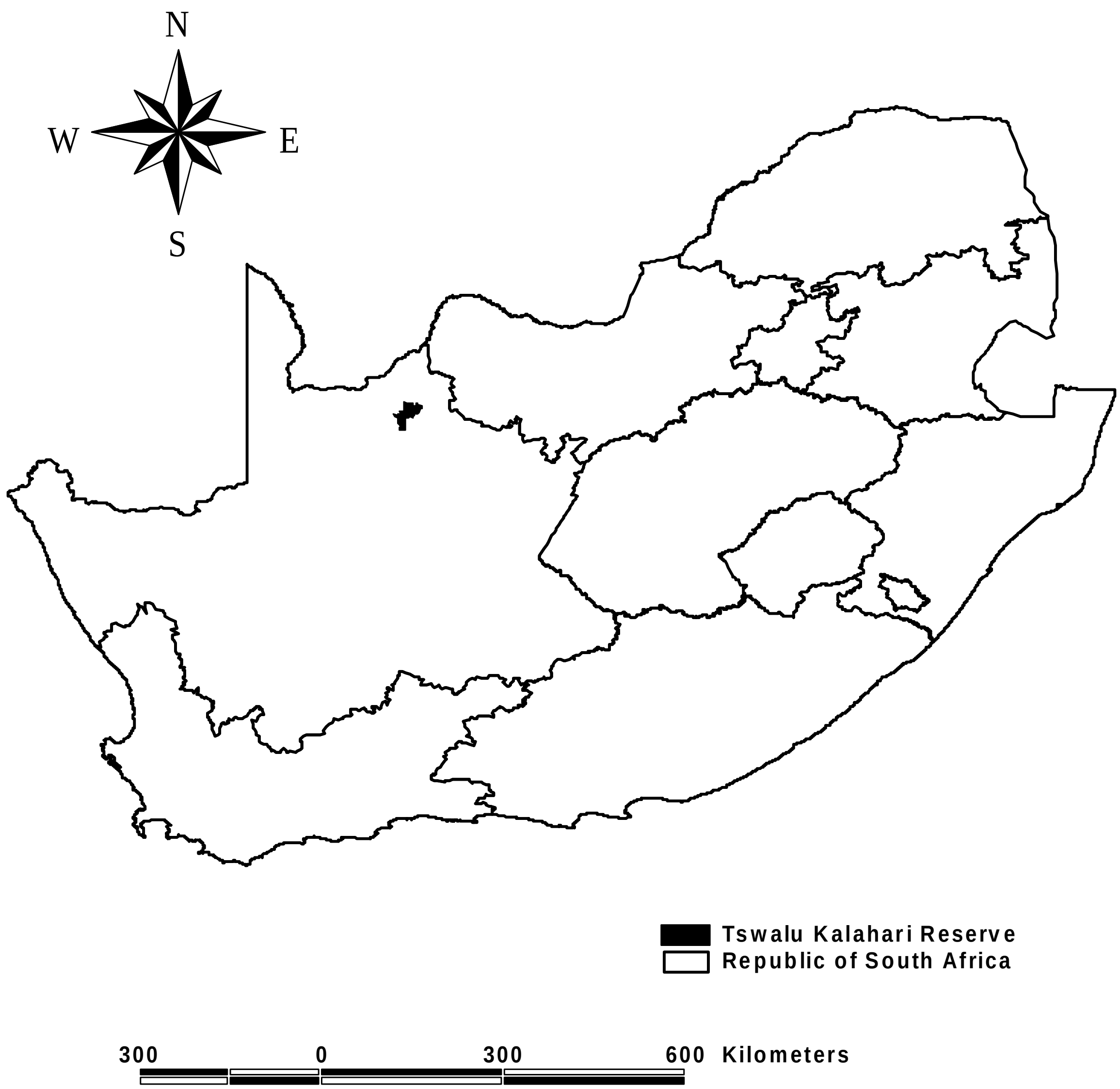

Figure 1: The Tswalu Kalahari Reserve in the Northern Cape Province of the Republic of South Africa.

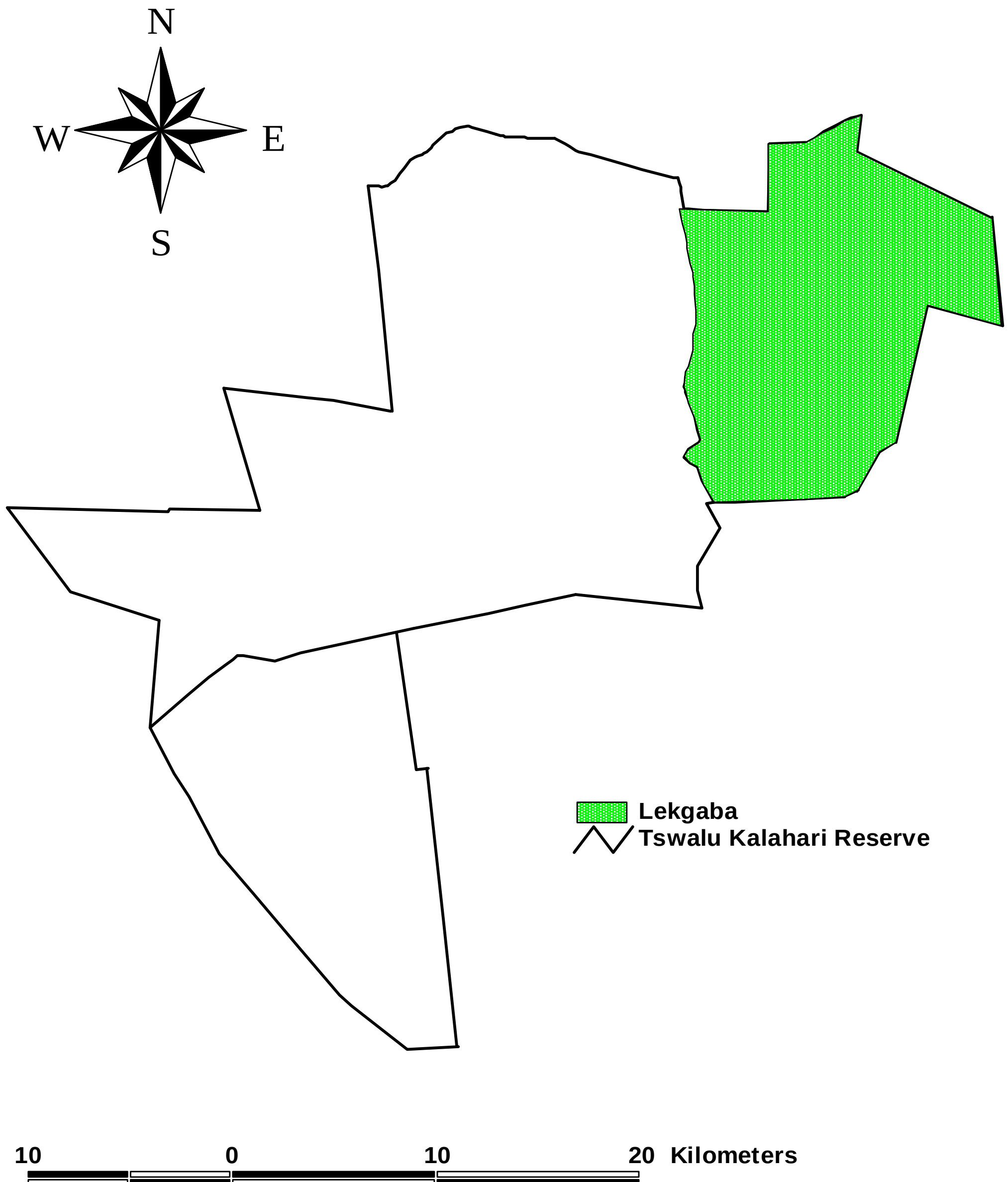

Figure 2: The predator section of Tswalu Kalahari Reserve, known as the Lekgaba section. The western boundary is a wildlife-proof fence on both sides of the gravel road.

Tswalu Kalahari Reserve management staff are hoping to amalgamate the Lekgaba and Korannaberg sections by taking down the fences along the Deben road (Jordaan 2008, *pers. comm.*[1]). This will depend on approval from local and provincial authorities and available funding. The presence of lions and wild dogs on the Korannaberg section will necessitate the need to electrify the fencing around the entire new area.

Climate

The climate of Tswalu is highly variable. Rainfall and temperature data have been recorded at the Vanzylsrus weather station, which lies just to the north of Tswalu and is 932 meters above sea level (Van Rooyen 1999). Tswalu is an arid savanna in the summer rainfall area of southern Africa (Low and Robelo 1998), with a relatively high rainfall occurring from October to April but with a distinct peak in March (Figure 3). The mean annual rainfall is 253.3 mm. The dry season occurs from May to September with less than 10 mm of rainfall annually. The peak dry season occurs from June to August with little or no rainfall occurring. A rainfall gradient is evident on Tswalu, with an increase from the southwest to the northeast (Van Rooyen 1999). Kuruman, which lies to the east of Tswalu, receives a mean annual rainfall of 450 mm per annum.

Data recorded for the last eleven years, 1994-2004, indicate that the temperature varies from –1.2 °C to 38.2 °C (Figure 3). The highest and lowest temperatures recorded by the Vanzylsrus weather station are a minimum of –6.6 °C and a maximum of 42.5°C (Van Rooyen 1999). Therefore Tswalu has a more moderate climate than Vanzylsrus.

Terrain morphology, geology and soils

A variety of terrain types occur on Tswalu. Large tracts of sandy plains extend to the west of the reserve. Several dunes and dune streets have been formed on these plains. The dunes and dune streets are formed by the prevailing east-west winds. The Korannaberg Mountains are found to the north and east of the Korannaberg section and to the east and south of the Lekgaba section

[1] Mr W. Jordaan, Ecologist, Tswalu Kalahari Reserve, conservation@tswalu.com

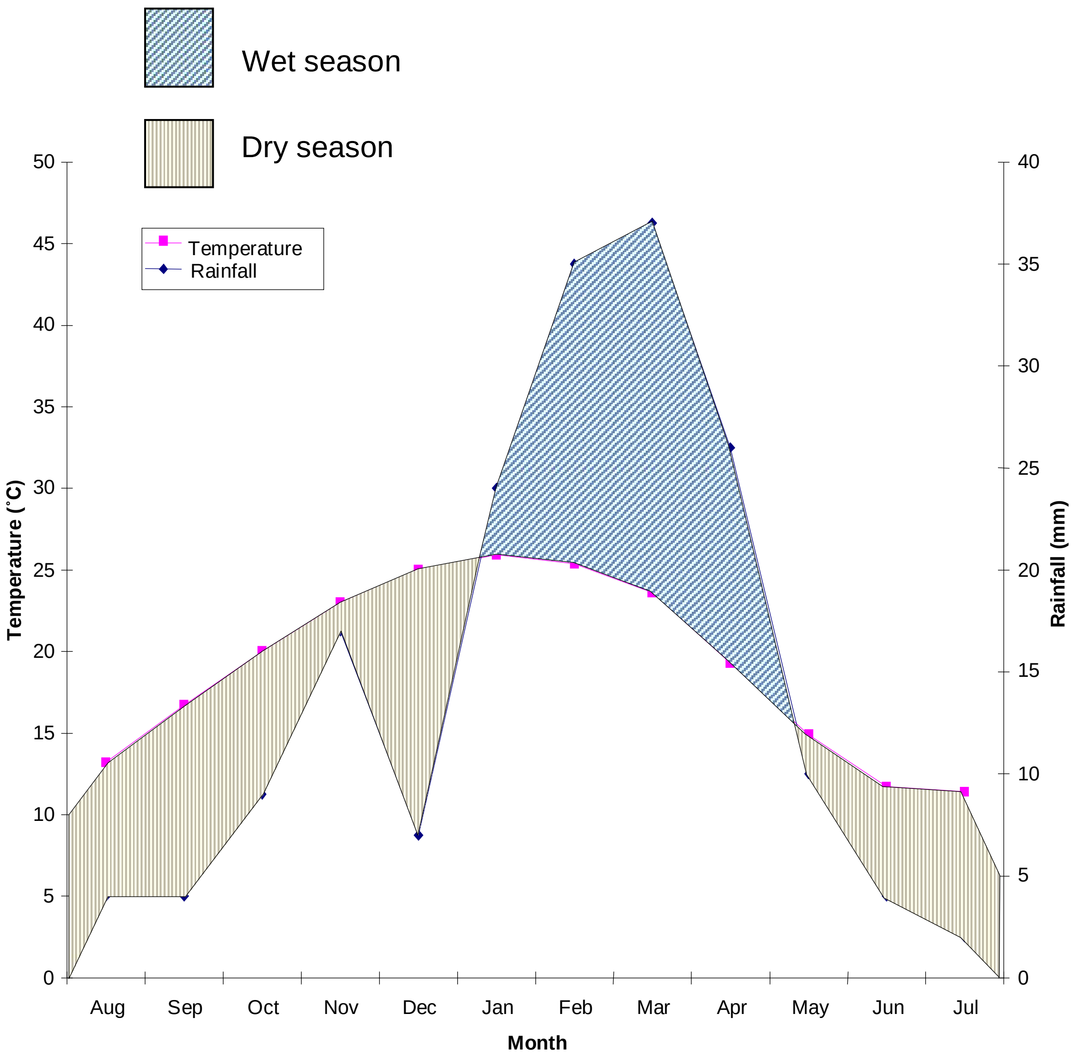

Figure 3: Climate diagram for Tswalu Kalahari Reserve in the Northern Cape Province (Source: Vanzylsrust Weather Station, No: 0427083A3, 2003).

(Figure 4). These mountains range in altitude from 1020 to 1586 m above sea level. The height and slope of these mountains offer spectacular scenery at sunrise and sunset (Van Rooyen, Theron & Bredenkamp 1991). Sandy valleys occur between the mountains and hills. Seasonal pans and artificial water points are scattered throughout the reserve (Figure 4). Water drains into seasonal streams as there are no major rivers running through Tswalu (Van Rooyen *et al.* 1991).

Van Rooyen (1999) describes the area as having two major geological formations. The mountains and hills consist of the matsap formation containing quartzite, conglomerate and subgreywacke. Acid banded ironstone and lava are also present (Low and Robelo 1998). The sandy plains and dunes consist of the Kalahari Group of the Gordonia formation. Aeolian surface sand, alluvium, gravel, limestone, silcrete and calcrete are also found (Low and Robelo 1998, Van Rooyen 1999)

The soils on Tswalu are poorly structured red soils with a high base status; well-drained red, sandy soils with a high base status; red and yellow, well-drained sandy soils with a high base status; and rocky areas with little or no soil (Van Rooyen 1999) (Figure 5).

Vegetation

Tswalu has been described by Low and Robelo (1998) as occurring in the shrubby Kalahari dune bushveld, Kalahari plains bushveld and Kalahari mountain bushveld areas of the Savanna Biome. Acocks (1988) described the area as Kalahari Thornveld. The reserve is characterized in certain areas by scattered shrubs and well-developed grass layers, in other areas by a well-developed tree layer and moderately developed grass and shrub layers, and by a poorly developed tree layer and moderately developed grass layers on the mountains and hills (Van Rooyen 1999). Some dominant plant species include the trees *Acacia erioloba, Boscia albitrunca, Terminalia sericea,*

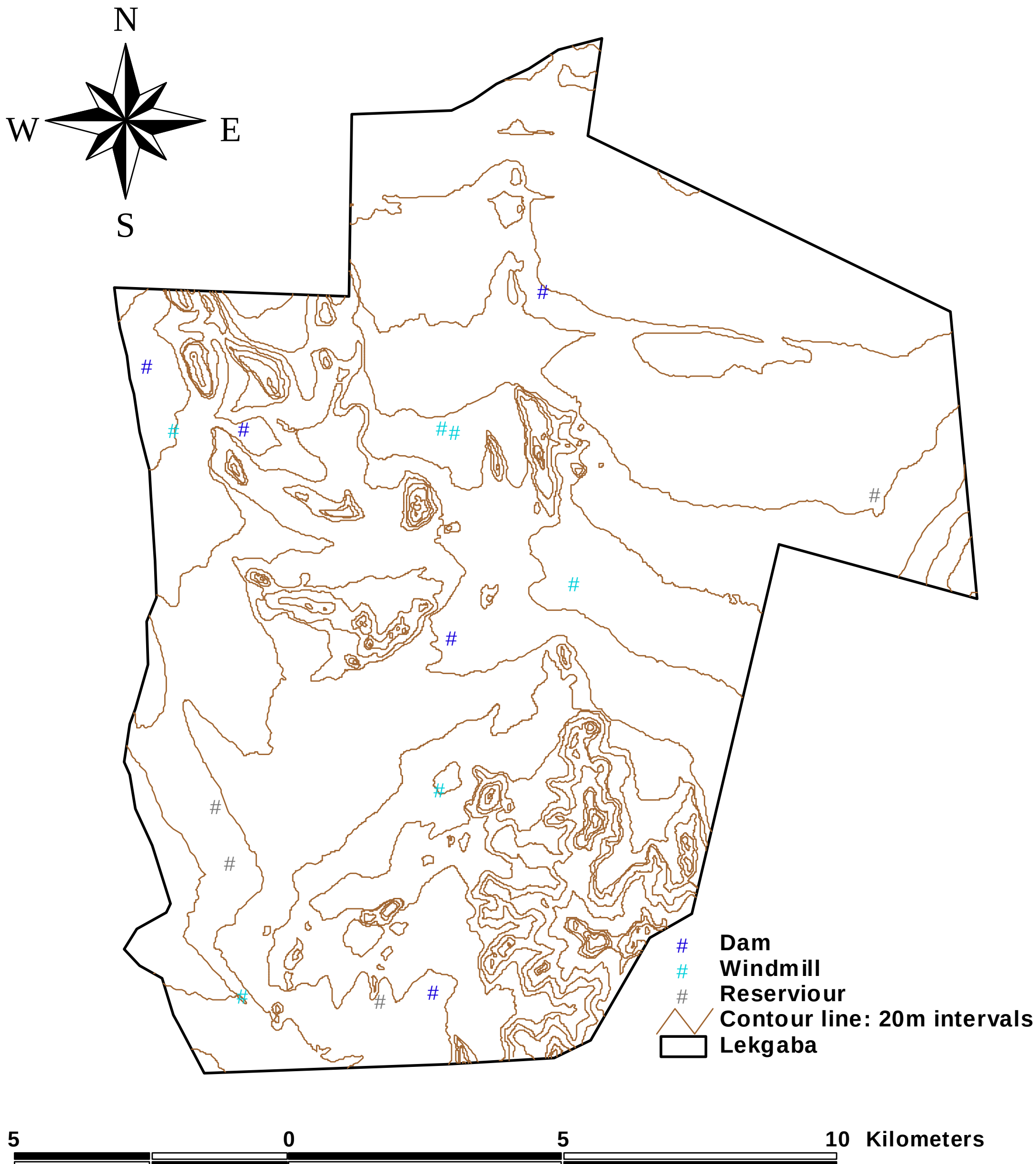

Figure 4: Terrain morphology and water sources of Lekgaba in Tswalu Kalahari Reserve (Source: ESRI Inc. 1998; Van Rooyen 1999).

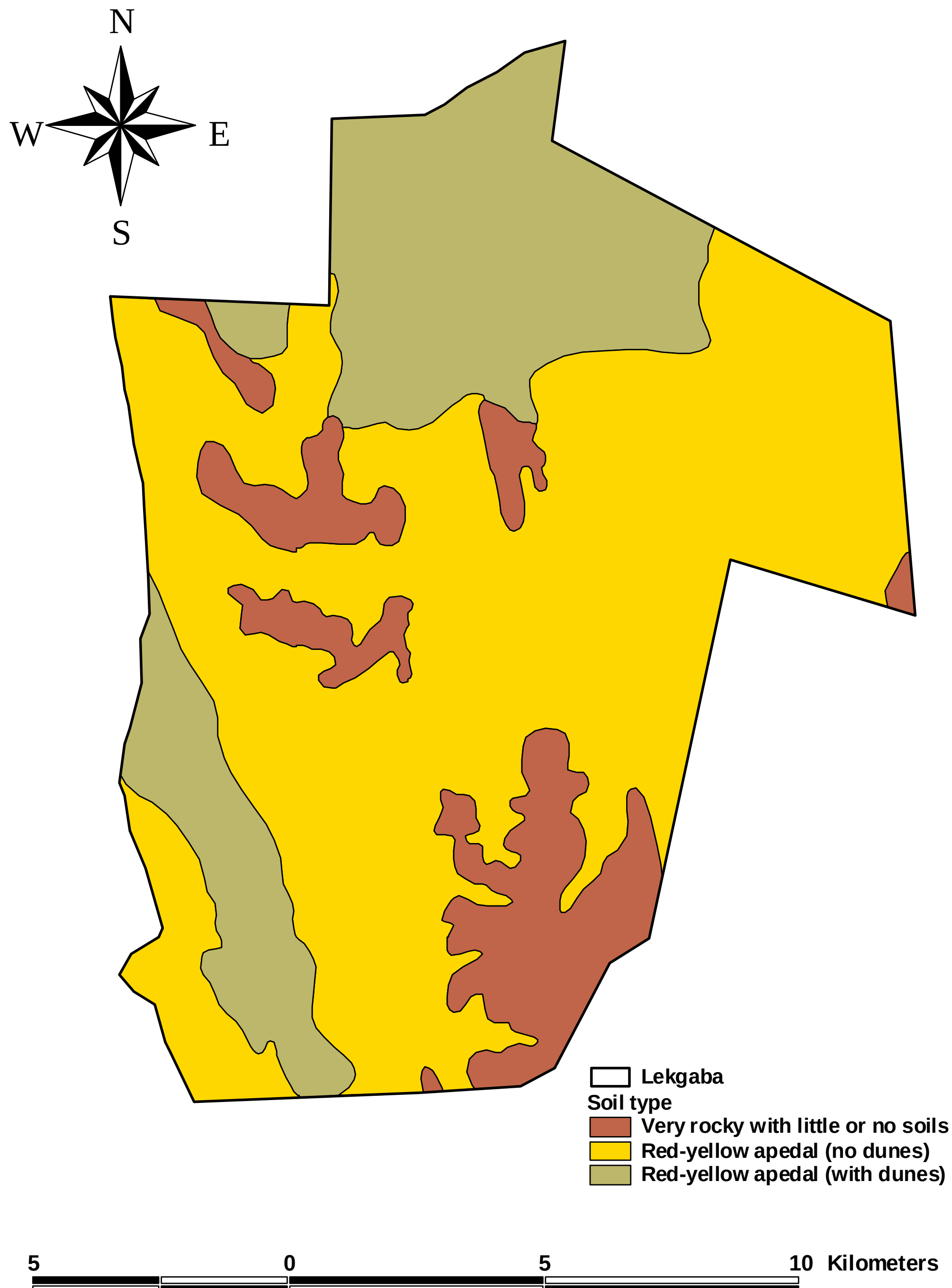

Figure 5: The soil types found on Lekgaba in Tswalu Kalahari Reserve (ESRI Inc. 1998)

the shrubs *Grewia flava, Rhus* spp., *Acacia* mellifera and Tarconanthus *camphorates* and the grasses *Eragrostis lehmanniana, Stipagrostis amablis, Stipagrostis uniplumis* and *Schmidtia kalahariensis*.

In a study conducted by Van Rooyen (1999) it was found that the Lekgaba section is composed of three major plant communities. They are:

- The *Acacia erioloba – Acacia haematoxylon – Eragrostis pallens* dune streets: This plant community occurs on the deep, sandy areas in the dune streets and in-between the mountains and hills. Trees and shrubs are sparse with *Acacia erioloba*, *Acacia haematoxylon*, *Grewia flava* and *Rhus tenuinervis* the most conspicuous species. Dwarf shrubs include *Elephantorrhiza elephantina* and *Senna italica.* The herbaceous layer is conspicouos covering approximately 35% of the surface area. Species such as *Stipagrostis uniplumis, Eragrostis pallens, Eragrostis lehmanniana, Aristida congesta* subsp. *congesta, Aristida stipitata* and *Anthephora pubescens* dominate the grass stratum. Forbs occur in a low percentage cover and include *Orthanthera jasminiflora, Herrmania tomentosa, Sesamum triphyllum* and *Asparagus africanus*.
- *Acacia mellifera – Rhigozhum trichotomum – Stipagrostis uniplumis* bushy plains and valleys: This community occurs on the open plains, in the dune streets and valleys, and in some mountainous regions of Lekgaba. Trees are sparse with *Acacia erioloba and Boscia albitrunca* the most abundant woody vegetation. Shrubs and dwarf shrubs are densely scattered, with the most abundant species being *Acacia mellifera, Grewia flava, Rhigozum trichotomum, Lycium bosciifolium*, *Ehretia rigida, Senna italica* and *Monechma incanum*. The herbaceous layer has a moderate cover of approximately 31%, with *Stipagrostis uniplumis, Schmidtia pappophoroides*, *Eragrostis lehmanniana*, *Schmidtia kalihariensis* being dominant. There is a low covering of forbs including *Monsonia angustifolia*, *Portulaca kermisina, Jatropha erythropoda*, *Trochomeria debilis* and *Solanum capense*. Three

variations of this community exist, they are the *Acacia mellifera – Rhigozum trichotomum – Euphorbia rectirama* plains, *Acacia mellifera – Rhigozum trichotomum – Eragrostis rigidior* valleys and the *Acacia mellifera – Rhigozum trichotomum – Senseveria aethiopica* dune streets.

- *Croton gratissimus – Digitaria polyphylla* mountains and hills: This plant community variation occurs on all the mountains and hills throughout Tswalu and Lekgaba, covering approximately 3250.6 ha in Lekgaba alone. *Croton gratissimus, Rhus burchellii, Euphorbia avasmontana, Ehretia rigida, Ziziphus mucronata, Boscia albitrunca, Grewia flava* and *Acacia mellifera* dominate a sparse tree and moderately sparse shrub layer. A high rock cover influences the herb layer with *Digitaria polyphylla, Brachiaria nigropedata, Aristida diffusa, Stipagrostis uniplumis, Schmidtia pappophoroides, Eragrostis lehmanniana* and *Melinis repens* dominating. The forb layer has a low cover and includes *Rhynchosia totta, Pegolettia retrofracta, Indigofera heterotricha, Tephrosia longipes, Leucas capensis* and *Ceratotheca triloba*. Two vartiations to this community occur: the *Croton gratissimus – Euphorbia avasmontana* mountains and hills and the *Croton gratissimus – Pellaea calomelanos* mountains and hills.

For the present study, eight habitat types in the three major communities were used and their relative sizes are provided in Table 1. Each habitat type was delineated by van Rooyen (1999) and was processed in ArcView ver 3.2. (Figure 6).

Tyson & Crimp (1998) have called for greater research into the climatic conditions occurring in the Kalahari. Temperature, rainfall, evapotranspiration and atmospheric moisture all contribute to the growth and development of the vegetation in any area, and as such have to be understood for wildlife management purposes (Tyson & Crimp 1998).

Table 1: The habitat types occurring on Lekgaba, and their respective sizes (Van Rooyen 1999)

Habitat type	**Size (km^2)**	**Proportion of total area (%)**
Anthephora pubescens dunes	5.2	2.7
Digitaria polyphylla mountains and hills	32.5	17.3
Eragrotis lechmanniana dune valleys and plains	8.3	4.4
Eragrostis pallens dune streets	55.7	29.6
Opuntia ficus-indica disturbed areas	2.5	1.3
Stipagrostis amabilis dune crests	1.2	0.6
Stipagrostis uniplumis bushy plains and valleys	78.0	41.4
Stipagrostis uniplumis plains	4.9	2.6
Total	188.3	100.0

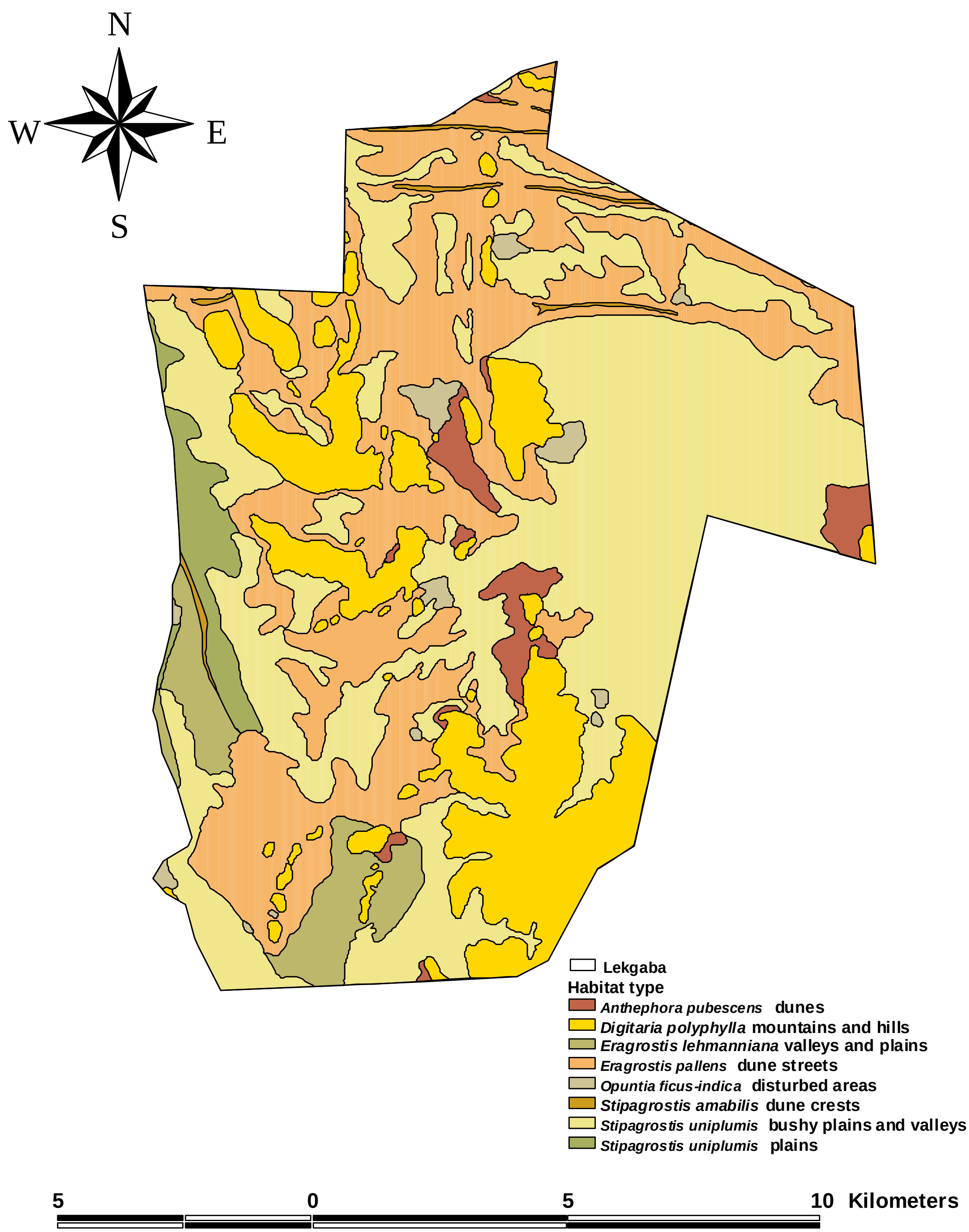

Figure 6: The eight habitat types found on Lekgaba in Tswalu Kalahari Reserve (Van Rooyen 1999).

Wildlife

Tswalu Kalahari Reserve houses a number of indigenous and exotic species of mammals and birds. Annual wildlife counts are undertaken on all three sections of Tswalu. Several types of wildlife that are present on Tswalu do not occur on the Lekgaba section including the roan antelope, the sable antelope, the tsessebe *Damaliscus lunatus lunatus* and the African savanna buffalo *Syncerus caffer caffer.* A list of the wildlife occurring on the Lekgaba section occurs in Table 2.

Table 2: The common and scientific names of the larger mammals and birds found on Lekgaba in the Tswalu Kalahari Reserve

Common name	**Scientific name**
Mammals:	
Aardvark	*Orycteropus afer*
Chacma Baboon	*Papio hamadryas ursinus*
Cheetah	*Acinonyx jubatus*
Grey duiker	*Sylvicapra grimmia*
Eland	*Taurotragus oryx*
Bat-eared fox	*Otocyon megalotis*
Cape fox	*Vulpes chama*
Gemsbok	*Oryx gazella*
Giraffe	*Giraffa camelopardalis*
Cape hare	*Lepus capensis*
Scrub hare	*Lepus saxitilis*
Red hartebeest	*Alcelaphus caama*
Impala	*Aepyceros melampus*
Black-backed jackal	*Canis mesomelas*
Greater kudu	*Tragelaphus strepsiceros*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Yellow mongoose	*Cynictis penicillata*
Striped polecat	*Ictonyx striatus*
African porcupine	*Hystrix africaeaustralis*
Mountain reedbuck	*Redunca fulvorufula*
Black rhinoceros	*Diceros bicornis bicornis*
White rhinoceros	*Ceratotherium simum simum*
Springbok	*Antidorcas marsupialis*
Springhare	*Pedetes capensis*
Ground squirrel	*Xerus inauris*
Suricate	*Suricata suricatta*
Warthog	*Phacochoerus africanus*
Waterbuck	*Kobus ellipsiprymnus*

Table 2: continued

Common name	Scientific name
African wild dog	*Lycaon pictus*
Blue wildebeest	*Connochaetes taurinus taurinus*
Burchell's zebra	*Equus burchellii*
Hartmann's mountain zebra	*Equus zebra hartmannae*
Birds:	
Kori bustard	*Ardeotis kori*
Ostrich	*Struthio camelus*
Secretary bird	*Sagittarius serpentarius*

CHAPTER 3

GENERAL METHODS

The methods describes in this chapter are a general outline as to the procedure that was followed in the study period. Detailed and specific methods are provided in each relevant chapter.

Maps of each lion or lion group's range, scat sites and kill sites were constructed using GIS software packages. These software packages were used to determine range size and any indications of habitat preferences.

The Department of Statistics at the University of Pretoria analysed the entire data set for any statistical results which are described in each relevant chapter.

Prey use of lions in a semi-arid, enclosed Kalahari nature reserve

Submitted to: South African Journal of Wildlife Research

D.J. Roxburgh[1*]

james.roxburgh@gmail.com

C.J. Tambling[2] &

cjtambling@gmail.com

J. du P. Bothma[1]

liset@wildlife.up.ac.za

[1]*Centre for Wildlife Management, Department of Animal and Wildlife Sciences, University of Pretoria, Pretoria, 0002, South Africa*

[2]*Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa*

*To whom correspondence should be addressed

ABSTRACT

Prey use and biomass removal were determined for a lion *Panthera leo* population in the Lekgaba predator camp at Tswalu Kalahari Reserve of 18800 ha in the south-eastern Kalahari region consisting of nine lions. Nineteen prey types were used, with prey size ranging from springhare *Pedetes capensis* to eland *Taurotragus oryx*. Kill and scat data indicated that gemsbok *Oryx gazella* and blue wildebeest *Connochaetes taurinus taurinus* were utilized most. Scat data were corrected for relative biomass, making smaller prey types significantly more prominent than in kill or uncorrected scat data. Jacobs' Index and 95% confidence limits indicated significant preference for warthog *Phacochoerus africanus* and steenbok *Raphicerus campestris*, and significantly infrequent use of gemsbok and Burchell's zebra *Equus burchellii*. The greater kudu *Tragelaphus strepsiceros* was utilized more than its proportional abundance, while Hartmann's mountain zebra *Equus zebra hartmannae* was underutilized relative to its abundance. The lions removed 9.9kg/Lion Feeding Units/day, while using 13 % of the available edible biomass per prey. Lion and prey management strategies on smaller, enclosed reserves are given.

Key words: Lion *Panthera leo*, enclosed reserve, prey selection, prey preference, biomass removal, scat analysis, Kalahari.

Word count: 5535

Note: This chapter is written in journal format

INTRODUCTION

The African lion *Panthera* leo once roamed freely throughout the African continent, but now the majority reside in protected areas such as national parks, large wildlife ranches and privately owned nature reserves. The current boom in ecotourism in Africa has necessitated that these reserves house so-called charismatic wildlife, with the lion being one of the important animals for ecotourism (Chardonnet 2002). Lion predation on small, enclosed nature reserves of <1000 km^2 can affect the survival of the prey population in that specific area, especially where immigration and emigration are hindered by wildlife-proof fences (Power 2002; Druce *et al*. 2004; Tambling & Du Toit 2005). Lions are opportunistic predators, but usually have a limited range of optimal prey on such ranches and reserves (Hayward *et al.* 2007a). Sedentary prey animals that are unable to move away from persistent predation pressure by lions tend to occur at lower numbers, and are more susceptible to population declines from predation pressure when compared to migratory populations that are generally more numerous (Fryxell *et al*. 1988).

Any prey preferences by lions must be taken into consideration in a study of lion prey selection. When such predators have access to a wide range of prey to hunt they will often show a preference for one or some of them (Cock 1978). Prey preference is here defined as predator utilization of a prey type that happens more frequently than expected relative to the proportional abundance of the prey. A predator may also underutilize certain prey types relative to their proportional abundance (Hayward & Kerley 2005).

Effective management of predator-prey interactions is an important goal for all small, privately owned wildlife ranches and reserves. The predator population must be managed to maintain prey type diversity, density and genetic variability (Lehmann *et al*. 2008). The correct management techniques can only be applied with a clear understanding of the predator population and its effect on the specific prey population.

Prey use can determined by using a number of techniques, which include opportunistic observations and direct observations (Mills & Shenk 1992), spoor tracking (Eloff 1973; Stander *et* al. 1997), stomach content analysis (Smuts 1976) and scat analysis (Perrin & Campbell 1980; Bothma & Le Riche 1994). Prey selection requires knowledge of relative prey abundance.

Opportunistic observations overestimate the proportion of larger kills (> 100 kg) in the diet of predators, while continual, direct observations are more reliable for determining kill rates and actual numbers of prey (Mills 1992). Prey use studies to date, mostly overestimated the detection of larger, visible prey items, whereas smaller, inconspicuous and completely consumed prey were underrepresented in the data (Radloff & Du Toit 2004; Rapson & Bernard 2007). In a semi-arid system, such as the Kalahari, smaller prey are utilized to a greater extent than in the more mesic savanna ecosystems (Eloff

1973). For example, porcupines *Hystrix africaeaustralis* form a large proportion of the diet of lions in the southern Kalahari (Eloff 1973).

Where direct observation is not possible, spoor tracking can provide biologically meaningful results. It has the advantages that such observations are completely non-intrusive and can indicate the behaviour and activity of the animal being tracked (Stander *et al*. 1997). However, potential bias can occur through observer error and poor tracking conditions in certain habitat types (Mills 1992), where tracking is difficult, but this does not include the open, sandy substrate of the Kalahari region.

Scat analysis is a non-invasive and relatively easy method to apply (Mukherjee *et al*. 1994; Marucco *et al*. 2008). However, potential bias occurs when scats are collected non-independently, such as at clusters or kill sites, which can over-represent a specific prey type in the diet (Marucco *et al*. 2008). Bias also occurs when variable digestion and size are not taken into account for each prey type. These uncorrected data can overestimate the biomass of small prey and underestimate the actual number of small prey in the diet of a predator (Karanth & Sunquist 1995; Marker *et al*. 2003). The scat sample size can also cause a statistical error if it is too small (< and unrepresentative of the total number of scats produced by the predator in question (Marucco *et al*. 2008).

In this study, we aim to determine the prey selection, specific prey preferences and prey biomass removal of the lion population on a small, enclosed reserve in the Kalahari ecosystem. This knowledge will allow managers to improve conservation and management practices and is so doing ensure that the lion population has an adequate prey base to survive indefinitely. Their survival will enhance the eco-tourism potential of these small, enclosed reserves. The hypothesis to be tested in the current study is that the lion population on the Lekgaba predator section on Tswalu Kalahari Reserve utilize a wide variety of prey types and favour the use of specific prey types over others. Consequently three questions arouse: what is the prey use by the lion population? Are there any clear preferences for certain types of prey? And what is the annual prey biomass removal found in the predator section?

STUDY AREA

The study was done from March 2003 to October 2004, on the Tswalu Kalahari Reserve, a 1000 km^2 private nature reserve in the Northern Cape Province of South Africa (Fig. 1). Tswalu is divided into three sections with the predator section, Lekgaba, along the eastern boundary of the reserve. Lekgaba is circa 188 km^2 in size with artificial water sources and wildlife-proof fences surrounding it.

The mean annual rainfall on Tswalu is 253.5 mm, with a distinct precipitation peak in March. Low & Rebelo (1998) have classified Tswalu as occurring in the Shrubby Kalahari Dune Bushveld, the Kalahari Plains Bushveld and the Kalahari Mountain Bushveld regions of the Savanna Biome.

Lekgaba has three major plant communities, the *Acacia erioloba* – *Acacia haemotoxylon* – *Eragrostis pallens* dune streets, the *Acacia mellifera* – *Rhigozhum trichotomum* – *Stipagrostis uniplumis* bushy plains and valleys and the *Croton gratissimus* – *Digitaria polyphylla* mountains and hills (Van Rooyen 1999).

The current lion population on Lekgaba numbers nine individuals of varying age and sex. Four lions (two males and two females) were captured in the Kalahari Gemsbok National Park in 2001 and were translocated to Lekgaba, where they were kept in a holding boma to acclimatise to the surroundings and each other. The younger, less dominant male was pushed out of the reserve by the dominant male in March 2003 and as was then recaptured and sold to another reserve. The dominant male fathered three sets of cubs, two to a 10-year old female and one to a five-year old female. The two reproducing females dispersed to different areas of the predator camp. The older lioness, her older cubs of three years, and two young cubs born in late December 2003, established a range in the northern region of the predator camp. The younger adult female dispersed to the southern region of the predator camp with her two subadult cubs, which were then two years old.

METHODS

Prey selection

Active fieldwork was done for 121 days during the study period. All kill and scat locations were located by using a combination of opportunistic observations, direct observations and spoor tracking (Mills 1992; Stander *et al*. 1997). Data were also collected by field rangers and game scouts during the study period. When a kill or scat was found, a GPS (Garmin E-trex) location fix and the time and the date were recorded and where possible the age and sex of the carcass. The scats that were collected were placed in brown paper bags and stored for further analysis. Kill and scat data were tested for significance by using Fishers exact test for goodness of fit, as some frequency values were < 5 % of the total scat sample (Zar 1999).

Scat analysis and scat correction

The scats were first washed in metal sieves until only insoluble material (hair, teeth and bone fragments) remained. The sample was then air dried in a convection oven at 70˚C for 24 hours (Melville *et al*. 2004). Hair, teeth and bone fragments were then analysed and compared to keys and templates that were available (Keogh 1979; Perrin and Campbell 1980; Hildyard 1983; Keogh 1983). Hair samples were identified macroscopically by colour, texture and length, and microscopically according to the cuticular patterns and cross-sectional structures (Putman 1984). Mukherjee *et al.* (1994) suggest that a minimum of 20 hairs should be analysed per scat sample so as to avoid any prey types being missed. The method of Douglas (1989) was adapted to make cross-sections of hair samples. A frequency of occurrence of each prey type in the total scat sample and 95% confidence limits were generated from 1000 bootstrap simulations (Andheria *et al*. 2007). All non-lion scats were removed and kept in the lab for any further research purposes.

To correct for possible bias associated with scat analysis, a correction factor was applied for each prey type found in the scats. This correction factor takes into account the frequency of occurrence of a particular type of prey and converts it into relative biomass and actual number of prey types (Floyd *et al*. 1978; Karanth & Sunquist 1995; Andheria *et al*. 2007). Such correction factors were first developed for wolves *Canis lupus lupus* (Floyd *et* al. 1978) and have since been adapted by Karanth & Sunquist (1995) for the tiger *Panthera tigris* and leopard *Panthera pardus*. Due to the lack of available data on feeding trials and passage rates on ingesta through the lion's gut, it was assumed that the digestive system of lions and tigers were broadly similar. This may be especially true for lions living in semi-arid environments in which they tend to hunt alone or in small groups (Eloff 2002). The following regression equation relates the live weight of prey (X) to the weight of prey type found in each scat (Y) (Karanth & Sunquist 1995; Bagchi *et al*. 2003):

$$Y = 1.980 + 0.035(X)$$

The live weight of prey types in any given population (Ebedes & Bothma 2002; Skinner & Chimimba 2005) were calculated as being 75 % of the adult female weight to account for juveniles and young prey types that were utilized (Hayward *et al*. 2007b). Solving the equation yields the weight of prey consumed per collectable scat. This value was then multiplied by the occurrence of each prey type in the total scat sample, which yields the total weight of each prey type consumed and the ratio of weights consumed between different prey types. The relative weight of each prey type was then used to determine the relative number of individuals consumed (Marker *et al*. 2003), and the ratios were determined relative to the live weight of a gemsbok, which was the prey type most utilized by the lion population in the study area. These corrected values for each prey type take into account the presence of small mammals in the prey selection data. The corrected scat data were compared to the observed kill numbers and the uncorrected scat data using by Fisher's exact test for goodness of fit (Zar 1999).

Species accumulation curve

It was also determined if the scats collected and analysed were an accurate representation of the diet during the study period by using a cumulative Brillouin's index (Glen & Dickman 2006), with the equation:

$$H = \frac{\ln N! - \sum \ln n_i!}{N}$$

Where *H* is the diversity in the scats, *N* the total number of prey recorded and n_i the number of individual prey prey items in the *i*th category (Brillioun 1956). Fifty randomised iterations of the cumulative Brillioun's index were generated and the cumulative diversity was plotted against the cumulative number of scats collected to determine whether an asymptote was reached (Landman *et al*. 2008).

Prey preference

Observed kills, uncorrected scat data and corrected scat data were compared against the observed population sizes, where such abundance data existed for the prey by using a Fisher's exact test for goodness of fit (Zar 1999). Sequential Bonferroni corrections were performed to account for Type 1 errors that are associated with multiple tests (Quinn & Keough 2002). Only prey types with known abundance were used in the analyses. The proportional availability of all prey types was determined from annual aerial census data for Lekgaba conducted at the end of August each year to maximise visibility (Bothma 2002). Prey selection was determined for each data set by calculating Jacobs' Electivity Index (Jacobs 1974) by using the equation:

$$D = \frac{r - p}{r + p - 2rp}$$

Where *r* is the proportion of kills of each prey type and *p* is the proportional availability of each prey type (Hayward & Kerley 2005). *D* yields values ranging from +1 to -1, where +1 indicates maximum selection and -1 indicates maximum absence of use (Hayward *et al.* 2006). Then 95% confidence intervals were constructed for each prey type's kill proportion (Neu *et al*. 1974). Significant preference occurs when the proportional availability of the prey item falls below the lowest limit of the confidence interval around the kill proportion (Landman *et al*. 2008). Significant lack of use occurs when the proportional availability of the prey type is higher than the highest limit of the confidence interval. All values that fall within the confidence interval range mean that there is no significant preference or lack of use.

Biomass removal

The amount of meat consumed and the biomass removed per prey type were determined by using Lion Feeding Units, standing crop biomass and available edible biomass (Van Orsdol 1981). Lion Feeding Unit classification centres around an adult female eating a relative proportion of 1.0 of prey units. Adult males eat 1.5 times as much as females, large cubs (2-3 years old) eat 0.75 times as much as an adult female, medium sized cubs (< 2 years, but at least 1 year old) eat 0.5 times as much as an adult female and small cubs (<1 year old) eat 0.25 times as much as an adult female (Van Orsdol 1981; Lehmann *et al*. 2008). Standing crop biomass of prey was calculated as 75 % of the adult female weight to account for juveniles and young prey types that were utilized, and was multiplied by the abundance of each particular prey type (Hayward *et al*. 2007b). The amount of edible material on a carcass was based on data in Mills & Biggs (1993) and Funston *et al*. (1998) who list the amount of edible meat per prey carcass as: very small animals (< 25 kg) 100% edible meat, small animals (25-100 kg) 90%, medium-sized animals (101-300 kg) 67% and large animals (> 300 kg) 60 % edible meat. The edible biomass removed and the available edible biomass removed were calculated for each kill.

All the statistical analysis were done by using the program R 2.7.0. (R Development Core Team 2008).

RESULTS

Prey selection

In total, data on 88 kills and 109 scats were collected during the study period. In all, 118 prey items were identified in the scat sample, with two prey types occurring in nine scats and only a single one occurring in the other 100 scats. Nineteen prey types were utilized by the lion population, with the gemsbok (n = 21), blue wildebeest (n = 16), greater kudu (n = 14), eland (n = 8) and red hartebeest *Alcelaphus caama* (n = 7) being the most abundant prey items when using observed kill data. The most abundant prey items found in the scats were gemsbok (n = 23), blue wildebeest (n = 16), greater kudu (n =

13), warthog (n = 10) and eland (n = 9). Mammals weighing < 100 kg (Karanth & Sunquist 1995) were more abundant in scats than in carcasses and kills (Fig. 2). The porcupine (n = 8), aardvark *Orycteropus afer* (n = 5), steenbok (n = 3) and springbok *Antidorcas marsupialis* (n = 7) were all more abundant in the scats than in the carcasses located in the field. However, there was no significant difference in prey occurrences between kill and scat data (Fisher's exact test: $p = 0.2821$). Other prey types included springbok, ostrich *Struthio camelus*, baboon *Papio hamadryas ursinus*, bat-eared fox *Otocyon megalotis*, large spotted genet *Genetta tigrina*, scrub hare *Lepus saxitilis* and impala *Aepyceros melampus*.

There was a significant difference between kills and corrected scat values (Fisher's exact test: $p < 0.001$) and between uncorrected scat data and corrected scat values (Fisher's exact test: $p < 0.005$) (Table 1). The most abundant prey types in the corrected scat values were the springhare, porcupine, gemsbok, scrub hare and steenbok (Fig. 3).

The diversity in the scats determined from Brillioun's index indicated that an asymptote was reached at a sample size of *c*. 110 scats (Fig. 4). The sample size of 109 scats should therefore be an adequate representation of prey types that were utilized by the lion population.

Prey preference

The most abundant potential larger prey type on Lekgaba was the gemsbok, followed by the red hartebeest, eland, springbok and Burchell's zebra (Table 2). Jacobs' Electivity Index values, using corrected scat values, show that warthog (0.76), steenbok (0.74) and greater kudu (0.49) are utilized to a greater degree than their proportional availability (Fig. 5), while Hartmann's mountain zebra (-0.54) and Burchell's zebra (-0.51) were used infrequently compared to their relative availability.

These differences were significant (Fisher's exact test: $p < 0.001$ in all cases) (Fig. 5), while the other prey items were used according to their abundance.

Biomass removal

A total of 6.5 Lion Feeding Units were used to determine the prey biomass removal by the lion population. The available standing crop biomass was 261 460.5 kg and available edible biomass 176 769.9 kg, with the largest contributors being the gemsbok (54 028.8 kg) and eland (41 814.0 kg) (Table 2). The lions were estimated to remove 7850.1 kg of meat during the study period when visible kill records are used, although it is assumed that this is a minimum figure because some kills were missed during non-observation days while smaller prey were entirely consumed and therefore not found. The meat consumption rate was 9.9 kg/Lion Feeding Units/day, or 3643.1 kg/Lion Feeding Units/year. The total lion population removed 23 860.1 kg of meat annually, which is 9.1% of standing crop biomass and 13.3% of available edible biomass.

DISCUSSION

The results show that within the Lekgaba predator section of the Tswalu Kalahari Reserve, the lions utilized 19 different prey types, which is consistent with other studies of lions in enclosed reserves (Rapson & Bernard 2007; Lehmann *et* al. 2008) and consistent with the findings of Eloff (2002) for the Kalahari lion.

Kill data showed that gemsbok were preyed upon more than any other prey type on Lekgaba. Gemsbok are also the preferred prey of lions elsewhere in the Kalahari ecosystem (Eloff 2002; Hayward & Kerley 2005). The Kalahari lions have developed specific techniques for killing gemsbok, which are known as notoriously difficult prey to kill (Eloff 2002). Gemsbok were also the most abundant prey type found on Lekgaba (n = 512), which could explain the large proportion of use of the gemsbok as a prey item. Blue wildebeest, which were the second most abundant prey, are also a general preferred prey item of lions in southern Africa (Hayward & Kerley 2005). Other larger prey types such as the eland and red hartebeest are also important prey items for lions living in a Kalahari ecosystem (Van Vuuren *et al*. 2005).

As was expected from most studies on lions, the kill data contained a greater proportion of larger prey (> 100kg, 81.8 %) and a low proportion of smaller prey (≤ 100 kg) (18.2 %). Scat analysis results were not significantly different to kill results, although smaller prey were found at a seemingly higher proportion than in the kills. Smaller prey types represented 33.9% of the total scat sample, which is almost double than that of the results of studying carcasses alone. It is likely that scat analysis provides a more reliable estimate of prey selection of the lion population. However, scat analysis does not take into account that large prey animals have a high quantity of edible meat on the carcass and that several hairless scats may be produced following the consumption of these prey types (Marker *et al.* 2003) which would make the identification of the prey from these scats impossible.

Small prey types are usually overestimated in biomass and underrepresented when using uncorrected scat data (Marker *et al.* 2003). The corrected scat data (Table 1) were significantly different to kill and uncorrected scat data, indicating that uncorrected scats analyses may not be a true reflection of the diet. Therefore scat data corrections should be used when describing the diet selection of larger predators such as lions, especially in areas where small prey are regularly consumed. The corrected scat data indicated the occurrence of small prey types at a much higher frequency (n = 66%) than either the kill or uncorrected scat data. The use of smaller prey types is typical of Kalahari lion behaviour (Eloff 2002), with especially the springhare, porcupine, warthog and springbok being used. However, due to the lack of feeding trials and data on the longevity of prey items in the digestive tract of lions and the known correction factors that were developed for tigers, show that such correction factors should be specifically developed for all larger predators.

Prey selection of lions in general shows that lions utilize some prey types more often than others, even if those prey types occur at low densities. The lions population on the Lekgaba predator camp showed a preference for warthog and steenbok, but it was difficult to determine the proportional availability of these animals from the air (Mills & Biggs 1993; Owen-Smith & Mason 2005). The annual aerial count may have underestimated the actual occurrence of these smaller prey types on Lekgaba. Burchell's zebra and gemsbok were not used proportional to their relative abundance as were giraffe, mountain reedbuck, grey duiker and waterbuck. The lack of interest in the giraffe may be a consequence of Kalahari lion behaviour, where the lions tend to hunt in smaller groups or alone (Eloff 2002). The killing of large prey requires several pride members and males (Funston *et al*. 2001). Burchell's zebra on the other hand prefer open plains (Skinner & Chimimba 2005) and on Lekgaba these open plains provide little stalking cover for the lions. Greater Kudu are utilized more frequently than their relative occurrence, as they already occur at a low density, care should be taken that the lions do not overuse the greater kudu population. Hartmann's mountain zebra are generally not used as a food source because these animals usually used the mountainous regions of Lekgaba which were avoided by the lion population (*pers. obs.*).

The daily consumption of the lions of 9.9 kg/Lion Feeding Units/day was high when compared to other studies of lions in enclosed reserves (Viljoen 1997; Rapson & Bernard 2007; Lehmann *et al*. 2008). The high prey density on Lekgaba could be the reason for these high consumption rates, as could the regular use of smaller prey. The edible biomass removed is higher than found in other studies, again suggesting that the Tswalu lions kill more often and kill larger prey more often than what would be expected from lions living in arid areas. Lehmann *et al*. (2008) suggest that the biomass removal is more important for management than the actual number killed.

The current lion population on Lekgaba is expected to grow to an established ecological capacity of 17 individuals (dealt with elsewhere). Thus research and monitoring are required to establish the prey use, prey preferences and prey biomass removal of the larger population. Care should also be taken that the population is kept at this ecological capacity to ensure survival of both the prey population and long-term survival of the lion population.

The management of a lion population in a confined environment requires knowledge of the prey selection, preference and actual biomass removal. Each study on prey selection of lions is site specific and detailed information can be garnered from studying the predator population closely. The economic benefit of housing lions should not overshadow the ecological constraint placed on the prey population by the lions. Managers should be aware that they might have to consider replacement of prey types and the utilization of buffer prey types to alleviate pressure on other prey types.

ACKNOWLEDGEMENTS

We would like to thank the staff of Tswalu Kalahari Reserve, especially the late Johan Lensing, Mark Rutherford, Gus van Dyk, Murray Letcher and Keith Jenkinson. Bridgestone-Firestone South Africa, GPTech/Garmin and Safari Centre are thanked for their sponsorship. E. Oppenheimer and Son and Duncan MacFadyen are thanked for providing accommodation and support. The Centre for Wildlife Management at the University of Pretoria provided financial assistance. Our thanks are also extended to Dr. M. Somers for useful comments.

REFERENCES

ANDHERIA, A.P., KARANTH, K.U. & KUMAR, N.S. 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *J. Zool., Lond.* 273: 169-175.

BAGCHI, S., GOYAL, S.P. & SANKAR, K. 2003. Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *J. Zool., Lond.* 260: 285-290.

BOTHMA, J. DU P. 2002. Counting wild animals. In J. du P. Bothma (Ed.) Game Ranch Management (pp. 335-357). Van Schaik Publishers, Pretoria.

BOTHMA, J. DU P. & LE RICHE, E.A.N. 1994. Scat analysis and aspects of defecation in northern Cape leopards. *S. Afr. J. Wildl. Res.* 24: 21-25.

BRILLOUIN, L. 1956. Scientific and information technology. Academic Press, New York.

CHARDONNET, PH. (ED.) 2002. *Conservation of the African lion: contribution to a status survey*. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA.

COCK, M.J.W. 1978. The assessment of preference. *J. Animal Ecol.* 47: 805-816.

DOUGLAS, R.M. 1989. A new method of cross-sectioning hair of large mammals. *S. Afr. J. Wildl. Res.* 19: 73-76.

DRUCE, D., GENIS, H., BRAAK, J., GREATWOOD, S., DELSINK, A., KETTLES, R., HUNTER, L. & SLOTOW, R. 2004. Prey selection by a re-introduced lion population in the Greater Makalali Conservancy, South Africa. *Afr. Zool.* 39: 273-284.

EBEDES, H. & BOTHMA, J. DU P. 2002. Ostriches. In: J. du P. Bothma (Ed.), Game Ranch Management (pp. 220-226). Van Schaik Publishers, Pretoria.

ELOFF, F.C. 1973. Lion predation in the Kalahari Gemsbok National Park. *S. Afr. J. Wildl. Res.* 3: 59-63.

ELOFF, F.C. 2002. Hunters of the dunes: the story of the Kalahari lion. Sunbird Publishing, Cape Town.

FLOYD, T.J., MECH, L.D. & JORDAN, P.A. 1978. Relating wolf scat to prey consumed. *J. Wildl. Manage.* 42: 528-532.

FUNSTON, P.J., MILLS, M.G.L. & BIGGS, H.C. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool., Lond.* 253: 419-431.

FUNSTON, P.J., MILLS, M.G.L., BIGGS, H.C. & RICHARDSON, P.R.K. 1998. Hunting by male lions: ecological influences and socioecological implications. *Anim. Behav.* 56: 1333-1345.

FRYXELL, J.M., GREEVER, J. & SINCLAIR, A.R.E. 1988. Why are migratory ungulates so abundant? *Am. Nat.* 131: 781-798.

GLEN, A.S. & DICKMAN, C.R. 2006. Diet of the spotted-tailed qoull (*Dasyurus maculates*) in eastern Australia: effects of season, sex and size. *J. Zool., Lond.* 269: 241-248.

HAYWARD, M.W. & KERLEY, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). *J. Zool., Lond.* 267: 309-322.

HAYWARD, M.W., HENSCHEL, P., O'BRIEN, J., HOFMEYR, M., BALME, G. & KERLEY, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *J. Zool., Lond.* 270: 298-313.

HAYWARD, M.W., O'BRIEN, J., HOFMEYR, M. & KERLEY, G.I.H. 2007a. Testing the predictions of prey of lion (*Panthera leo*) derived from modelled prey preferences. *J. Wildl. Manage.* 71: 1567-1575.

HAYWARD, M.W., O'BRIEN, J. & KERLEY, G.I.H. 2007b. Carrying capacity of large African predators: predictions and tests. *Biol. Conserv.* 139: 219-229.

HILDYARD, C.J. 1983. The identification of mammals using hair samples. B.Sc. (Hons) (Wildlife Management) Project Report, University of Pretoria, Pretoria.

JACOBS, J. 1974. Quantitative measurement of food selection. *Oecologia* 14: 413-417.

KARANTH, K.U. & SUNQUIST, M.E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *J. Animal Ecol.* 64: 439-450.

KEOGH, H.J. 1979. An atlas of hair from southern African mammal species, with references to its taxonomic and ecological significance. D.Sc. Thesis, University of Pretoria, Pretoria.

KEOGH, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *S. Afr. J. Wildl. Res.* 13: 89-94.

LANDMAN, M., KERLEY, G.I.H. & SCHOEMAN, D.S. 2008. Relevance of elephant herbivory as a threat to important plants in the Addo Elephant National Park, South Africa. *J. Zool., Lond.* 274: 51-58.

LEHMANN, M.B., FUNSTON, P.J., OWEN, C.R. & SLOTOW, R. 2008. Feeding behaviour of lions (*Panthera leo*) on a small reserve. *S. Afr. J. Wildl. Res.* 38: 66-78.

LOW, A.B. & REBELO, A.G. 1998. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

MARKER, L.L., MUNTIFERING, J.R., DICKMAN, A.J., MILLS, M.G.L. & MACDONALD, D.W. 2003. Quantifying prey preferences of free-ranging Namibian cheetahs. *S. Afr. J. Wildl. Res.* 33: 43-53.

MARUCCO, F., PLETSCHER, D.H. & BOITANI, L. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. *J. Mammal.* 89: 665-673.

MELVILLE, H.I.A.S., BOTHMA, J. DU P. & MILLS, M.G.L. 2004. Prey selection by caracal in the Kgalagadi Transfrontier Park. *S. Afr. J. Wildl. Res.* 34: 67-75.

MILLS, M.G.L. 1992. A comparison of methods used to study food habits of large African carnivores. In: D.R. McCullough & R.H. Barrett (Eds.), Wildlife 2001: Populations (pp. 1112-1124). Elsevier, London.

MILLS, M.G.L. & BIGGS, H.C. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symp. Zool. Soc. Lond.* 65: 253-268.

MILLS, M.G.L. & SHENK, M. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *J. Anim. Ecol.* 61: 693-702.

MUKHERJEE, S., GOYAL, S.P. & CHELLAM, R. 1994. Standardisation of scat analysis techniques for leopard (*Panthera pardus*) in Gir National Park, Western India. *Mammalia* 58: 139-143.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38: 541-545.

OWEN-SMITH, N. & MASON, D.R. 2005. Comparative changes in adult vs. juvenile survival affecting population trends in African ungulates. *J. Anim. Ecol.* 74: 762-773.

PERRIN, M.R. & CAMPBELL, B.S. 1980. Key to the mammals of the Andries Vosloo Kudu Reserve (Eastern Cape), based on their hair morphology, for use in predator scat analysis. *S. Afr. J. Wildl. Res.* 10: 1-14.

POWER, R.J. 2002. Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe* 45: 67-75.

PUTMAN, R.J. 1984. Facts from faeces. *Mammal Rev.* 14: 79-97.

QUINN, G.P. & KEOUGH, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

R DEVELOPMENT CORE TEAM. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org

RADLOFF, F.G.T. & DU TOIT, J.T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *J. Anim. Ecol.* 73: 410-423.

RAPSON, J.A. & BERNARD, R.T.F. 2007. Interpreting the diet of lions (*Panthera leo*); a comparison of various methods of analysis. *S. Afr. J. Wildl. Res.* 37: 179-187.

SKINNER, J.D. & CHIMIMBA, C.T. 2005. The mammals of the Southern African subregion. Cambridge University Press, Cape Town.

SMUTS, G.L. 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe* 19: 153-164.

STANDER, P.E., GHAU, //., TSISABA, D., □OMA, //. & I UI, I. 1997. Tracking and the interpretation of spoor: a scientifically sound method in ecology. *J. Zool., Lond.* 242: 329-341.

TAMBLING, C.J. & DU TOIT, J.T. 2005. Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. *J. Appl. Ecol.* 42: 431-441.

VAN ORSDOL, K.G. 1981. Lion predation in Rwenzori National Park, Uganda. Ph.D. Thesis, University of Cambridge, Cambridge.

VAN ROOYEN, N. 1999. The vegetation types and veld condition of Tswalu Private Desert Reserve. Unpublished report to the management of Tswalu Kalahari Reserve. University of Pretoria, Pretoria.

VAN VUUREN, HERRMANN, E. & FUNSTON, P.J. 2005. Lions in the Kgalagadi Transfrontier Park: modelling the effect of human-caused mortality. *Int. Trans. Op. Res.* 12: 145-171.

VILJOEN, P.C. 1997. Ecology of lions in northern Botswana. In: J. van Heerden (Ed.), Proceedings of a symposium on lions and leopards as game ranch animals (pp. 37-46). The Wildlife Group, South African Veterinary Association, Onderstepoort.

ZAR, J.H. 1999. Biostatistical analysis. Prentice-Hall, New Jersey.

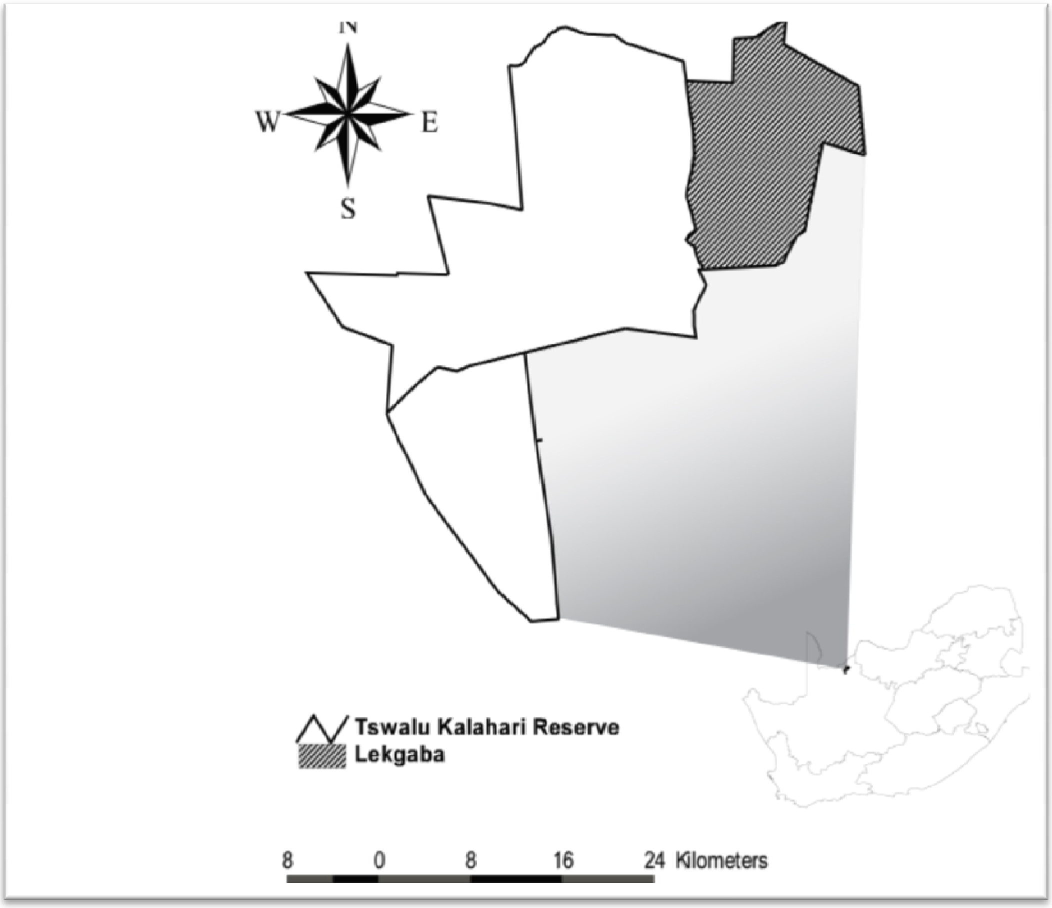

Fig. 1. The predator camp, Lekgaba (hatched), located in the eastern region of Tswalu Kalahari Reserve in the Northern Cape Province of South Africa.

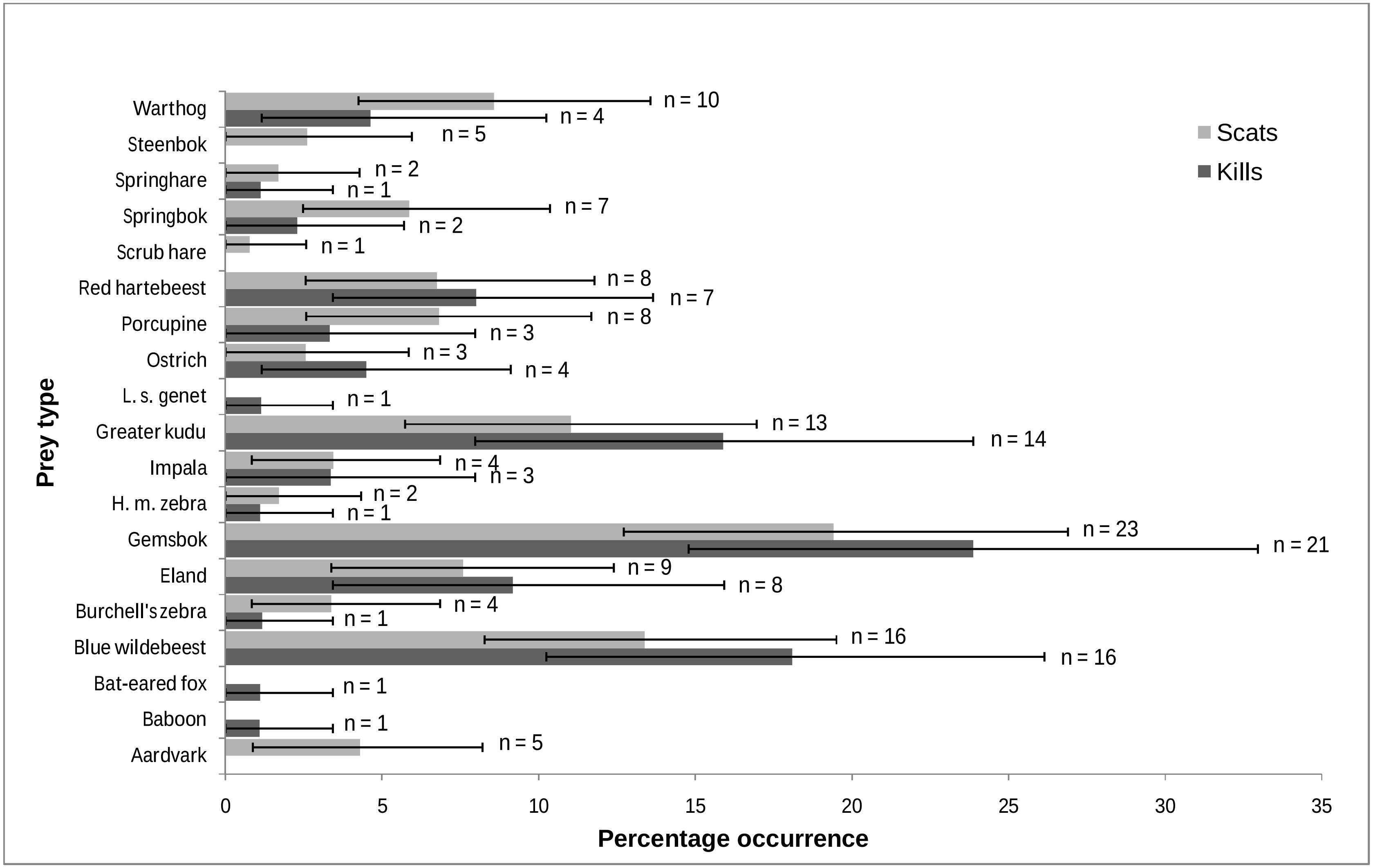

Fig. 2. Percentage occurrence of prey types of lions in observed kill and scat data, with 95% confidence limits and the total number of observations for each prey type (n) for the Lekgaba lion population on Tswalu Kalahari Reserve.

Table 1. Ratios and percentage occurrence of each prey type of lions when using corrected scat analysis (Karanth & Sunquist 1995; Marker *et al*. 2003) on Tswalu Kalahari Reserve.

Prey type	Weight of prey (kg)*	y	No. of scats	Weight of meat consumed	Ratio of weight consumed	Individuals consumed	Ratio of individuals consumed	Percentage occurrence in all scats
Aardvark	39.75	3.37	5	16.85	0.10	0.42	0.39	3.75
Blue wildebeest	135.00	6.71	16	107.28	0.62	0.79	0.73	7.02
Burchell's zebra	240.00	10.38	4	41.52	0.24	0.17	0.16	1.53
Eland	345.00	14.06	9	126.54	0.73	0.37	0.34	3.24
Gemsbok	157.50	7.49	23	172.27	1.00	1.09	1.00	9.67
Hartmann's mountain zebra	206.25	9.20	2	18.40	0.11	0.09	0.08	0.79
Impala	33.75	3.16	4	12.64	0.07	0.37	0.34	3.31
Greater kudu	116.25	6.05	13	78.65	0.46	0.68	0.62	5.98
Ostrich	101.25	5.52	3	16.56	0.10	0.16	0.15	1.45
Porcupine	12.75	2.43	8	19.44	0.11	1.52	1.39	13.45
Red hartebeest	90.00	5.13	8	41.04	0.24	0.46	0.42	4.03
Scrub hare	2.06	2.05	1	2.05	0.01	1.00	0.91	8.79

Table 1. (continued)

Prey type	Weight of prey (kg)	y	No. of scats	Weight of meat consumed	Ratio of weight consumed	Individuals consumed	Ratio of individuals consumed	Percentage occurrence in all scats
Springbok	27.75	2.95	7	20.65	0.12	0.74	0.68	6.58
Springhare	2.25	2.06	2	4.12	0.02	1.83	1.67	16.17
Steenbok	8.25	2.27	3	6.81	0.04	0.83	0.75	7.29
Warthog	45.00	3.56	10	35.60	0.21	0.79	0.72	6.98

*weight taken as 75 % of the adult female weight to compensate for juveniles and young that are killed (Hayward *et al.* 2007b).

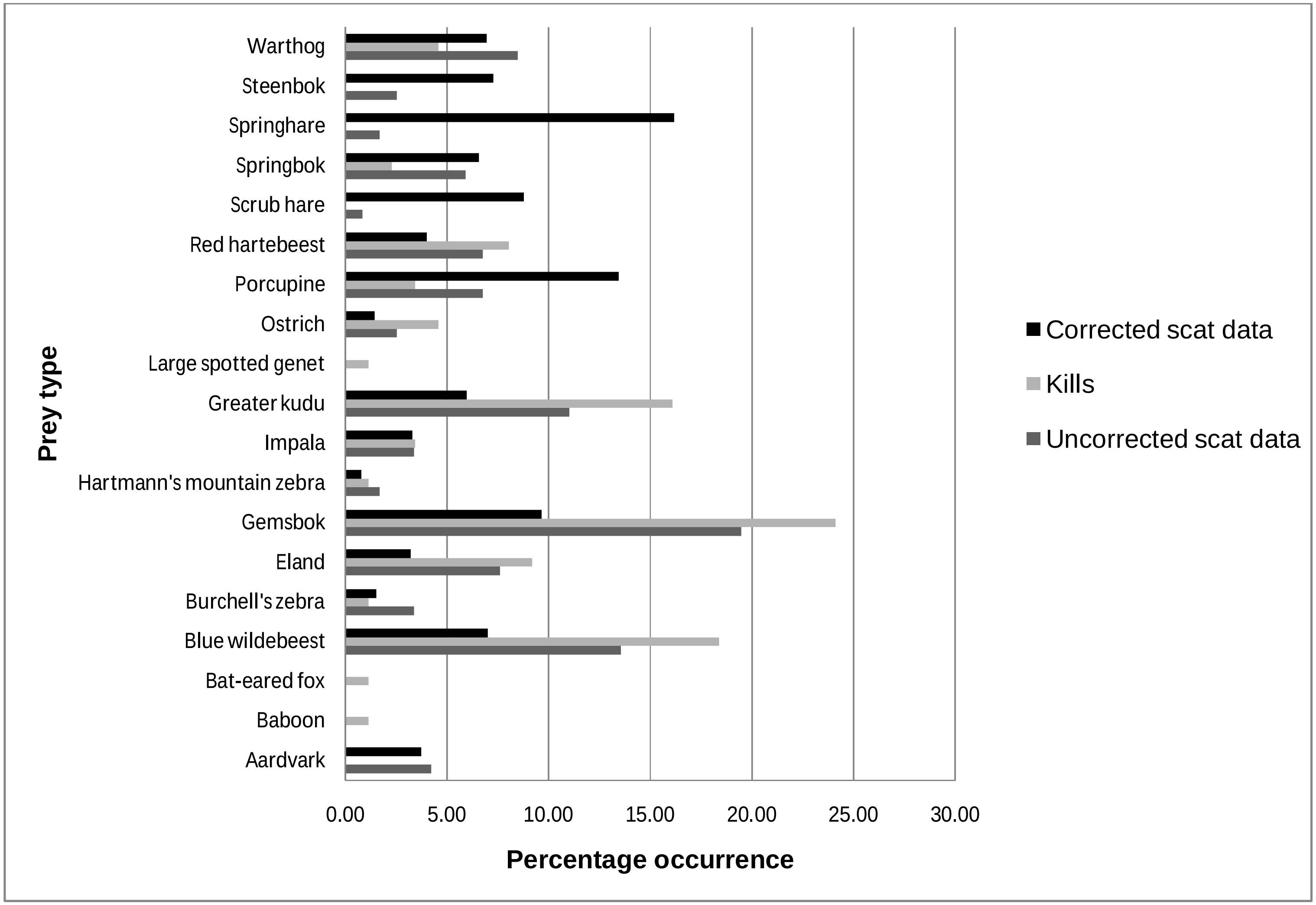

Fig. 3. Percentage occurrence of all prey types in the diet of lions on Tswalu Kalahari Reserve when using observed kills, uncorrected and corrected scat data.

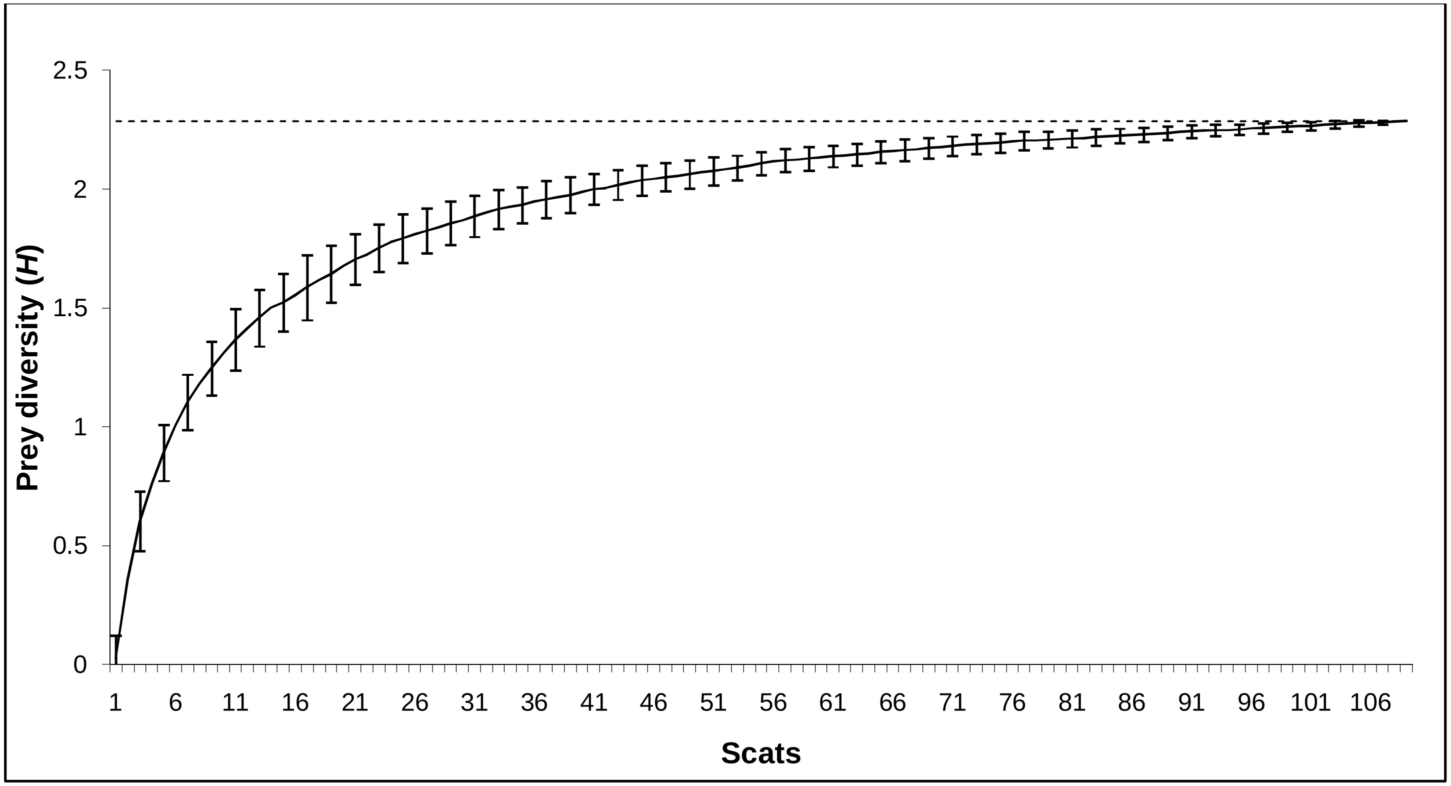

Fig. 4. Prey diversity relative to sample size increases in all collected uncorrected scats of lions on Tswalu Kalahari Reserve, with 95 % confidence limits (Brllioun1956).

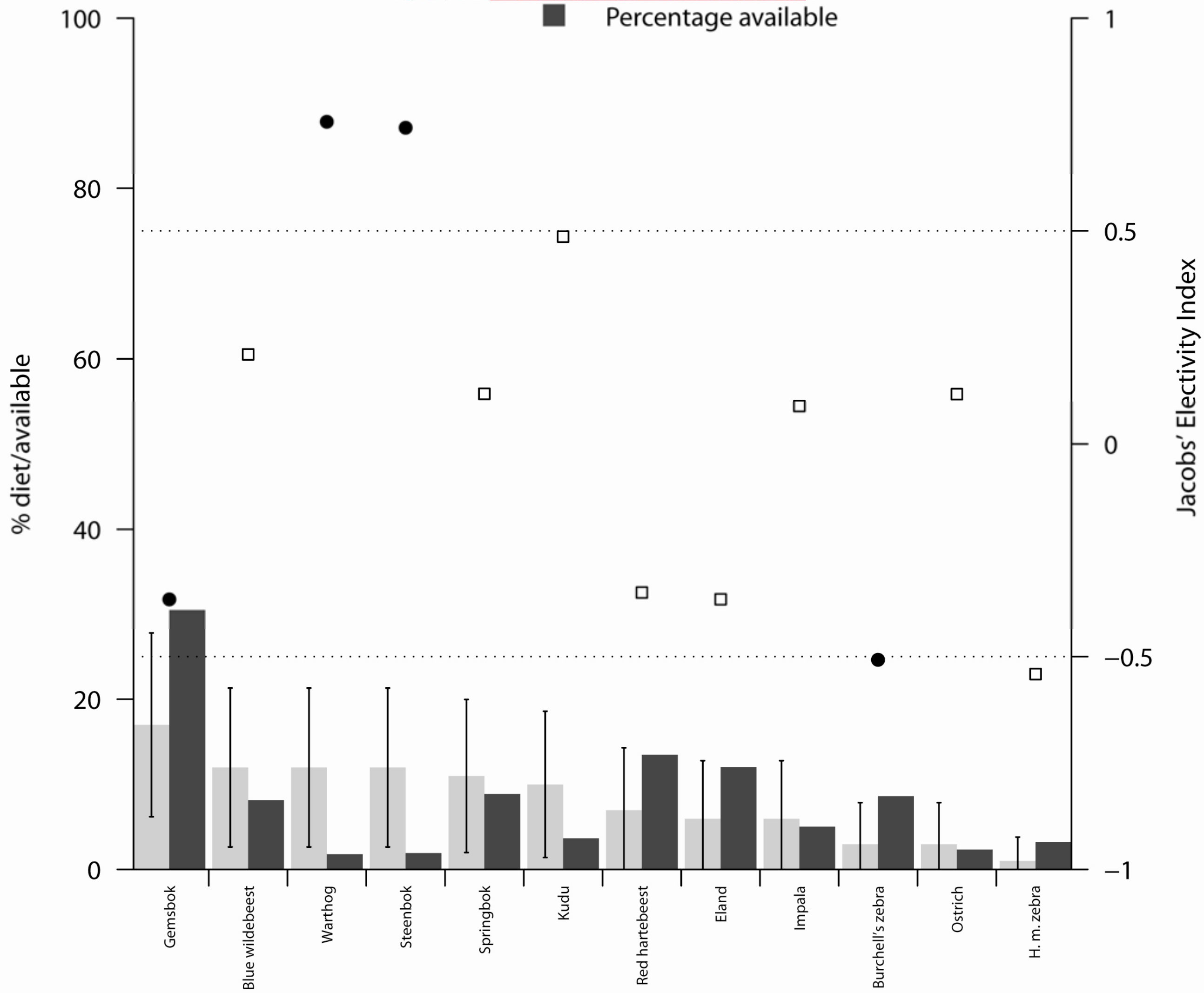

Fig. 5. Prey preference of the lion population on Tswalu Kalahari Reserve when using Jacobs' Electivity Index (Jacobs 1974). Values of +1 indicate maximum preference and -1 indicate maximum lack of use. 95% confidence intervals (Neu *et* al. 1976) are also shown where open squares indicate non-significant use and closed circles indicate significant preference or lack of use.

Table 2. Live weight and edible weight of prey types used to calculate available biomass and biomass removal by a lion population in Lekgaba on Tswalu Kalahari reserve.

Prey type[1]	Number	Live weight[2] (kg)	Estimated edible meat weight[3] (kg)
Gemsbok	512	157.5	105.53
Blue wildebeest	137	135.00	90.45
Eland	202	345.00	207.00
Kudu	62	116.25	77.89
Red hartebeest	226	90.00	81.00
Ostrich	40	101.25	67.84
Warthog[4]	31	45.00	40.50
Impala	85	33.75	30.38
Burchell's zebra	145	240.00	160.80
Hartmann's mountain zebra	55	206.25	138.19
Springbok	149	27.75	24.98
Steenbok	33	8.25	8.25

Table 2. (Continued)

Prey type	**Number**	**Live weight[2] (kg)**	**Estimated edible meat weight[3] (kg)**
Giraffe	9	600.00	360.00
Grey duiker	28	12.0	12.0
Mountain reedbuck	5	22.5	22.5
Waterbuck	2	187.50	126.63
Total	1721	261 460.5	176 769.9

[1]Abundance values for the aardvark, porcupine, springhare, baboon, bat-eared fox, large spotted genet and scrub hare were not available. The white rhinoceros and the black rhinoceros were excluded from the biomass calculations.

[2] 75 percent of the weight of an adult female was used to account for juveniles and young (Skinner & Chimimba 2005; Hayward *et. al.* 2007b).

[3] Dressing percentages of carcasses (Mills & Biggs 1993).

[4] Warthog numbers are difficult to assess as they take shelter in burrows when disturbed during aerial counts.

CHAPTER 5

RANGE USE AND HABITAT SELECTION

Introduction

Historically, lions ranged throughout Africa, Europe and Asia (Nowell & Jackson 1996; Bothma & Walker 1999; Chardonnet 2002; Sunquist & Sunquist 2002; Bauer, De Iongh, Princée & Ngontou 2003). As stated in Chapter 1, these ranges have since diminished to a fraction of the previous sizes. Lions are now only found in various fragmented ranges and habitats throughout the African continent (Hanby, Bygott & Packer 1995; Estes 1997; Chardonnet 2002). Several studies have been conducted on these lion populations with regard to their spatial movements and habits (Spong 2002; Ogutu & Dublin 2004).

The range of any animal is associated with the spatial distribution of limiting resources (Mizutani & Jewell 1998; South 1999; Mitchell & Powell 2004). These limiting resources determine the size and utilization of that range. Several factors determine the range size and its use by predators. These relate to energy requirements and energy availability (Macdonald 1983; Lindstedt, Miller & Buskirk 1986; Horne & Garton 2006), and include factors related to hunting success and hunting opportunities (Bothma & Le Riche 1994b), the presence of other competing predators, opportunities for reproduction (Rowlands & Sadleir 1968; Turner 2005), unique qualities of different habitats (Turner 2005) and reducing variation in their life processes (Ferguson, Taylor, Born, Rosing-Asvid & Messier 1999)

Lion prides live in ranges or territories (Smuts 1982; Apps 1992; Estes 1997; Sunquist & sunquist 2002; Spong & Creel 2004), each one differing in size, scale and characteristics if another territory or area of use (Schaller 1972; Bothma 1998). A territory is defined as the area in which an animal survives and protects its own resources and offspring (Maher & Lott 1995). This is especially evident in lion sociality in which a territory is fiercely protected from conspecifics (Maher & Lott 1995). Prides occupy territories, while nomadic lions wander into several ranges, often causing their own death if they come across the resident pride (Smuts 1982; Estes 1997). Territories are delineated by scent-marking, head-rubbing and constant patrolling (Smuts 1982; Briscoe, Lewis & Parrish 2002; Sunquist & Sunquist 2002). Prides of females can occupy the same territory for a number of years and live in stable family groups with the prides consisting of siblings and related individuals. On the other hand males are not related to the females and only have tenure over a certain territory for 2.5 to 3 years (Nowell & Jackson 1996; Estes 1997). Males are replaced by other males, preventing inbreeding. Males do form coalitions, which are small groups of related individuals, which allow them to occupy a territory for longer, and improve their competing abilities with other males (Funston, Mills, Richardson & van Jaarsveld 2003). Males protect their territories vigorously, and expend an enormous amount of energy in patrolling and maintaining territory boundaries.

Territory sizes are dynamic and change with regard to environmental conditions and resource availability (Stander & Albon 1993). General territory sizes are a function of resource abundance and availability and the size of the pride that inhabits that specific territory. Generally prides with greater numbers and higher numbers of males occupy larger territories because they require more resources than smaller prides. The range size of females is dependent on prey density and distribution (Fisher & Owens 2000; Dahle & Swenson 2003; Killian 2003), while the range sizes of the males is dependent on the availability of mating opportunities, i.e. the distribution of prides (Gehrt & Fritzell 1998; Fisher & Owens 2000; Sunquist & Sunquist 2002; Funston *et al.* 2003). Prides of females occupy separate adjacent ranges, while the males can occupy ranges that overlap several pride’s territories.

Males seem to have three distinct phases of range use (Turner 2005). Young males are evicted from their natal prides and disperse into neighbouring territories (Hanby & Bygott 1987). In this first phase they do not defend any resources. Males or coalitions of males then attempt to take over a pride of females. If successful at the takeover, the males spend most of their rime courting and mating with the pride females. The males protect mating rites to the females in this second phase. After the birth of the cubs the males spend less time with the females and cubs and spend more time patrolling their territory.

If two rival prides meet, they usually retreat to their own territories, or in rare cases they can be hostile towards each other (Spong & Creel 2004). Nomadic lions are also not tolerated in a pride's territory. The range sizes of nomadic lions are often much larger than that of the prides. Lions living in harsh environments exhibit larger range use patterns than other lion populations (Eloff 2002). During extremely unfavourable environmental conditions territory breaks down (Eloff 2002) as hunting grounds are expanded into rival territories.

Studying range sizes, utilization and preference is important for ecological and behavioural studies, which is emphasized in social species (Swihart & Slade 1985; Guasp, De Torres Curth & González 1996; Blackwell 1997; Ogutu & Dublin 1998; Horne & Garton 2006). This knowledge is can be used to correctly understand a population's movement patterns and for making management decisions aimed at its conservation (Van Winkle 1975; Guasp *et al.* 1996; Seaman & Powell 1996). Range use studies are an important biological tool to determine an animal's behaviour, habitat selection, population density and foraging behaviour (Harris, Creswell, Forde, Trewhella, Woollard & Wray 1990; Schooley 1994; Arthur, Manly, McDonald & Garner 1996). Correct management of the Tswalu lion population will therefore only be maintained through a thorough understanding of the range use patterns and habitat selection of these lions. These range use patterns and habitat selection were determined by using a number of statistical and methodological tools which are described below. In doing so, the hypothesis that the Tswalu lion population uses its range and habitat proportionally to its availability was tested by researching the following key questions:

- To what extent do the lions utilize the current available range?
- Do the lions utilize the range and habitats within the range proportionally to the habitat availability?
- If the lions do not use the habitats proportionally to their availability, is there any indication of specific habitat preference?

Methods

The following specific methods of study were used:

Field study

The range use patterns and habitat selection of lions in this enclosed, arid area were investigated. Eight lions were followed and studied during the study period. These eight lions were divided into two prides and consisted of six focal groups. This was done because the lions spent a large portion of their time alone or with a sibling. The six focal groups and their ages, at the start of the study were as follows:

Northern Pride:

- F1: adult female, circa 8 years old. F1 gave birth to two female cubs in December 2003 and they were included in focal group F1 because they were still being weaned.
- M2: subadult male, circa 30 months old, M2 was pushed out of the pride in late 2003 and then established his own range.
- F3: subadult female, circa 30 months.

Southern Pride:

- F2: adult female, circa 6 years old. F2 gave birth to two cubs in September 2004 which were only seen once.

- M3, F4: brother and sister, born to F2 in June 2002. They were considered to be one focal group because they were seen together on all occasions.

The dominant male, M1, was not included in the prides because he visited both prides on a random basis.

The focal lion groups were located by spoor tracking, direct observation, opportunistic observations and reports from rangers and staff working in the area. Spoor tracking of lions was done by driving a designated route, along pre-determined roads. Spoor tracking has been used in many studies in which the habitat is restrictive to studying the animal population in question (Eloff 1973a; Stander, Ghau, Tsisaba, □oma & I ui 1997). Spoor-tracking is also an unobtrusive, passive method of determining animal behaviour and movement (Bothma & Le Riche 1993; Stander 1997). Once the spoor of a lion was detected, it was followed until a positive sighting of the animal was obtained. Once the lion was spotted and identified, a GPS fix was taken of its original position. If the lion continued to move, a new point was taken every 100 m from the point of first contact. The entire day was spent with one particular pride or focal group. It was not possible to track the lions at night because of logistical problems. If the lions moved off-road it was also nearly impossible to find them in the dark. Several aardvark holes made driving at night almost impossible. If no tracks were located on the marked route, searching was continued at waterholes and areas of known use by the lions. Several opportunistic sightings and sightings that were called in by rangers and field guides were also included in the data set. Direct observation and opportunistic sightings were considered to be the least biased and easiest method to determine range use characteristics of the Tswalu lion population based on Bryden 1978), Mills & Schenk (1992) and Funston (1999).

M1 and F1 were fitted with radio-collars when they were released in 2001. These collars were removed for aesthetic reasons and because the battery life had expired on both collars before the study had started. In January 2004, M2 was fitted with a radio collar by the Tswalu management staff. Tswalu borders on cattle and sheep farms and it was feared that M2 would break out of Lekgaba and raid the neighbouring farms. Despite the radio-collar on M2, the original data collection methods were used so as not to bias the data toward M2.

Range use analysis

Two statistical range use methods, the minimum convex polygon method and the Kernel density estimate method were used to determine the range sizes and use of the lion population on Tswalu. These two methods allow for spatial analysis of range size and use (Harris *et al.* 1990). The ArcView Global Information System Package (ArcView 3.2a) along with the Home Range Extension (Carr & Rodgers 1998) and the Animal Movement Extension for ArcView (Hooge 1999; Hooge & Eichenlaub 2000) were used in the range use and size determination.

Minimum convex polygon (MCP) method

The minimum convex polygon method is described as the simplest and oldest of all range use calculation techniques (Worton 1987; Harris *et al.* 1990). Despite its early development, it is still widely used today in many studies involving range use by animals (Harris *et al.* 1990; Burgman & Fox 2003). The minimum convex polygon method is highly comparable between studies and is valuable when it is being used in conjunction with other methods (Harris *et al.* 1990).

The peripheral locations of an animal are joined to create a minimum area which incorporates all the data location points (Worton 1987). The range size is highly correlated with the number of data points that are collected for each animal, especially when working with a small sample size (Worton 1987). Although this method is relatively simple to apply, it does have deficiencies. Because all positional fixes are taken into account, areas that are only visited occasionally are included in the polygon. This creates an overestimation of the actual range size and shape (Harris *et al.* 1990). This method also does not give an indication of the intensity of range use (Worton 1987; Harris *et al.* 1990), and it is known that certain animals utilize areas of their range more frequently than others (Turner 2005)

Kernel analysis

The Kernel density analysis method of range use analysis is a non-parametric method that is used for estimating range use and size (Broomhall 2001; Seaman & Powell 1996; Bothma, Knight, Le Riche & van Hensbergen 1997; Hemson, Johnson, South, Kenward, Ripley & Macdonald 2005). Kernel density estimates provide an ideal basis for quantitative analysis of the data set (Seaman & Powell 1996; Hemson *et al.* 2005). The Kernel method can be used to determine the density estimation in any number of dimensions, where different observation parameters characterise a population of interest (Seaman & Powell 1996). In the context of range use, the intensity of use that is generated by this method is an estimation of the amount of time that is spent by the animal at any given location (Seaman & Powell 1996). This estimation allows for the development of a basis for ecological investigations of habitat use and preference (Seaman & Powell 1996). Worton (1989) states that the kernel density estimation method of range use provides a good means of determining range use because of the well understood theoretical properties of this method.

The kernel density estimation method in essence functions by placing a kernel (a probability density) over each positional fix in the sample (Seaman & Powell 1996; Gallerani Lawson & Rodgers 1997). A rectangular grid is placed over the data and an estimate of the density of fixes is determined at each grid intersection. The density estimations of each individual positional fix combine to form a mixture distribution that is used to estimate a probability density function (Worton 1989). A 50%, 75% and 95% utilization distribution were calculated for each of the six lion groups. The 50% and 75% isopleths were used to estimate the core area of use (Lent & Fike 2003) of the lions, while the 95% isopleths were used to remove the effect of outliers or random excursions outside the normal range on the calculation of the range size (Mizutani & Jewell 1998). Core areas of use are those areas of habitat being used more frequently by the population in question and they more than likely contain refuges and dependable food sources (Samuel, Pierce & Garton 1985)

Much debate centres on the efficacy of a range use estimator and whether or not a range is actually definable (Gautestad & Mysterud 1995; Börger, Franconi, De Michele, Gantz, Meschi, Manica, Lovari & Coulson 2006; Millspaugh, Nielson, McDonald, Marzluff, Gitzen, Rittenhouse, Hubbard & Sheriff 2006; Nilsen, Pedersen & Linnell 2008). Range estimation models should calculate range use contours from a complete utilization distribution while also comparing probability densities from the utilization distribution (Worton 1989; Kernohan, Millspaugh, Jenks & Naugle 1998). Many authors have stated the need to avoid autocorrelation of data sets to obtain statistically relevant results (Reynolds & Laundre 1990; Marzluff, Millspaugh, Hurvitz & Handcock 2004; Turner 2005; Cromhout 2006). However, autocorrelation appears to not have an effect on the estimates of range size (Blundell, Maier & Debevec 2001; Cushman, Chase & Griffin 2005) and so all location fixes were used to determine range size.

The minimum convex polygon method has been found to be less efficient than kernel density estimators when determining range size (Blundell *et* al, 2001; Börger *et* al. 2006; Nilsen *et al*. 2008). Kernel density estimators have become the standard for models of animal movements (Kernohan *et* al. 1998; Seaman, Millspaugh, Kernohan, Brundige, Raedeke & Gitzen 1999; Marzluff *et al*. 2004; Nilsen *et al*. 2008). The kernel density estimate method was considered to be biased by a lion study in Botswana (Hemson *et* al. 2005), but was resurrected by several studies later, notably by Nilsen *et al*. (2008).

Seaman & Powell (1996) suggest that at least 100 positional fixes must be recorded for robustness of the data. This number has since been revised by a number of authors, with a minimum number now being placed at between 30 and 50 location fixes (Seaman *et* al. 1999, Marzluff *et al*. 2004). More recently the minimum required number of location fixes for statistical use has been placed at 10 location fixes (Börger *et al*. 2006).

Habitat selection analysis

Habitat selection by the Tswalu lion population was determined by comparing patterns of habitat use with habitat availability. An Arcview (ver. 3.2a) vegetation map (Van Rooyen 1999) was used to determine the proportion of each habitat type in the range used by each of the six lion groups. A 100% minimum convex polygon was used, which encompassed all location fixes, including all excursions out of the normal range area. The location fixes in each habitat type were counted for each lion group and tabulated.

A habitat selection index was calculated for each of the habitat types in the ranges of the six focal lion groups by using an adaptation on Ivlev's Electivity Index (Jacobs 1974). Several studies have used this method successfully to determine a measure of selectivity e.g. Viljoen (1989), Pienaar, Bothma & Theron (1992), Jansen, Little & Crowe (2000); Admasu, Thirgood, Bekele & Laurenson (2004), Biró, Szemethy & Heltai (2004), Turner (2005), Cromhout (2006) and Landman, Kerley & Schoeman (2008). The following equation (adapted from Jansen *et al.* 2000) indicates Jacobs' preference index:

$$P = (R_1/R_2 - A_1/A_2) / (R_1/R_2 - A_1/A_2)$$

Where:

P = Jacobs' preference index

R_1 = number of fixes in a particular habitat type

R_2 = total number of fixes per lion

A_1 = surface area of particular habitat type in hectares

A_2 = total surface area of all habitat types in hectares

By using the equation results in values range from +1 to -1 (Hayward, Henschel, O'Brien, Hofmeyr, Balme & Kerley 2006), with +1 being the maximum preference for a specific habitat type and -1 indicating maximum avoidance of a specific habitat type. Cromhout (2006) stated that values ranging from +0.5 to -0.5 indicate a habitat type that was used in proportion to its availability, while values greater than +0.5 indicated a habitat type that was used in a greater proportion to its availability. Values less than -0.5 indicated that a habitat type was used less often than its proportional availability. Jacobs' preference Index is merely an indication of habitat use compared to habitat availability and is not based on a statistical test (Hayward *et al*. 2006).

For statistical analyses a chi-square goodness-of-fit test was conducted on the data set (Neu *et al*. 1974; Alldredge & Ratti 1992; Turner 2005). The chi-square analyses were done to determine if a specific habitat type was preferred or underutilized by each lion group. The data were tested for significance at the 5% level (α = 0.05). The chi-square ($\mathcal{X}^2$) values were compared to values found in the upper percentage chi-square distribution tables (Samuels 1989; Nelson 2004), by using the degrees of freedom relevant to the study and the set significance level. If the chi-square values exceeded the value listed in the table, the data were significant at the 5% level of error or less (Nelson 2004).

When significant differences were detected between the frequencies of utilization and availability, Bonferroni Z-statistics were used to construct 95% simultaneous confidence intervals (Cromhout 2006; Watson & Chadwick 2007) by using the following equation (adapted from Neu *et al*. 1974)

$$P_i - Z(1\text{-}\alpha/2k)\sqrt{Pi(1-Pi)/n} \leq P_i \leq P_i + Z(1\text{-}\alpha/2k)\sqrt{Pi(1-Pi)/n}$$

Where:

P_i	= proportion of use of a habitat type
Z(1-α/2k)	= the upper standard normal distribution value corresponding to a tail area of α/2k
n	= total number of observations for each lion group
α	= significance level = 5%
k	= number of habitat types available

To determine preference, underutilization or no discernible pattern of habitat use the proportions of each habitat type were compared to the 95% confidence intervals (Marcum & Loftsgaarden 1980). A habitat type was considered to be preferred if the habitat type proportion was less than the lower limit value of the confidence interval of use for that specific habitat. No pattern was observed if the habitat type proportion value fell within the confidence interval values. A habitat type was considered to be underutilized if the habitat type proportion value exceeded the upper limit value of use of the confidence interval (Byers, Steinhorst & Krausman 1984).

Results

A total of 860 confirmed GPS fixes for the entire lion population was recorded in the study period (Table 1). There was a lion density of 0.04 lions/km^2 of habitat.

Range use

According to the 100% minimum convex polygon method the range sizes of the lion population varied from a maximum of 109.1 km^2 (LM1) to a minimum of 70.2 km^2 (LF1) with a mean of 91.9 km^2 (Table 1). The 100% minimum convex polygon method results appear in Figures 1 to 6 as ArcView maps. The kernel density estimate maps (95%, 75% and 50% isopleths) for each lion group appear in Figures 7 to 12.

Table 1: Range sizes (km^2) for all lion groups in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon (MCP) method and various kernel density estimates

Lion group	**Location fixes**	**Minimum convex polygon**	**Kernel isopleth estimate**		
			95%	75%	50%
LM1	191	109.1	111.1	48.3	11.7
***Northern pride*:**					
LF1	108	70.2	65.0	24.4	6.6
LM2	173	102.8	103.7	34.5	11.8
LF3	110	76.8	56.6	22.2	8.1
***Southern pride*:**					
LF2	145	91.8	63.9	23.6	4.3
LM3, LF4	133	96.4	80.4	30.6	8.9
Mean	-	91.1	80.1	30.6	8.6

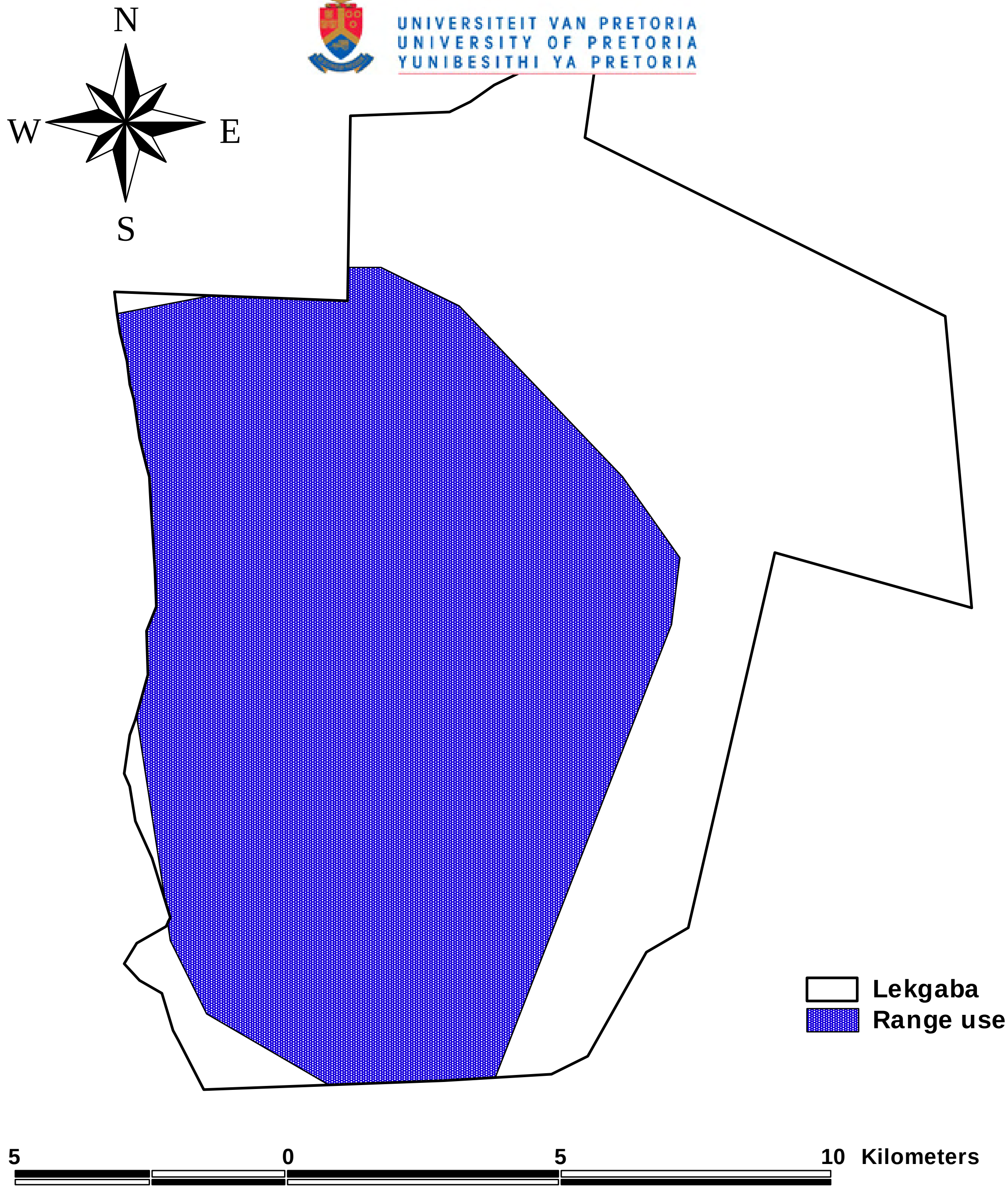

Figure 1: Range use of lion LM1 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

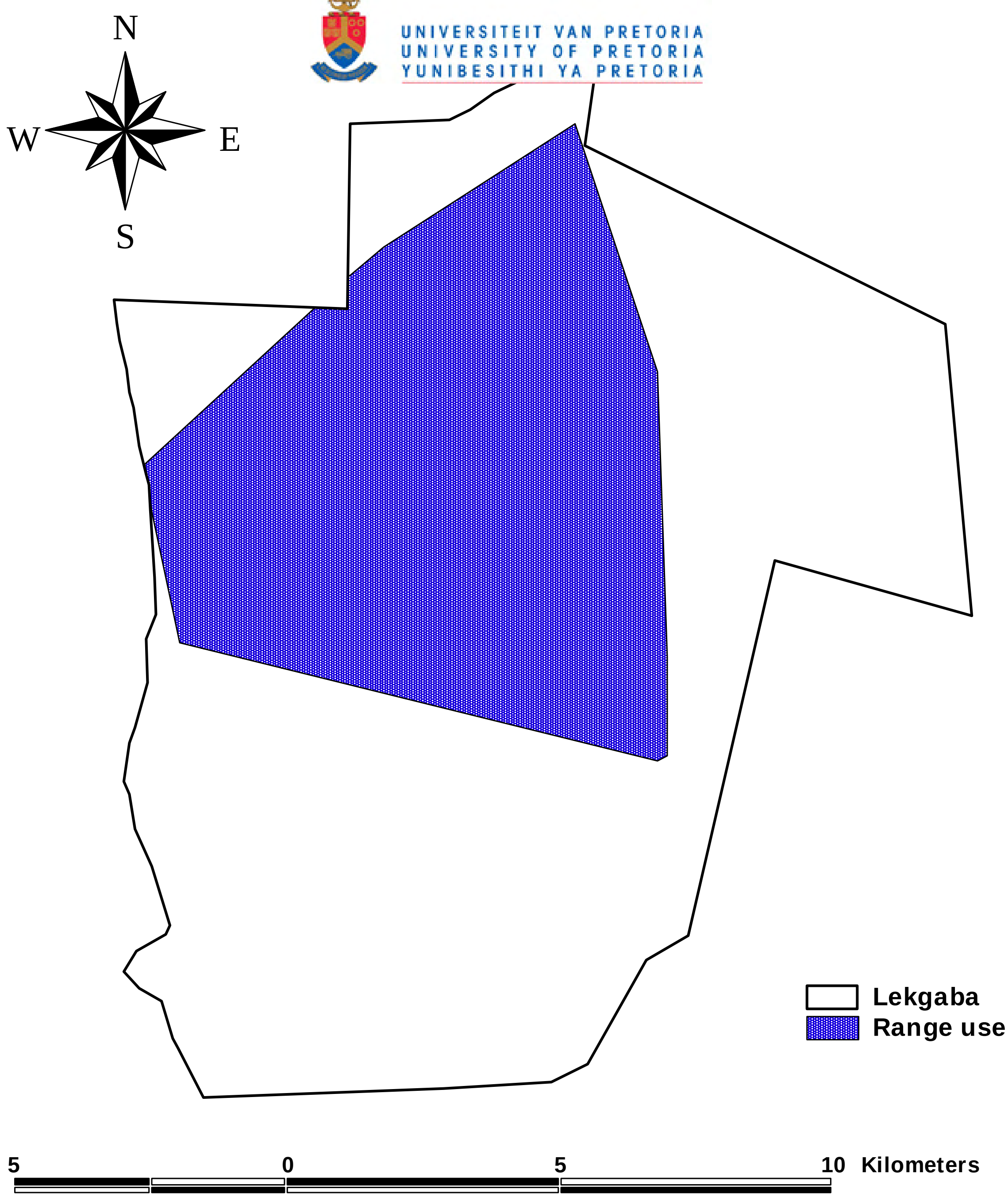

Figure 2: Range use of lioness LF1 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

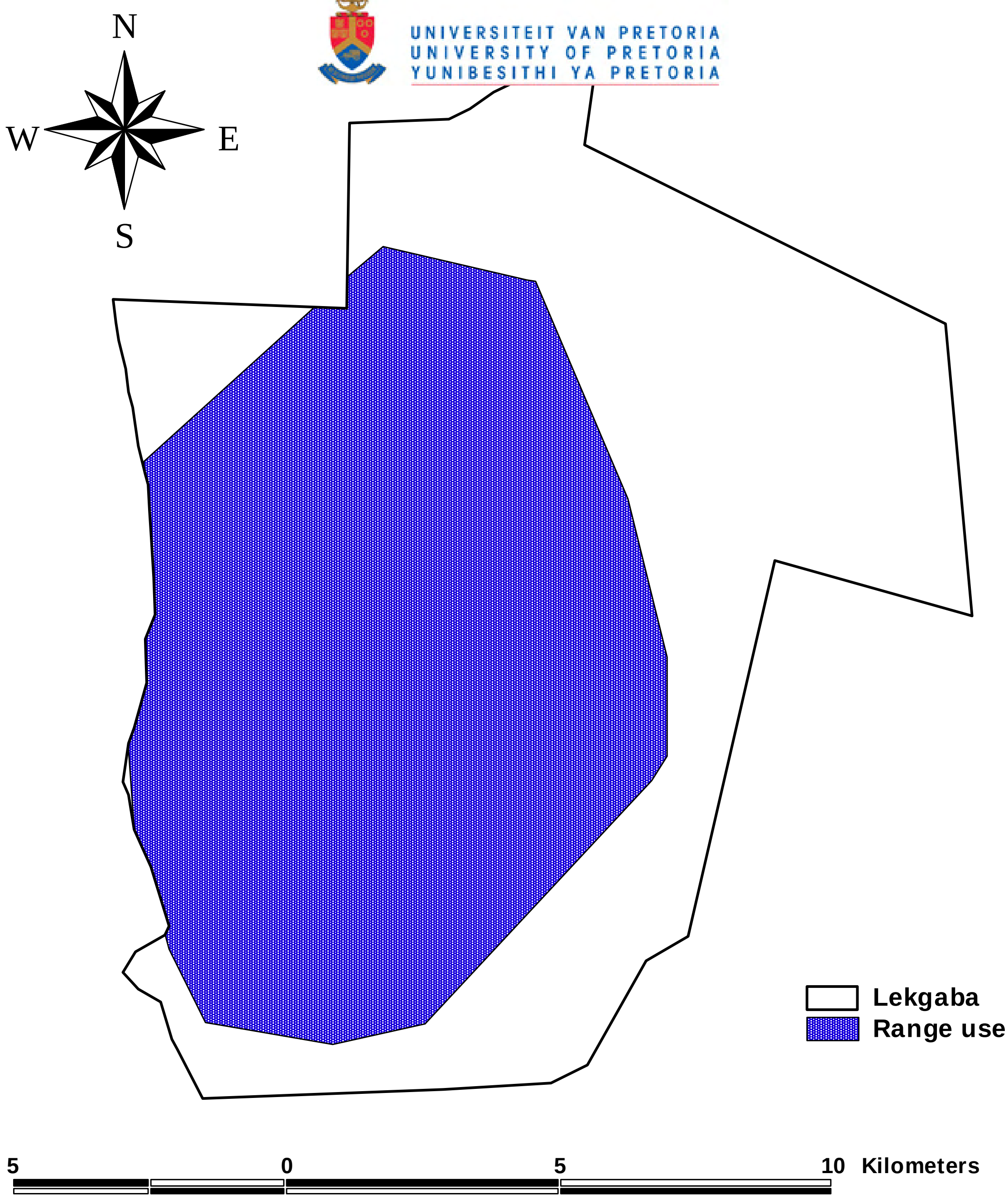

Figure 3: Range use of lion LM2 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

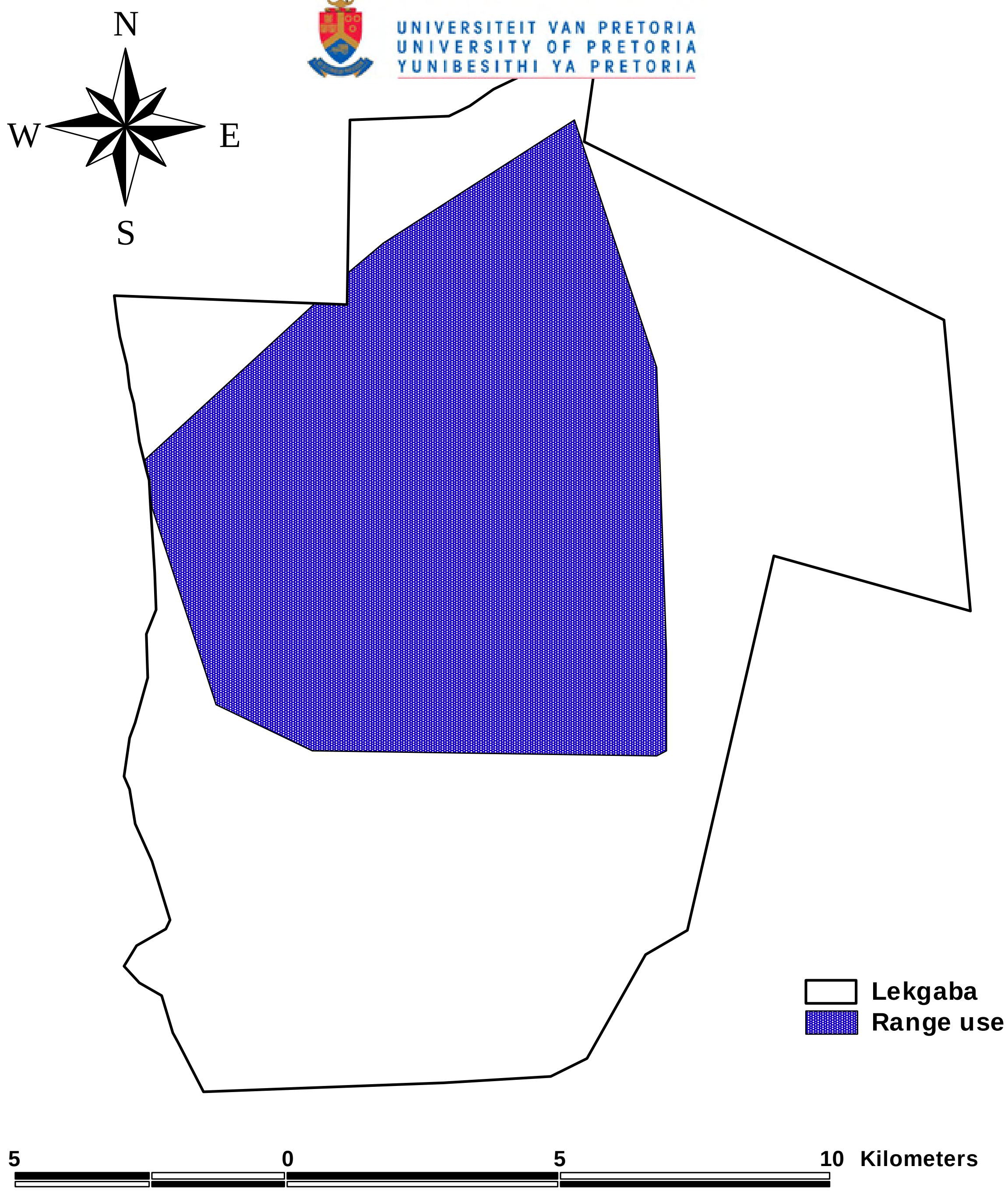

Figure 4: Range use of lioness LF3 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

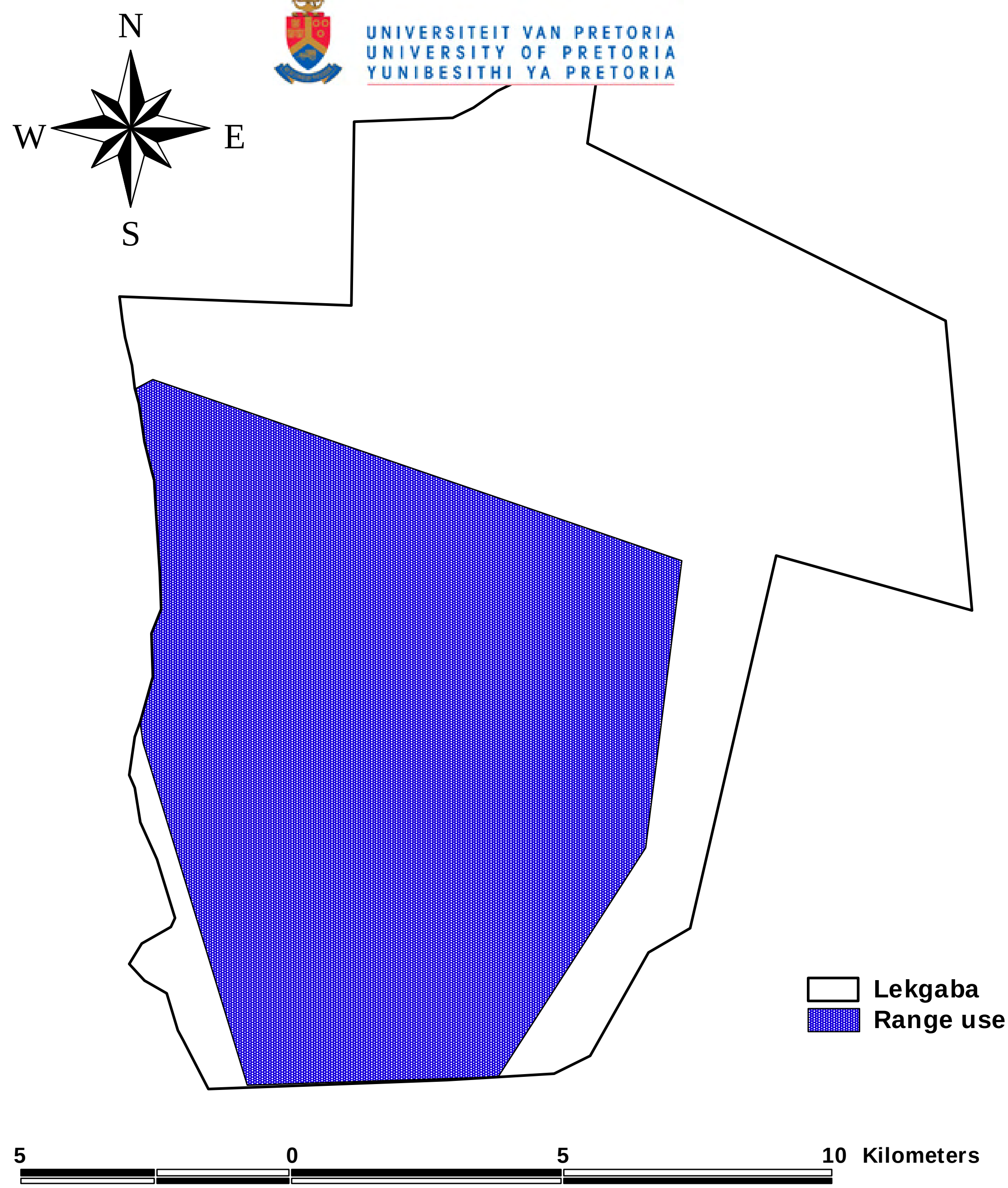

Figure 5: Range use of lioness LF2 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

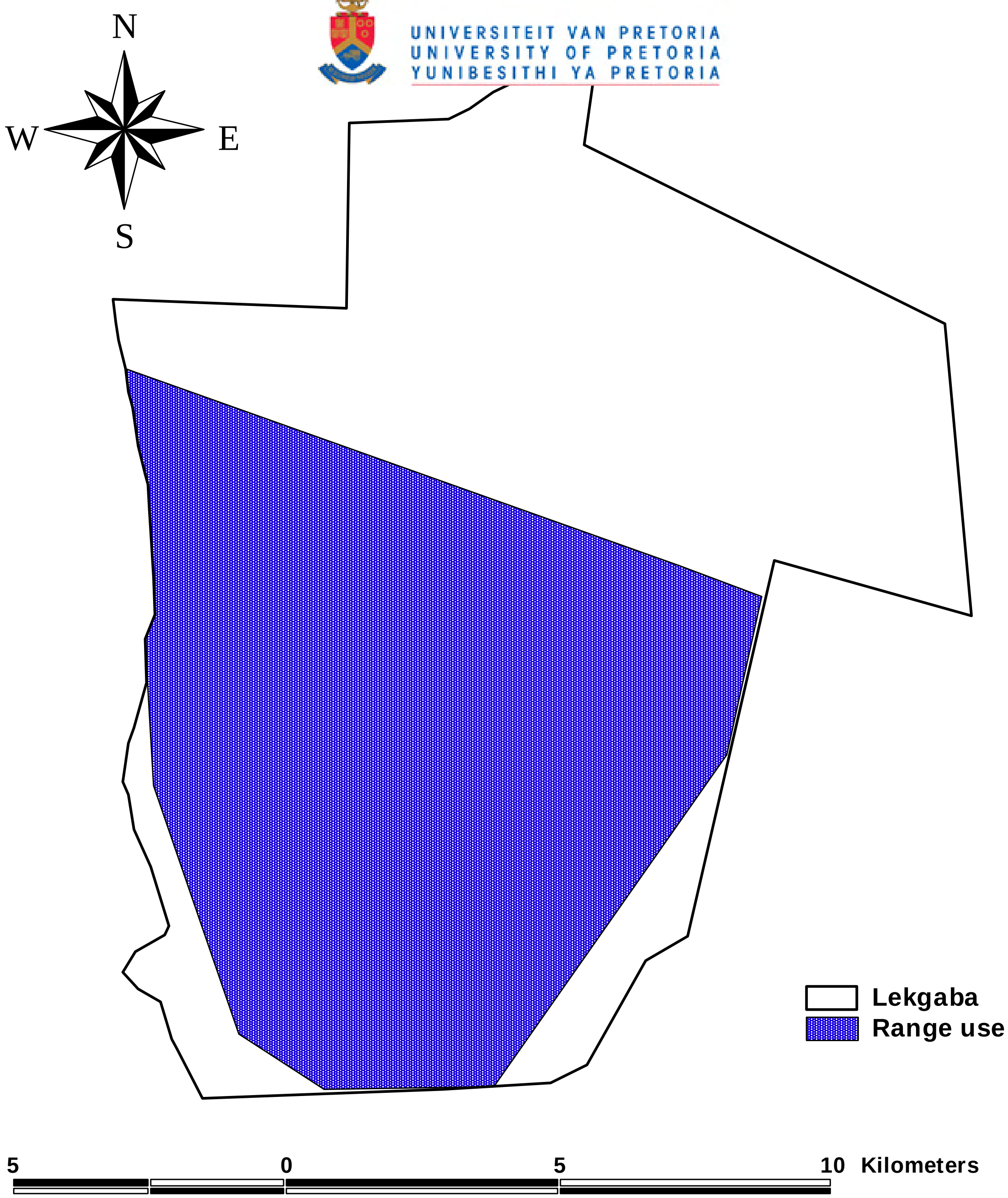

Figure 6: Range use of lion LM3 and lioness LF4 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

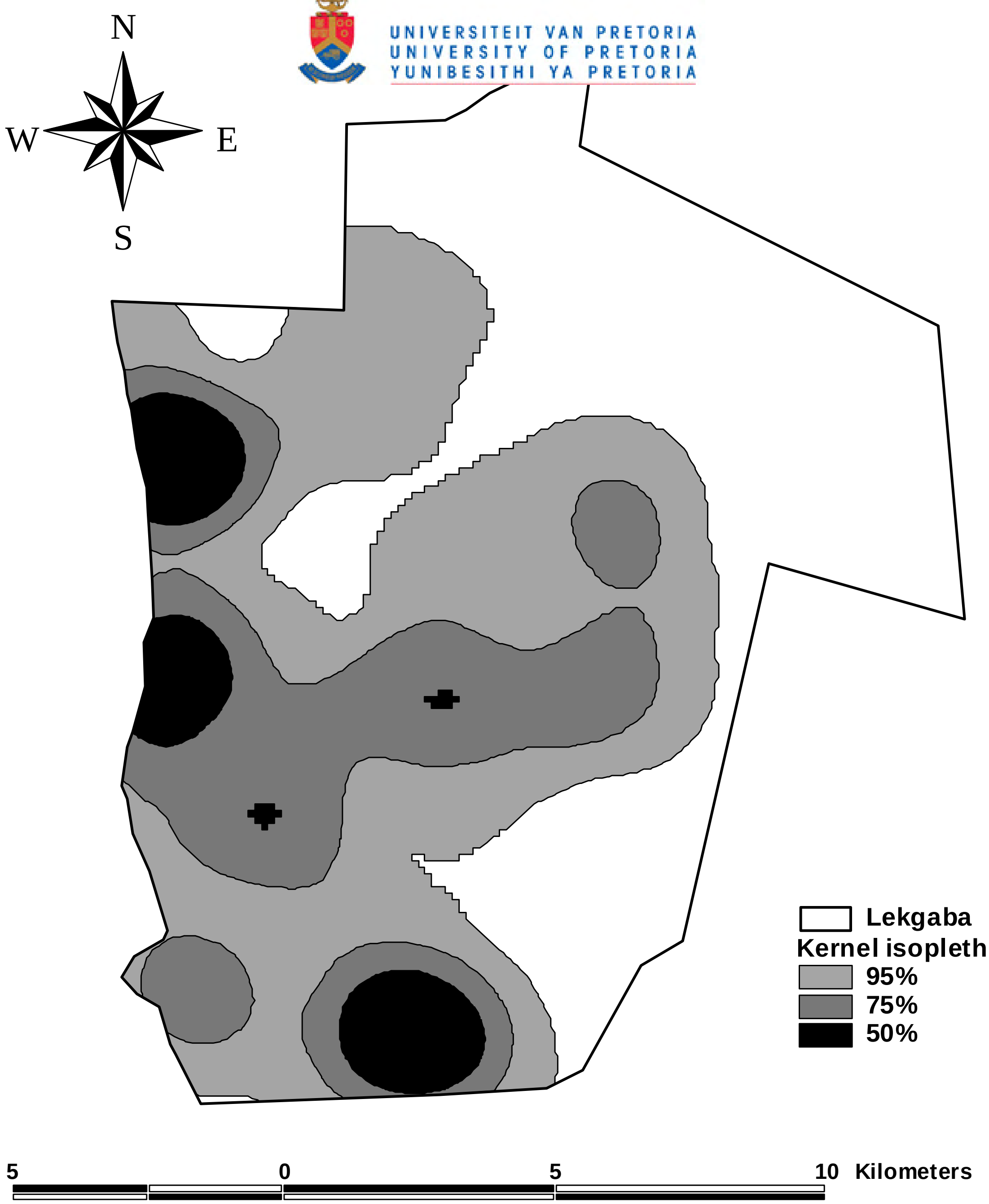

Figure 7: Range use of lion LM1 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

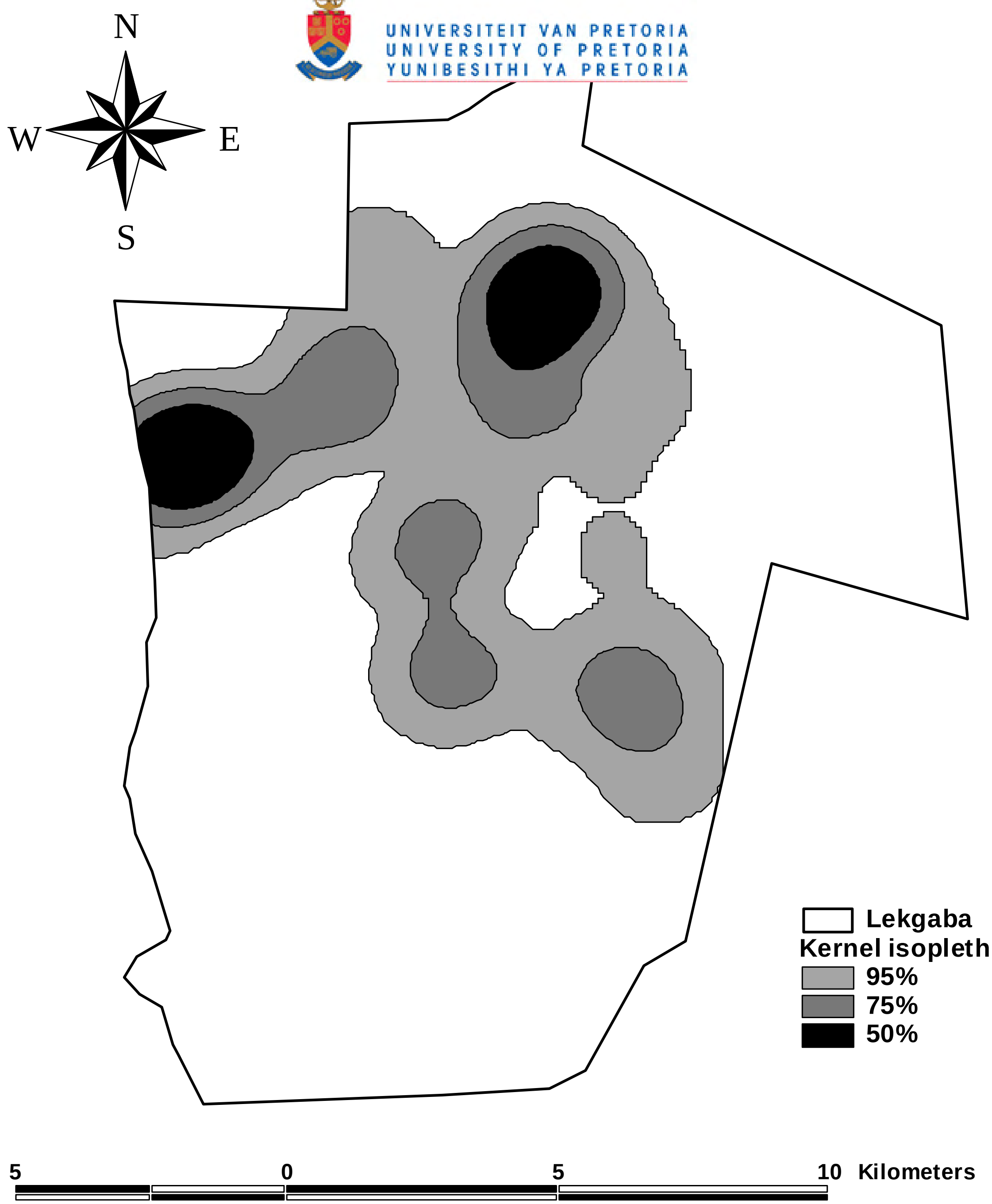

Figure 8: Range use of lioness LF1 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2a (Hooge 1999).

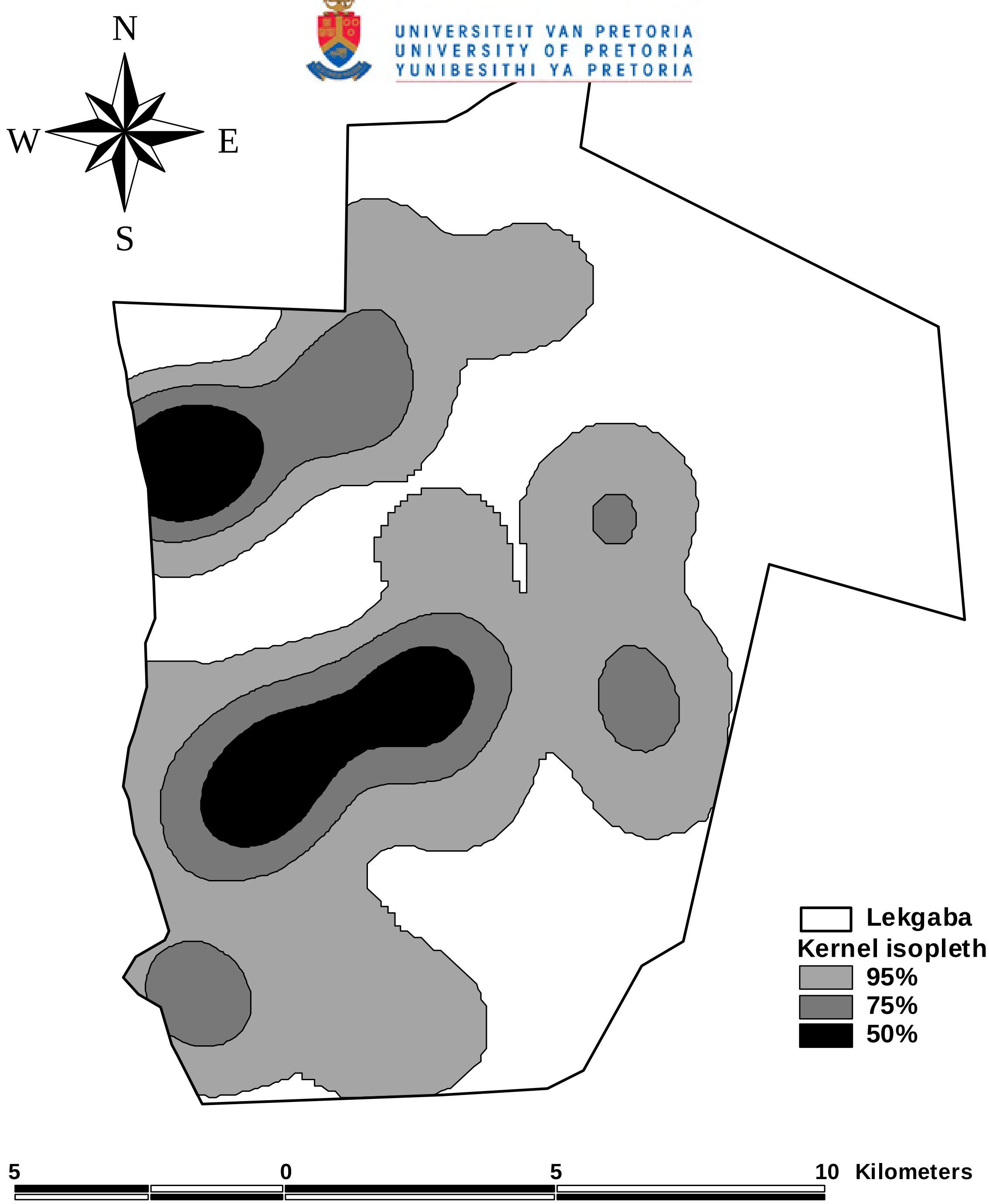

Figure 9: Range use of lion LM2 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2a (Hooge 1999).

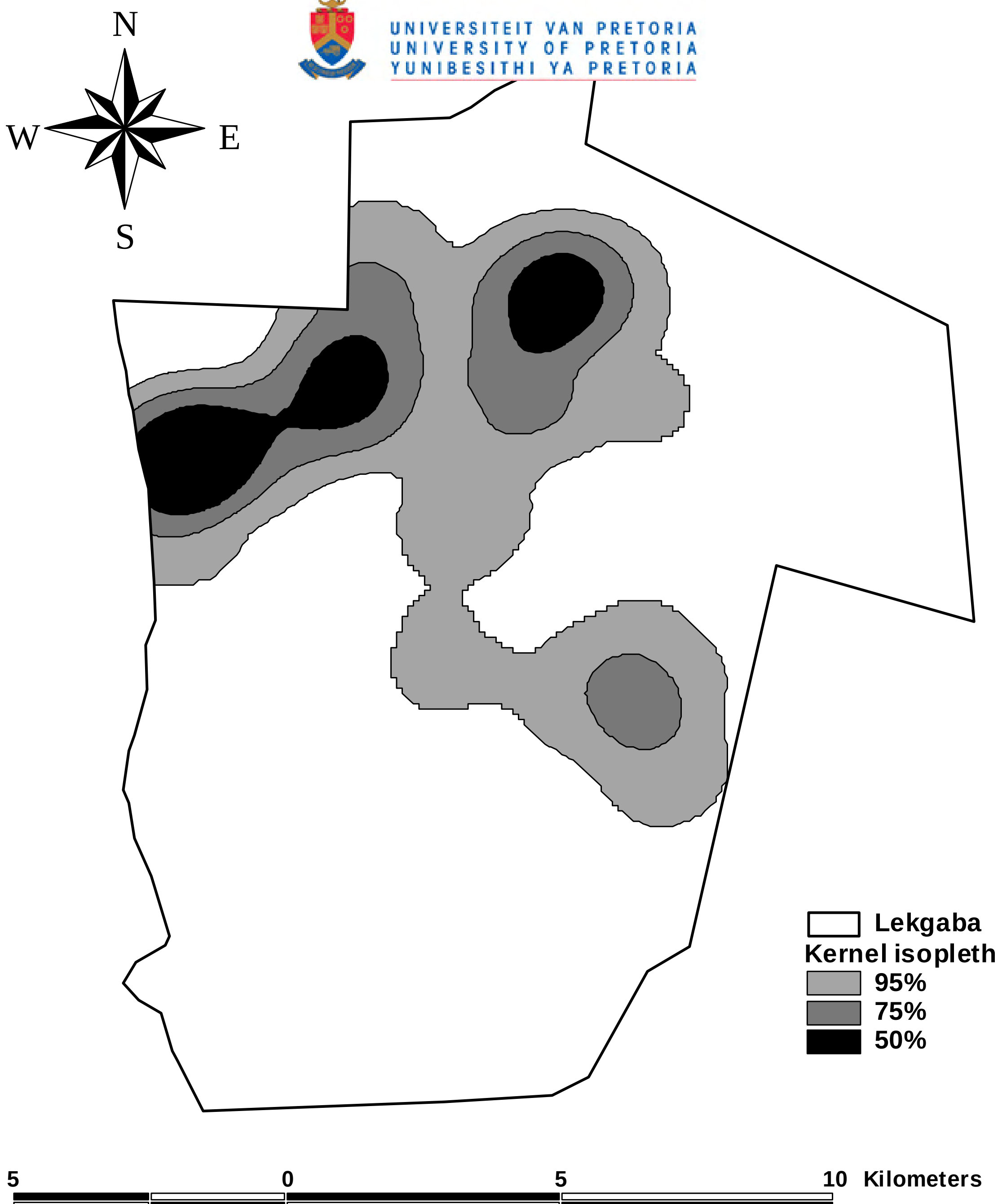

Figure 10: Range use of lioness LF3 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2a (Hooge 1999).

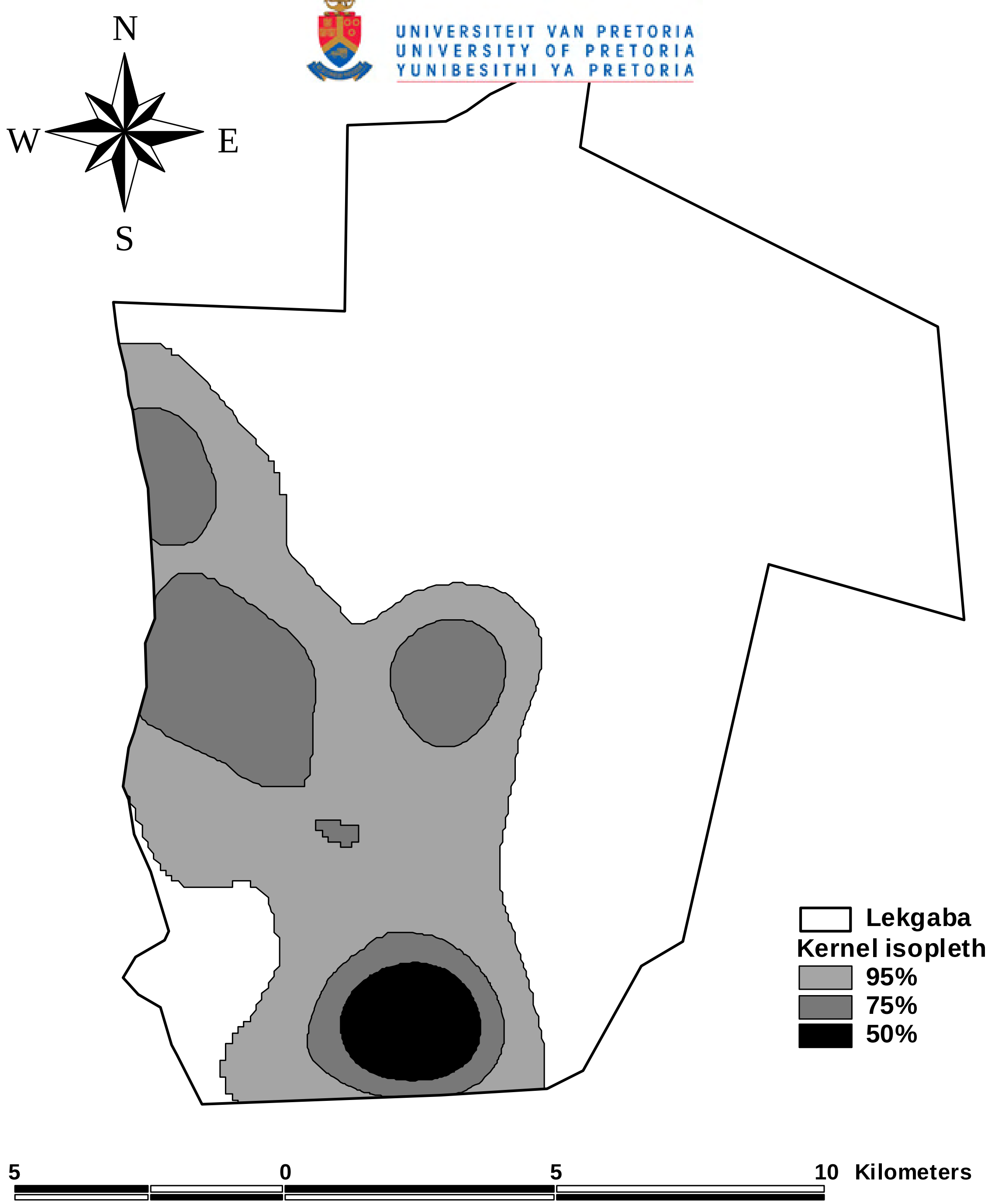

Figure 11: Range use of lioness LF2 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2a (Hooge 1999).

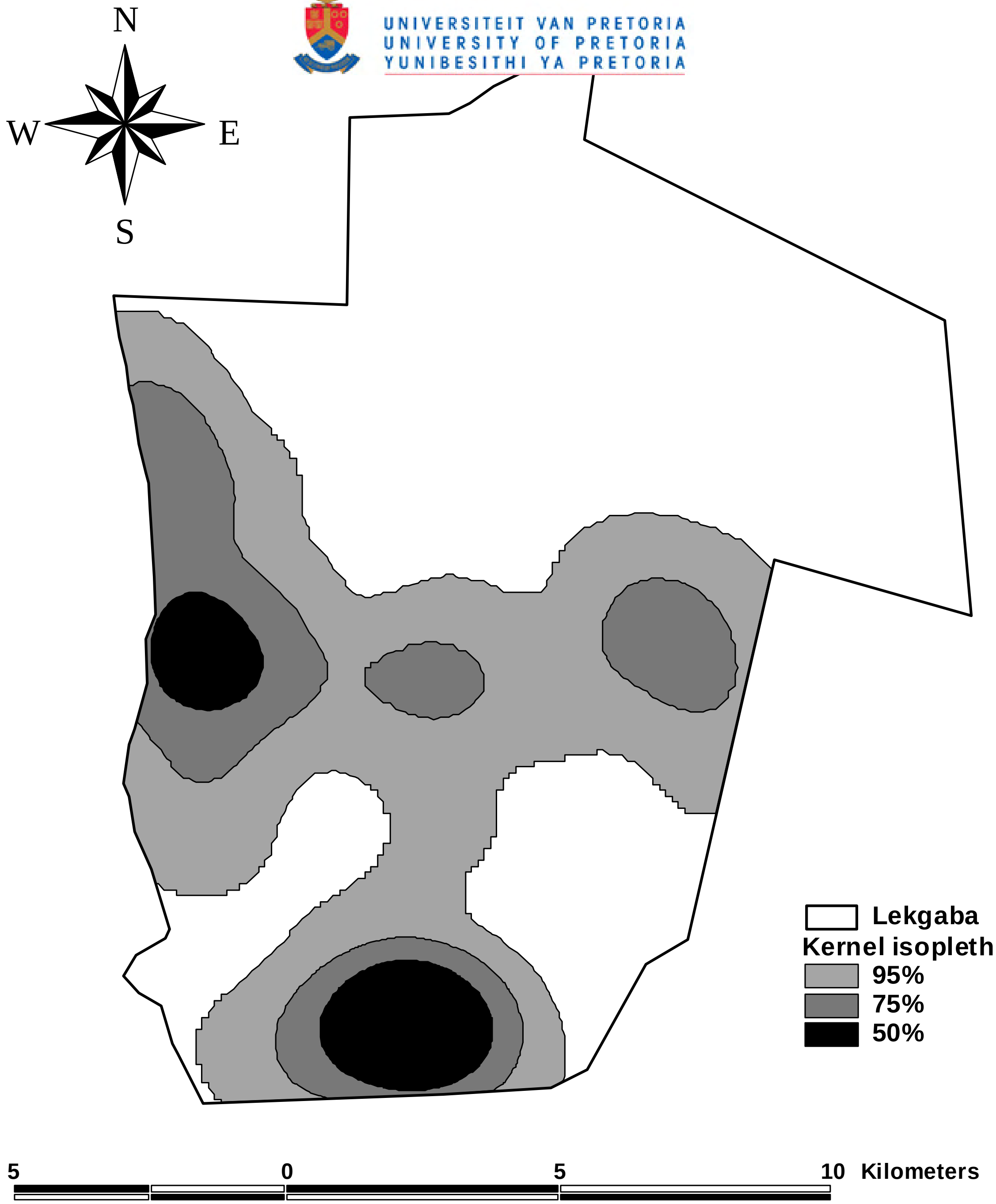

Figure 12: Range use of lion LM3 and lioness LF4 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for Arcview 3.2a (Hooge 1999).

The older and dominant male (LM1) had the largest range according to both the 100% minimum convex polygon method and the 95% kernel density estimate. The core area of use (50% kernel density estimate) for LM1 was the second highest at 11.7 km^2.

The northern pride, consisting of LF1, LM2 and LF3, showed varying degrees of range use. The dominant female with the two young cubs (LF1) utilized the smallest range of 70.2 km^2 (100% minimum convex polygon), based on 108 confirmed locations. Kernel density estimates, however, showed that her core area of use and 95% kernel range use size estimates were not the smallest. The young male, LM2, had the second largest range of the lion population, utilizing 102.8 km^2 of the 188.3 km^2 predator section of Tswalu. Based on a 50% kernel isopleth density, LM2, had the largest core area of use of the lion population (11.8 km^2). Female 3 (LF3) utilized 76.8 km^2 of the total range (100% minimum convex polygon) based on 110 location fixes. The 95% kernel isopleth density estimate for LF3 was the smallest in the entire population at 56.6 km^2.

The southern pride utilizes large ranges based on the 100% minimum convex polygon analyses. The dominant female (LF2) had a range size of 91.8 km^2 (145 location fixes), while her subadult cubs (LM3 and LF4) had a range size of 96.4 km^2 (133 location fixes). The core area of use (50% kernel isopleths density estimate) for LF2 was the smallest recorded in the entire lion population, at just 4.3 km^2.

The mean range size of the Tswalu lion population is similar to studies conducted in other, more mesic environments (Table 2). Lions in the Associated Private Nature Reserves (Turner 2005), Kruger National Park (Funston 1999), Welgevonden Private Game Reserve (Killian 2003) and Phinda Resource Reserve (Hunter 1998) all show similar mean range sizes for their lion populations.

Table 2: Mean annual rainfall (mm) and mean range sizes (km^2) of lions in various conservation areas in Africa compared to those in Lekgaba, Tswalu Kalahari Reserve in South Africa and as calculated with the 100% minimum convex polygon method

Conservation area	Rainfall	Range size	Country	Source
Serengeti National Park	800.0	200.0	Tanzania	Hanby *et al.* (1995)
Ngorongoro Crater	772.2	45.0	Tanzania	Schaller (1972)
Welgevonden Private Game Reserve	641.5	176.0	South Africa	Killian (2003)
Phinda Resource Reserve	635.7	91.5	South Africa	Hunter (1998)
Kruger National Park	584.0	133.5	South Africa	Funston (1999)
Savuti Marsh	550.0	300.0	Botswana	McBride (1990)
Associated Private Nature Reserves	500.3	139.0	South Africa	Turner (2005)
Kaudom Game Reserve	450.0	1400.0	Namibia	Stander (1997)
Etosha National Park	351.0	1112.5	Namibia	Stander (1991)
Tswalu Kalahari Reserve	253.3	91.1	South Africa	Present study
Kgalagadi Transfrontier Park	250.0	861.0	South Africa, Botswana	Eloff (2002)
Central Kalahari	200.0	2301.0	Botswana	Owens & Owens (1984)

Habitat selection

The results of the Jacobs' Preference Index showed that some of the various habitat types (Figure 6, Chapter 1) were not used in proportion to their availability by the lions (Tables 3 to 8). The habitat use patterns showed the following:

- Habitat type 1, the *Anthephora pubescens* dunes, was used in proportion to its availability by lions LM1, LF1, LF3, LM3 and LF4. This habitat type was avoided (Index < -0.5) by lions LM2 and LF2.
- Habitat type 2, the *Digitaria polyphylla* mountains and hills, was avoided by lions LM1, LM2, LF2, LM3 and LF4 while females LF1 and LF3 used this habitat type proportional to its availability.
- Habitat type 3, the *Eragrostis lehmanniana* dune valleys and plains, was used more than its proportional availability by lions LM1, LF2, LM3 and LF4. This habitat type was avoided by lions LF1 and LF3 and was used proportional to its availability by lion LM2.
- Habitat type 4, the *Eragrostis pallens* dune streets, was used in proportion to its availability by lions LM1, LF1, LM2, LF3 and LF2. This habitat type was avoided by the subadult lions of the southern pride, LM3 and LF4.
- Habitat type 5, the *Opuntia ficus-indica* disturbed areas, was used in proportion to its availability by all the lion groups
- Habitat type 6, the *Stipagrostis amabilis* dune crests, was completely avoided (Index = -1.00) by all the lion groups other than lion LF2 which used the habitat in proportion to its availability
- Habitat type 7, the *Stipagrostis uniplumis* bushy plains and valleys, was used in proportion to its availability by all the lion groups
- Habitat type 8, the *Stipagrostis uniplumis* plains, was used in a greater proportion to its availability by all the lion groups

The chi-square goodness-of fit tests showed that all the lion groups showed a significant habitat selection and preference throughout the study period (Tables 3 to 8). For the data to be significant, a minimum value of 7.81 (upper percentage

Table 3: The habitat selection of lion LM1 in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon method, Jacobs' Preference Index (1974), a chi-square goodness-of-fit test value of χ^2 = 161.97, *df* = 7, P ≤ 0.05 and Bonferroni 95% simultaneous confidence intervals (CI) (α = 0.05, k = 8, Z = 2.73)

Habitat type	P_i	**Observations**	χ^2	**Jacobs' Index**	**Bonferroni 95% CI**	**Habitat use**
Anthephora pubescens dunes	0.03	6	0.11	0.07	$0.00 \le P_i \le 0.06$	No pattern
Digitaria polyphylla mountains and hills	0.17	8	18.76	-0.70	$0.00 \le P_i \le 0.08$	Underutilized
Eragrostis lehmanniana dune valleys and plains	0.04	29	50.08	0.63	$0.08 \le P_i \le 0.22$	Preferred
Eragrostis pallens dune streets	0.30	34	8.98	-0.43	$0.10 \le P_i \le 0.26$	Underutilized
Opuntia ficus-indica disturbed areas	0.01	5	2.27	0.33	$0.00 \le P_i \le 0.06$	No pattern
Stipagrostis amabilis dune crests	0.01	0	1.24	-1.00	$0.00 \le P_i \le 0.00$	Underutilized
Stipagrostis uniplumis bushy plains and valleys	0.41	84	0.29	0.36	$0.34 \le P_i \le 0.53$	No pattern
Stipagrostis uniplumis plains	0.03	25	80.24	0.73	$0.06 \le P_i \le 0.20$	Preferred
Total	1.00	191	161.97	-	-	-

P_i = proportion of habitat available

Table 4: The habitat selection of lioness LF1 in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon method, Jacobs' Preference Index (1974), a chi-square goodness-of-fit test value of χ^2 = 20.84, *df* = 7, P ≤ 0.05 and Bonferroni 95% simultaneous confidence intervals (CI) (α = 0.05, k = 8, Z = 2.73)

Habitat type	P_i	**Observations**	χ^2	**Jacobs' Index**	**Bonferroni 95% CI**	**Habitat use**
Anthephora pubescens dunes	0.03	3	0.00	0.01	$-0.01 \leq P_i \leq 0.07$	No pattern
Digitaria polyphylla mountains and hills	0.17	15	0.71	-0.13	$0.05 \leq P_i \leq 0.23$	No pattern
Eragrostis lehmanniana dune valleys and plains	0.04	1	2.96	-0.66	$-0.02 \leq P_i \leq 0.04$	No pattern
Eragrostis pallens dune streets	0.30	26	1.10	-0.14	$0.13 \leq P_i \leq 0.35$	No pattern
Opuntia ficus-indica disturbed areas	0.01	3	1.59	0.35	$-0.01 \leq P_i \leq 0.07$	No pattern
Stipagrostis amabilis dune crests	0.01	0	0.69	-1.00	$0.00 \leq P_i \leq 0.00$	Underutilized
Stipagrostis uniplumis bushy plains and valleys	0.41	51	0.87	0.12	$0.34 \leq P_i \leq 0.60$	No pattern
Stipagrostis uniplumis plains	0.03	9	13.63	0.55	$0.01 \leq P_i \leq 0.15$	No pattern
Total	1.00	108	20.84	-	-	-

P_i = proportion of habitat available

Table 5: The habitat selection of lion LM2 in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon method, Jacobs' Preference Index (1974), a chi-square goodness-of-fit test value of $\chi^2 = 53.90$, *df* = 7, P ≤ 0.05 and Bonferroni 95% simultaneous confidence intervals (CI) (α = 0.05, k = 8, Z = 2.73)

Habitat type	P_i	**Observations**	χ^2	**Jacobs' Index**	**Bonferroni 95% CI**	**Habitat use**
Anthephora pubescens dunes	0.03	1	0.46	-0.66	$0.00 \leq P_i \leq 0.00$	Underutilized
Digitaria polyphylla mountains and hills	0.17	10	13.20	-0.59	$0.01 \leq P_i \leq 0.11$	Underutilized
Eragrostis lehmanniana dune valleys and plains	0.04	10	0.74	0.15	$0.01 \leq P_i \leq 0.11$	No pattern
Eragrostis pallens dune streets	0.30	47	0.34	-0.08	$0.18 \leq P_i \leq 0.36$	No pattern
Opuntia ficus-indica disturbed areas	0.01	4	1.22	0.27	$-0.01 \leq P_i \leq 0.05$	No pattern
Stipagrostis amabilis dune crests	0.01	0	1.11	-1.00	$0.00 \leq P_i \leq 0.00$	Underutilized
Stipagrostis uniplumis bushy plains and valleys	0.41	84	2.11	0.35	$0.39 \leq P_i \leq 0.59$	No pattern
Stipagrostis uniplumis plains	0.03	17	34.72	0.63	$0.04 \leq P_i \leq 0.16$	Preferred
Total	1.00	173	53.90	-	-	-

P_i = proportion of habitat available

Table 6: The habitat selection of lioness LF3 in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon method, Jacobs' Preference Index (1974), a chi-square goodness-of-fit test value of χ^2 = 33.40, *df* = 7, P ≤ 0.05 and Bonferroni 95% simultaneous confidence intervals (CI) (α = 0.05, k = 8, Z = 2.73)

Habitat type	P_i	**Observations**	χ^2	**Jacobs' Index**	**Bonferroni 95% CI**	**Habitat use**
Anthephora pubescens dunes	0.03	4	0.33	0.14	$-0.01 \leq P_i \leq 0.09$	No pattern
Digitaria polyphylla mountains and hills	0.17	17	0.21	-0.07	$0.06 \leq P_i \leq 0.24$	No pattern
Eragrostis lehmanniana dune valleys and plains	0.04	1	3.10	-0.67	$-0.02 \leq P_i \leq 0.28$	No pattern
Eragrostis pallens dune streets	0.30	22	3.41	-0.26	$0.10 \leq P_i \leq 0.30$	No pattern
Opuntia ficus-indica disturbed areas	0.01	3	1.56	0.35	$-0.01 \leq P_i \leq 0.07$	No pattern
Stipagrostis amabilis dune crests	0.01	0	0.71	-1.00	$0.00 \leq P_i \leq 0.00$	Underutilized
Stipagrostis uniplumis bushy plains and valleys	0.41	52	0.90	0.13	$0.17 \leq P_i \leq 0.77$	No pattern
Stipagrostis uniplumis plains	0.03	11	23.17	0.62	$0.02 \leq P_i \leq 0.18$	No pattern
Total	1.00	110	33.40	-	-	-

P_i = proportion of habitat available

Table 7: The habitat selection of lioness LF2 in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon method, Jacobs' Preference Index (1974), a chi-square goodness-of-fit test value of χ^2 = 152.90, *df* = 7, P ≤ 0.05 and Bonferroni 95% simultaneous confidence intervals (CI) (α = 0.05, k = 8, Z = 2.73)

Habitat type	P_i	**Observations**	χ^2	**Jacobs' Index**	**Bonferroni 95% CI**	**Habitat use**
Anthephora pubescens dunes	0.03	1	2.21	-0.61	$-0.02 \leq P_i \leq 0.03$	No pattern
Digitaria polyphylla mountains and hills	0.17	2	21.29	-0.88	$-0.02 \leq P_i \leq 0.03$	Underutilized
Eragrostis lehmanniana dune valleys and plains	0.04	27	66.47	0.69	$0.10 \leq P_i \leq 0.28$	Preferred
Eragrostis pallens dune streets	0.30	25	7.47	-0.39	$0.08 \leq P_i \leq 0.26$	Underutilized
Opuntia ficus-indica disturbed areas	0.01	3	0.58	0.22	$-0.01 \leq P_i \leq 0.05$	No pattern
Stipagrostis amabilis dune crests	0.01	1	0.01	0.04	$-0.02 \leq P_i \leq 0.03$	No pattern
Stipagrostis uniplumis bushy plains and valleys	0.41	68	1.04	0.18	$0.36 \leq P_i \leq 0.58$	No pattern
Stipagrostis uniplumis plains	0.03	18	53.93	0.70	$0.05 \leq P_i \leq 0.19$	Preferred
Total	1.00	145	152.90	-	-	-

P_i = proportion of habitat available

Table 8: The habitat selection of lions LM3 and LF4 in Lekgaba, Tswalu Kalahari Reserve, from March 2003 to October 2004, based on the 100% minimum convex polygon method, Jacobs' Preference Index (1974), a chi-square goodness-of-fit test value of χ^2 = 173.47, *df* = 7, P ≤ 0.05 and Bonferroni 95% simultaneous confidence intervals (CI) (α = 0.05, k = 8, Z = 2.73)

Habitat type	P_i	Observations	χ^2	Jacobs' Index	Bonferroni 95% CI	Habitat use
Anthephora pubescens dunes	0.03	3	0.11	-0.09	$-0.01 \leq P_i \leq 0.05$	No pattern
Digitaria polyphylla mountains and hills	0.17	2	19.13	-0.87	$-0.01 \leq P_i \leq 0.05$	Underutilized
Eragrostis lehmanniana dune valleys and plains	0.04	25	62.34	0.68	$0.10 \leq P_i \leq 0.28$	Preferred
Eragrostis pallens dune streets	0.30	14	16.32	-0.60	$0.04 \leq P_i \leq 0.18$	Underutilized
Opuntia ficus-indica disturbed areas	0.01	4	2.77	0.39	$-0.01 \leq P_i \leq 0.07$	No pattern
Stipagrostis amabilis dune crests	0.01	0	0.85	-1.00	$0.00 \leq P_i \leq 0.00$	Underutilized
Stipagrostis uniplumis bushy plains and valleys	0.41	66	2.15	0.37	$0.29 \leq P_i \leq 0.71$	No pattern
Stipagrostis uniplumis plains	0.03	19	69.80	0.73	$0.06 \leq P_i \leq 0.22$	Preferred
Total	1.00	133	173.47	-	-	-

P_i = proportion of habitat available

points of the chi-square distribution, Nelson 2004) was required for significance at the 5% level, with degrees of freedom = 7. All the chi-square values for the lion groups exceeded this minimum value at the 5% level.

Since all the lion groups showed significant habitat selection and preferences, the Bonferroni 95% simultaneous confidence intervals were used to determine a preference, no discernable pattern, or underutilization for each lion group (Tables 3 to 8) (Neu *et al.* 1974). There was no discernable pattern for habitat preference in Habitat type 1, other than lion LM2, which underutilized this habitat type (P_i = 0.03). Habitat type 2 has a large surface area but was underutilized by the majority of the lion groups. Three lion groups have a preference for habitat type 3, while there was no discernable pattern of use for the remaining lion groups. Habitat type 4, the second largest habitat type in Lekgaba, was either underutilized or there was no pattern of use, meaning that the lions used the habitat in proportion to its availability. No pattern of use was by the lions was observed in habitat type 5. Habitat type 6 was underutilized by the majority of the lion population. No discernable use pattern was observed for any lion group in Habitat type 7. A preference of use was shown for Habitat type 8, with four of the six lion groups preferring these *Stipagrostis uniplumis* plains according to its proportional availability.

Discussion

An understanding of the range use and habitat selection of wild animals is integral to its conservation and management (Perrin & Bodbijl 2001; Turner 2005). The range use and habitat selection, in particular, of a predator are correlated to the range use and habitat preference of their prey (Sunquist & Sunquist 2002; Turner 2005). Spoor tracking was seen as an effective method in obtaining range use and habitat selection data for the lion population on Tswalu. There is, however, an inherent bias associated with spoor tracking, such as observer error and inexperience (Stander *et al.* 1997; Stander 1998), and more effective methods such as continuous GPS radio tracking could provide more insight into the movement patterns of the Tswalu lion population (Harris *et al*. 1990; Viljoen 1997; Van Heezik & Seddon 1998; Salvatori, Skidmore, Corsi & Van der Meer 1999; Turner 2005). However, spoor tracking provides data on behaviour of an animal, hunting success and type of prey hunted, which radio tracking does not provide (Melville, Bothma & Mills 2004).

Range use

The range sizes of felids in arid and semi-arid environments can be expected to be larger than those of the same type in more mesic environments (Bothma & Le Riche 1994b; Bothma *et* al. 1997; Van Heezik & Seddon 1998; Eloff 2002). However, on Tswalu Kalahari Reserve it was found that the range sizes of the focal lions were similar to areas with a higher annual rainfall, being similar to those found for lions in Phinda Resource Reserve (Hunter 1998), Welgevonden Private Game Reserve (Killian 2003) and the Associated Private Nature Reserves (Turner 2005) when based on the 100% minimum convex polygon method of range use analysis. According to Turner (2005), prey density is an important determinant in range sizes of lions. Ogutu and Dublin (2004) also suggested that the distribution of lions mirrors that of the resident herbivores and that there is a correlation between lion density and herbivore biomass.

The range sizes of lions across various habitat types are inversely related to lean season prey availability (Van Orsdol, Hanby & Bygott 1985; Ogutu & Dublin 2002; Sunquist & Sunquist 2002). However, on Tswalu the prey could not migrate to other areas in the dry season due to the presence of the wildlife-proof fences. The year-round water supply also meant that the prey did not have to move seasonally. The prey densities on Lekgaba are similar to those described by Hunter 1998, Killian 2003 and Turner 2005. Lekgaba has a prey density of 1508 kg/km^2, which is similar to both Welgevonden (1880 kg/km^2, Killian 2003) and Phinda (1996 kg/km^2, Hunter 1998). The Tswalu lion population also have a larger prey base from which to choose from than the lion population of the

Associated Private Nature Reserves, where a prey to lion ratio of 115 prey animals per lion was found, whereas on Tswalu the lions have a prey to lion ratio of 315 prey animals per lion.

The presence of management fences also does not allow the lions to expand their ranges into neighbouring farms (Turner 2005). The range size of the lion groups may have been larger and similar to other lions living in a semi-arid environment (Eloff 2002), were it not for the presence of these fences. Lekgaba also has many waterholes which are topped up regularly when there is not enough rainwater. The prey animals of the lions are dependent on water in semi-arid environments (Eloff 2002; Cromhout 2006), which would explain the use of waterholes by the lions when hunting. Lions are not dependent on water in the Kalahari ecosystem, but will drink it if the opportunity arises (Eloff 1973b, 2002; Sunquist & Sunquist 2002). The lions therefore do not have to move long distances to find prey animals at the water sources where they will hunt them (Scheel 1993).

As expected the range size of the males was larger than that of the females, which is consistent with the majority of felids (Bothma *et al*. 1997; Mizutani & Jewell 1998; Killian 2003; Turner 2005). The mean range size for the male lions was 105.9 km^2, while the mean range size for females was 79.6 km^2 (Table 2). The range size of the males is smaller than that found in other studies, with LM1 having the largest range at 109.1 km^2. Yet, this range is still smaller than that found for males in the Associated Private Nature Reserves, with a lower prey density, but again this particular male did not have to move far for mating opportunities or potential prey. The range size of the males on Tswalu is similar to that of females found on Welgevonden. The dominant lioness in the northern pride, LF1, had the smallest range size of all the focal lions which is consistent with the results of Killian (2003), who found that females with young cubs have smaller range sizes than females who are not nursing. The range overlap of the dominant male with the two dominant females in each pride is shown in Figure 13 and 14.

The range sizes of the lion population on Lekgaba, Tswalu Kalahari Reserve, do not concur with studies done on felids in arid and semi-arid regions (Castley, Knight, Mills & Thouless 2002).. The range sizes did follow a general trend in which range sizes of lions are smaller in prey rich areas and much larger in prey poor areas (Turner 2005).

Habitat selection

The habitat requirements of lions are considered to be areas of sufficient hunting opportunities, habitats with preferred prey types, mating opportunities and drinking water (Hanby *et al*. 1995; Turner 2005). Lions are and ambush predators, relying on good cover to attack their prey (Sunquist & Sunquist 2002; Hopcroft, Sinclair & Packer 2005). This means that the structure of the vegetation in each particular habitat type influences the hunting success of lions, as well as does prey availability (Funston 1999). On a broad habitat scale prey density and prey habitat selection are important factors in determining the habitat preference of a predator (Packer, Scheel & Pusey 1990; Mills & Gorman 1997; Lombardi, Fernandez, Moreno & Villafuerte 2003; Hopcroft *et al*. 2005; Turner 2005). According to Killian (2003), predators will naturally seek out high concentrations of available prey. Hopcroft *et al*. (2005) furthermore suggest that lions select habitats where prey animals are easier to catch, rather than where prey densities are high. They support an ambush-habitat hypothesis, which basically involves fine-scale habitat changes which affect the catchability of the prey.

The lion population on Lekgaba showed a definite preference for certain habitat types, while avoiding others. Some habitat types were also used in proportion to their relative availability. Individual animals selected habitats differently, despite relative availability (McClean, Rumble, King & Baker 1998). It was not logistically possible to study the habitat requirements and preferences of the prey animals

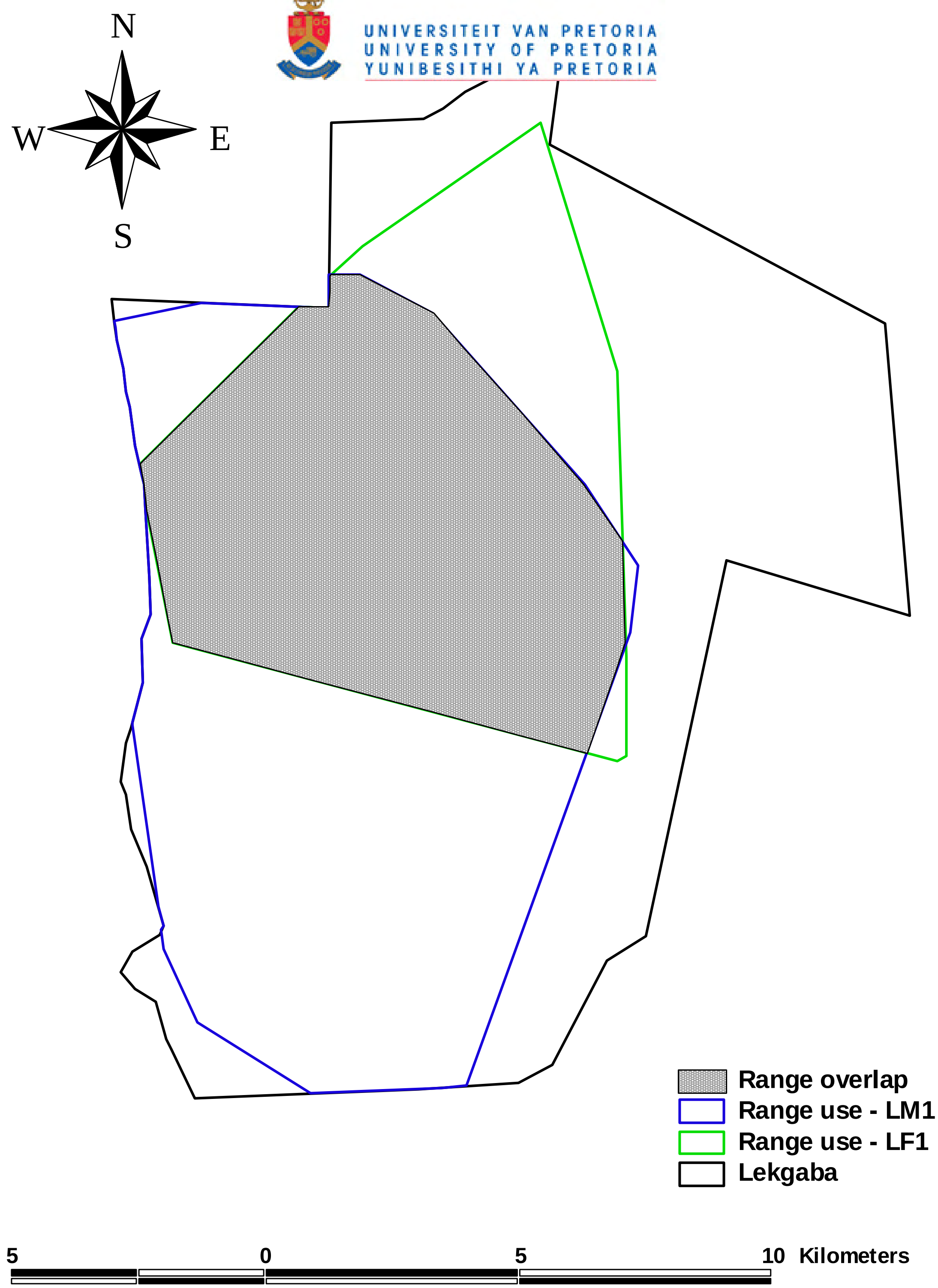

Figure 13: Range overlap of lion LM1 and lioness LF1 on Lekgaba, Tswalu Kalahari Reserve using the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

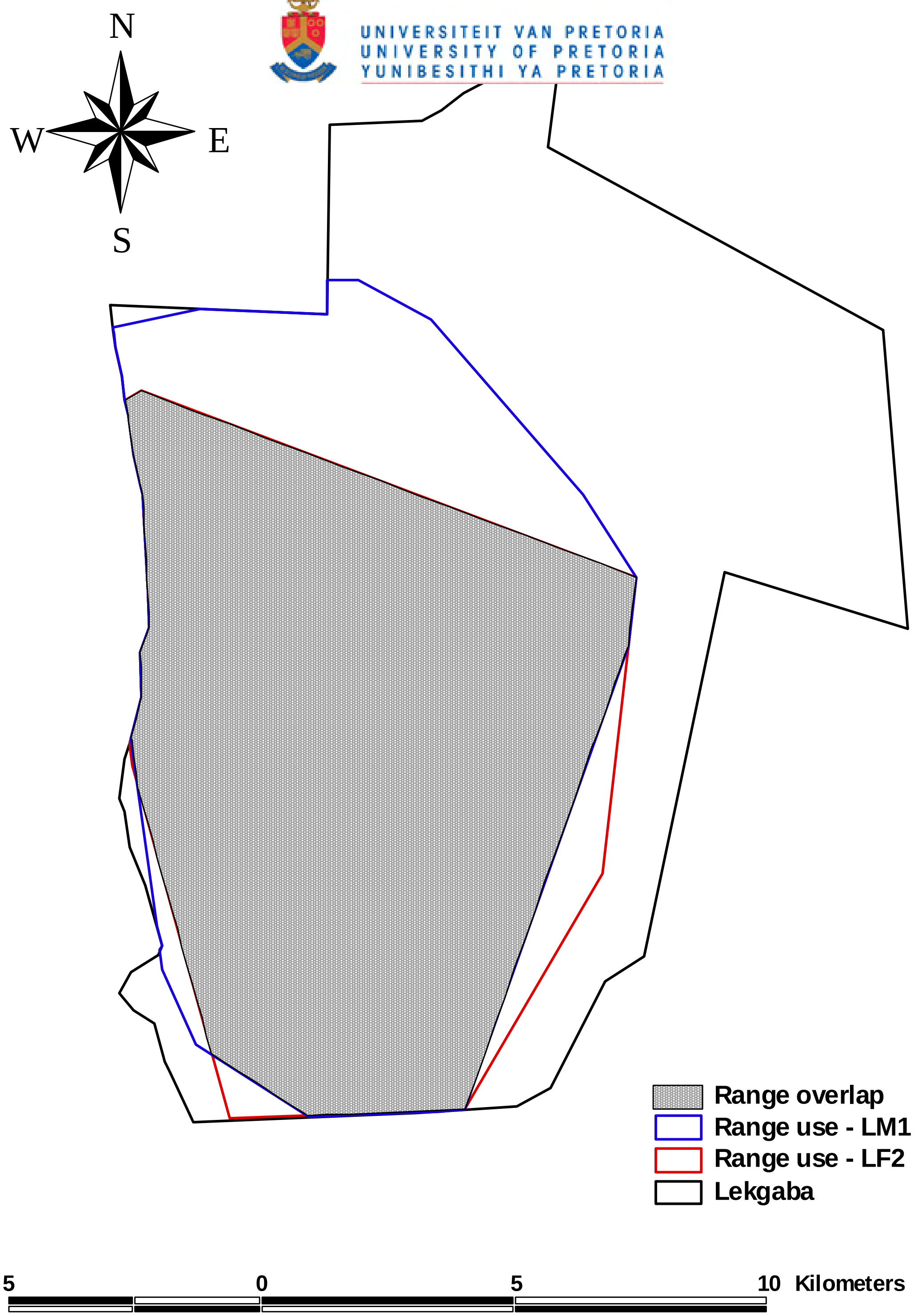

Figure 14: Range overlap of lion LM1 and lioness LF2 on Lekgaba, Tswalu Kalahari Reserve using the 100% minimum convex polygon method (Worton 1987) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

on Lekgaba and for this reason only habitat use for the lion population is indicated. Various types of prey prefer specific habitat types and are therefore unevenly distributed in an area (McNaughton & Georgiades 1986; Turner 2005). Where possible, prey habitat use and characteristics are given using the prey's general behavioural characteristics and personal observations made by researchers and field guides.

There was not a single habitat type that all the lion focal groups under-utilized or preferred. Two habitat types (the *Opuntia ficus-indica* disturbed areas and the *Stipagrostis uniplumis* plains) were used in proportion to their availability by all the focal lion groups. As was expected the majority of the observation locations were made in the most abundant habitat of *Stipagrostis uniplumis* bushy plains and valleys (405 locations in 41% of the available area, Tables 3 to 8).

The *Anthephora pubescens* dunes, covered only 3% of the total area of Lekgaba. This habitat type has a good veld condition score at 70% with a high incidence of Decreaser grass species (Van Rooyen 1999), which provides palatable grass for grazers. There is a poorly developed tree and shrub layer which does not provide adequate cover for lions when hunting. A total of 18 locations were recorded here for all focal lion groups, with only the young male, LM2, not using this particular habitat type in proportion with its availability.

The *Digitaria polyphylla* mountains and hills were underutilized by the two lone males and by the entire southern pride due to the lack of hunting opportunities on the rocky slopes. The northern pride females used this habitat type in proportion to its availability. LF1 gave birth to her cubs and nursed them on one of the mountains, while her daughter LF3, did not move far from her side during the nursing of the cubs. The rocky slopes are inaccessible to plains wildlife and only Hartmann's mountain zebra and the greater kudu were found on the mountains and hills of Lekgaba. Skilpad dam, one of the main dams, is located in this habitat type which was frequented by the northern pride (Figure 15). Skilpad dam

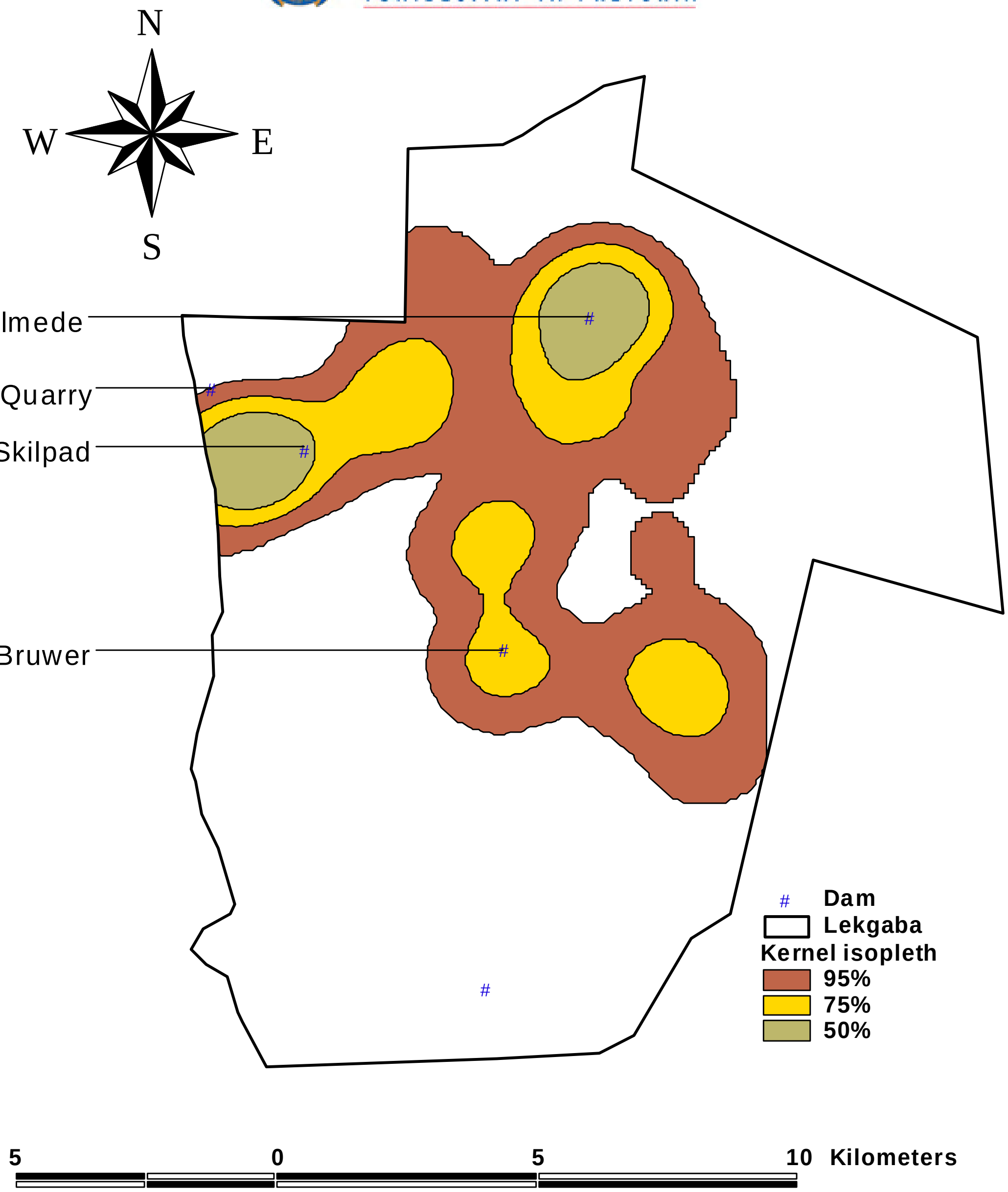

Figure 15: Overlap of water source use and core area of use of lioness LF1 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

was used for hunting and drinking. Several greater kudu herds and lone bulls would drink at this watersource and provided several hunting opportunities for the northern pride. The dominant female, LF1, would utilize various other habitat types, the *Eragrostis pallens* dune streets and the *Stipagrostis uniplumis* bushy plains and valleys, to hunt plains game while she was nursing her cubs.

The *Eragrostis lehmanniana* dune valleys and plains were preferred by the dominant male, LM1, by the southern pride consisting of LF2, LF4 and LM3. This habitat type covers only 4% of the total area of Lekgaba but the fourth highest number of observations (n = 93) was recorded here. This habitat type has a high veld condition score of 72.1%, a moderate herbaceous layer and sparse tree and shrub cover. The relatively high veld condition score meant that there is a high incidence of palatable vegetation for ungulate prey. The cover that is provided for the lions by the moderately developed grass layer contributes to the preference that was shown by the southern pride and the dominant male for this habitat type. The large number of lion observations in this relatively small habitat may also be attributed to the abundance of high quality feed for ungulate prey in this habitat type.

The *Eragrostis pallens* dune streets, is the second largest habitat type on Lekgaba covering approximately 30% of its total surface area. The second highest number of observations were made in habitat type (n = 168). There is a moderate grass cover and sparsely developed tree and shrub layer, and it has a moderate veld condition score of 55.2% (Van Rooyen 1999). None of the focal lion groups preferred this habitat type and LM1 and the southern pride underutilized this area. However, the northern pride's main waterhole, Deelmede, is found in this habitat which could explain their frequent use of it relative to its proportional availability (Figure 15). Deelmede was used by gemsbok, Burchell's zebra, blue wildebeest, eland and ostriches.

The *Opuntia ficus-indica* disturbed areas contribute only 1% of the total area of Lekgaba. As the name implies these disturbed areas have little herbaceous, tree and shrub growth. No veld condition score was given for these areas due to the lack of growth (Van Rooyen 1999). One of the five main waterholes, Bruwer, is found on the edge of such a disturbed area. This waterhole is popular with plains wildlife such as the blue wildebeest, gemsbok, springbok and red hartebeest. Several (n = 22) lion sightings were made there, but the lack of cover and ambushing opportunities limited the use of this particular habitat type by the lions for hunting.

The *Stipagrostis amabilis* dune crests were the least used by all the lions, and it also only contributed 1% to the total area of Lekgaba. Only one sighting of LF2 was made on a dune crest. There is a moderate veld condition score of 61.4% and poor ecological capacity of 52.8 hectares per large stock unit on these dune crests. The herbaceous layer is very poorly developed and does not provide adequate cover for predators nor adequate feeding opportunities for herbivores. The relatively small size, poor ecological capacity and limited hunting opportunities on dune crests are reflected by the low number of observations of lions that were made on this habitat type. There is also limited shade because of a poor occurrence of trees and shrubs. Lions do utilize dune crests as look-out points to find prey (Eloff 2002), but no evidence of this was found while spoor-tracking the lion population. The lions had adequate opportunities for hunting in the other habitat types.

The largest habitat type, the *Stipagrostis uniplumis* bushy plains and valleys, provided the most observational data with 405 confirmed lion locations. All the focal lion groups utilized this habitat type relative to its proportional availability. The main waterhole of the southern pride, Stoffberg dam (Figure 16), and the main waterhole of the northern pride, Deelmede (Figure 15), are both found in this habitat. A dense shrub layer provides adequate cover for hunting and ambushing opportunities for the lions. The bushy plains and valleys have a good

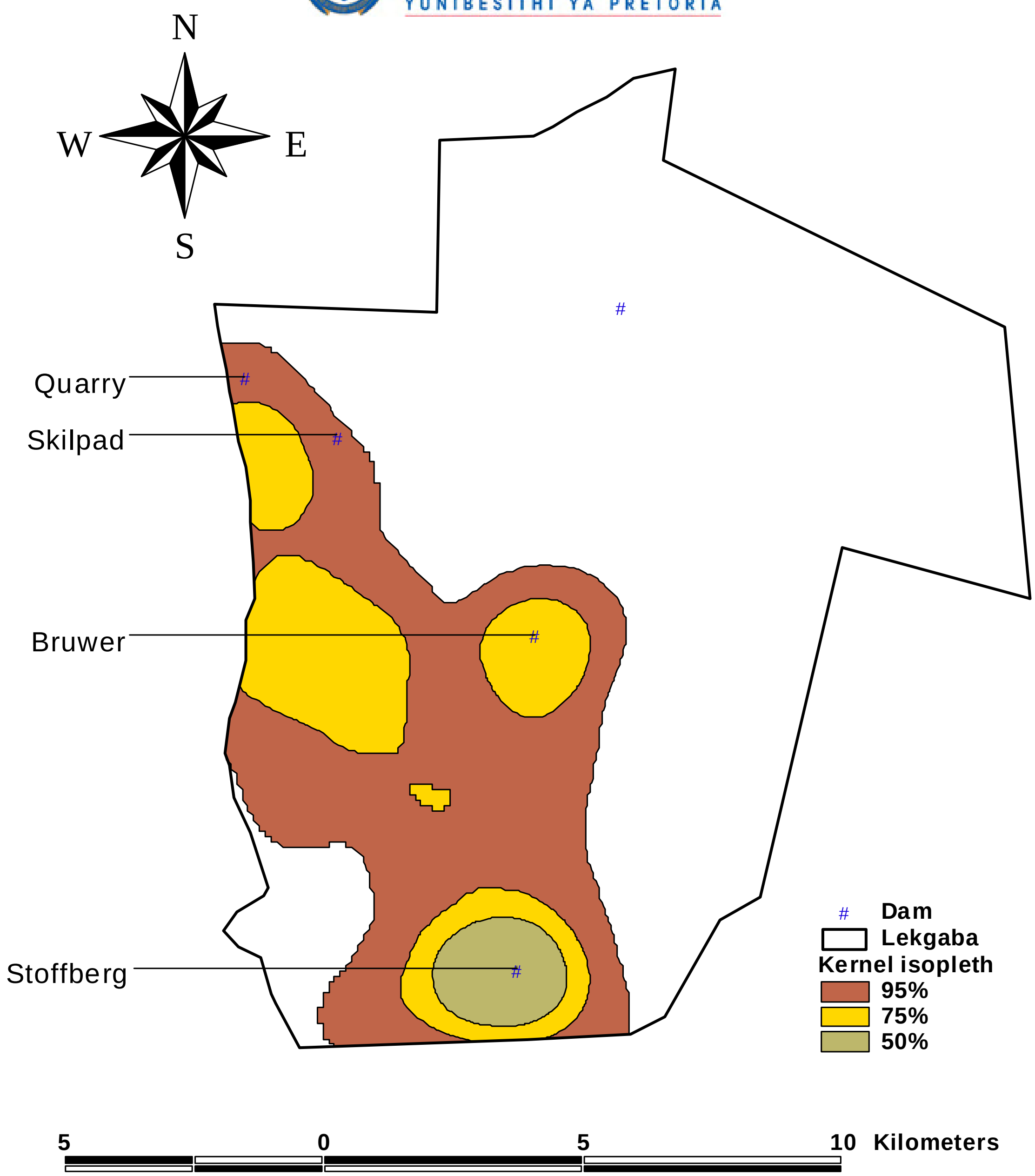

Figure 16: Overlap of water source use and core area of use of lioness LF2 in Lekgaba, Tswalu Kalahari Reserve from March 2003 to October 2004, based on kernel density estimates (Mizutani & Jewell 1998) and the Animal Movement Extension for ArcView 3.2a (Hooge 1999).

veld condition score of 64.1% (Van Rooyen 1999) and provide grazing and browsing for prey species. Their prey also prefer open plains to reproduce, feed and be vigilant for predators (Estes 1997). The high incidence of shrubs also provides adequate shade for the lions during the warm daylight hours. LF1 used a *Boscia albitrunca* tree, located right next to Deelmede dam, for cover for her two young cubs as they were growing up. Stoffberg dam is used by gemsbok, blue wildebeest, impala, red hartebeest, warthog and waterbuck.

The *Stipagrostis uniplumis* plains, was preferred by four of the six focal lion groups. The northern pride females utilized this area relative to its proportional availability. The quarry waterhole was frequented by the southern pride (Figure 16) and males LM1 and LM2. The original holding bomas, in which LM1 and LF2, were housed are located in this habitat type and were visited regularly by the southern pride and the two males, especially after a pack of four wild dogs was introduced into the boma. The herbaceous layer is moderately developed with an indication of moderate overutilization by herbivores. Several types of plains wildlife frequented this area, even with the large number of lion sightings being made in this area. Several herds of springbok, blue wildebeest and gemsbok also regularly drank water at the quarry waterhole. The cover provided by the vegetation around the quarry waterhole was relatively poor, however, and there were several large trees and shrubs from which the lions could hunt and where they could rest. The high potential prey abundance and the wild dogs in the holding boma probably contributed to the high level of preference shown for this habitat type by the lion population.

The hypothesis that the lions utilized the available habitat types relative to their proportional availability was therefore rejected and clear habitat preferences were shown, while other areas that did not meet their minimum habitat requirements were not utilized. Further studies of the habitat selection of the preferred prey of the lion population will provide more reliable answers as to the habitat selection of the lion population. It seems that both hypotheses, the ambush-habitat hypothesis and the prey-habitat hypothesis (Hopcroft *et al* 2005), are relevant for the Tswalu lion population. Water seems to play a large role in the movement patterns of the lions, as do cover, hunting opportunities, resting sites and prey habitat selection.

Conclusions

Range use and habitat selection of lions in a relatively small, enclosed and semi-arid environment has not been studied before. This study aimed to identify areas of use by the lions and identified whether there was any indication of habitat selection in the lion population. Range sizes of lions in small enclosed reserves are limited by the presence of management fences and management actions such as placement of waterholes and stocking rates of prey. Management decisions will influence the range use of the prey which in turn will affect the range use by the lion population. The range size and range use of the Tswalu lion population were not similar to those found for other lions in a semi-arid region, but were similar to lions of the more mesic savannas. The lions did not utilize the entire range and seemed to concentrate their activity around waterholes and dams. The prey density on Lekgaba was also higher than usual in other semi-arid areas, and was closer to that in more mesic savannas. The range size of the adult males was larger than that of the females which is found in most lion studies (Sunquist & Sunquist 1989; Eloff 2002; Killian 2003; Turner 2005).

The study of habitat selection indicated that there was a distinct selection for certain habitats by the lions. Each habitat type has unique qualities on a broad and fine scale which affect the hunting potential for the lions (Hopcroft *et al*. 2005). Certain habitat types do not meet the minimum habitat requirements for lions living in a semi-arid, enclosed reserve. The mountains and hills found on Lekgaba were mostly avoided, unless they were used to raise cubs. The dune crests seem to have been avoided but they are not large contiguous surface areas and as such cannot be considered to have been completely avoided. The more open habitat types, plains and bushy plains were favoured by the lions.

It seems therefore that range use and habitat selection of the lion population on Lekgaba, Tswalu Kalahari Reserve are determined by the location of the waterholes, the habitat preferences of the prey, the ecological capacity of each habitat type for ungulates, and the hunting opportunities provided by each habitat type.

CHAPTER 6

POPULATION VIABILITY ANALYSIS

Introduction

The reintroduction of large carnivores into areas of previous use is a controversial and difficult practice (Hayward, Adendorff, O' Brien, Sholto-Douglas, Bissett, Moolman, Bean, Fogarty, Howarth, Slater & Kerley 2007c). Several reintroduction attempts have failed due to a lack of knowledge regarding the actual animal being re-introduced and the area where it is to be introduced (Hayward *et al*. 2007c). This has led researchers and authors to conclude that reintroductions need to be sufficiently understood to be used as accurate conservation techniques (Killian 2003).

Lions play a large role in the ecotourism potential of South Africa, and their economic benefit for small enclosed reserves or wildlife ranches cannot be under-estimated (Packer 1996). However, provision should be made to accurately determine lion behaviour at each specific site to ensure the long-term survivability of the lion population while at the same time ensuring that the population is self-sufficient. The prey use, space use and population dynamics of lion populations should be studied to maximise the conservation and economic potential of reintroduced carnivores. An understanding of the area of introduction, its degree of isolation and habitat quality are also needed to ensure survival of the population (Carroll, Noss, Paquet & Schumaker 2003). Population dynamics such as reproduction and population growth are essential parameters in understanding a population. (Killian 2003). A high reproductive potential, successful breeding and a high growth rate are indicators that a reintroduction attempt was indeed successful (Killian 2003).

In general, lion population dynamics have been thoroughly studied (Van Orsdol 1981; Smuts 1982; Hunter 1998; Funston 1999; Eloff 2002; Sunquist & Sunquist 2002; Killian 2003; Turner 2005). These population parameters can be used in population viability analysis to determine the short- and long-term survivability of a small lion population in an isolated area. However, these demographic data should be treated with caution as they are difficult to determine while they may differ between areas or isolated populations (Münzbergová & Ehrlén 2005).

Population viability analysis is a method widely applied in ecology to predict the risk of extinction of a population and to test various management strategies to prevent extinction from occurring (Norton 1993; Hamilton & Moller 1995; Lindenmayer, Burgman, Akçakaya, Lacy & Possingham 1995; Taylor 1995; Brook, Lim, Harden & Frankham 1997; Somers 1997; Brook, Cannon, Lacy, Mirande & Frankham 1999; Ludwig 1999; Brook, O' Grady, Chapman, Burgman, Akçakaya & Frankham 2000; Reed, Mills, Dunning, Menges, McKelvey, Frye, Beissinger, Anslett & Miller 2002; Killian 2003; Cromhout 2006; Wilson 2006; Watson & Chadwick 2007; Leimgruber, Senior, Uga, Myint Aung, Sanger, Mueller, Wemmer & Ballou 2008). A population viability analysis involves the evaluation of population data and models to predict the likelihood of population persistence for a certain time period (Boyce 1992). Deterministic and stochastic events that affect populations are dealt with in a population viability analysis (Brook *et al*. 1997).

Stochastic events include demographic stochasticity, environmental variation, genetic drift and natural catastrophes (Lacy 1993; Brook *et al*. 1997). Demographic stochasticity is the fluctuation in the observed birth rate, mortality rate and sex ratio of a population (Lacy 1993). Environmental variation is the change in environmental conditions which affects the birth and mortality rates of a given population (Lacy 1993). Genetic drift is the cumulative and non-adaptive change in allele frequencies, which can result in an accelerated decline in a population or severely impede that population's recovery (Lacy 1993). Natural catastrophes are the extreme of environmental variation and include events such as prolonged drought, fire and disease (Lacy 1993).

Population viability analysis can provide an understanding of all interacting forces that contribute to a population's potential extinction, and how best to overcome these factors to ensure the long-term survival of a population. Several programs have been developed to construct population models to aid managers in creating strategies to avoid local population extinction. Various software packages such as GAPPS, INMAT, RAMAS, RAMAS/stage, Metapop and VORTEX, use Monte Carlo simulations to recreate survival and reproductive events in successive years (Harris, Maguire & Shaffer 1987; Lacy 1993; Hamilton & Moller 1995).

For the purposes of the present study, VORTEX ver. 9.72 (Lacy, Borbat & Pollak 2005; Miller & Lacy 2005) was used for a population viability analysis. VORTEX is a user-friendly software package that has been applied to several populations throughout the world (Song 1996; Brook *et* al. 1997; Somers 1997; Watson, Odendaal, Barry & Pietersen 2005; Leimgruber *et al*. 2008). VORTEX models the changes in a population that may occur as a result of deterministic and stochastic events in a series of discrete events that occur once per year (Lacy 2000). VORTEX requires several input parameters as specified by the user in the belief that they may have an impact on the population (Somers 1997). These parameters include mortality rates, reproductive rates, reproductive biology, initial population sizes and the ecological capacity of the population in question (Killian 2003).

The management of small isolated populations is essential for their future survival. The survivability of the lion population on Tswalu Kalahari Reserve is determined by answering the following questions:

- What are the population demographics of the lions?
- What is the ecological capacity for lions on the Lekgaba predator camp?
- What are the short- and long-term survival probabilities of the lion population?

Methods

The various input parameters required for VORTEX simulation modelling were studied and entered into the program to conduct a population viability analysis.

Scenario settings

The lion population demographics were modelled from 1000 iterations for greater accuracy over a period of 10, 20, 50 and 100 years to determine short- and long-term viability. Short time intervals were used to minimise error and to evaluate conservative probabilities of extinction (Beissinger & Westphal 1998). Extinction is defined here as only one sex remaining in the breeding pool.

Species description

Small isolated populations run the risk of inbreeding when no immigration or emigration can occur in the population. Inbreeding can have a severe effect on the survival probability of a population (Killian 2003). Inbreeding depression was set at the default value of 3.14, with 50% due to recessive alleles, as there was no published data on inbreeding depression for lions.

Reproductive system and reproductive rates

Lions are polygynous reproducers with one male siring several sets of cubs from various females (Estes 1997). Females start breeding at the age of four years (Van Vuuren *et al*. 2005), with males being able to mate successfully for the first time at 5 years old (Van Vuuren *et al*. 2005). The maximum age of reproduction varies from region to region, a mean of 13 years old for maximum reproduction was chosen. Females can produce up to six cubs per year (Schaller 1972), with a two year cessation in breeding. In most populations the sex ratio of cubs is at parity, except after a male takeover where the sex ratio favours the birth of male cubs (Van Vuuren *et al*. 2005). Both adult females were actively breeding in the population (100% breeding females), producing four cubs every two years.

Mortality rates

Lion survival is dependent on environmental and ecological conditions, which affects the numbers and availability of their preferred prey types (Van Vuuren *et al*. 2005). Cub survival is very low in arid and semi-arid conditions (Eloff 2002), and is dependent on the abundance of food, while that of adults is much higher. Under good environmental conditions, lion survival is assumed to be higher than under poor environmental conditions (Van Vuuren *et al*. 2005). For this study, three types of conditions and lion survival probabilities were modelled in VORTEX (Table 1). Good environmental conditions existed when the annual average rainfall exceeded 237 mm for the previous two years. Poor environmental conditions were modelled as years where average rainfall was below 165 mm. Average environmental conditions occurred in those years where the mean annual rainfall was from 165 to 237 mm (Van Vuuren *et al*. 2005). Lion survivability was modelled for each environmental variable by grouping the lions into age classes from 0-1 year, 1-2 years old, 2-3 years old, 3-4 years old, and adults over 4 years old.

Catastrophes

Extreme environmental changes, disease and fire are realities in wildlife management (Killian 2003). The catastrophes are modelled in VORTEX by obtaining the frequency of occurrence and the effect of that particular catastrophe on the reproduction and survivability of the lion population. The only catastrophe that was thought to have a possible effect on the lions in Lekgaba was disease. Lion sociality lends itself to the rapid spread of disease (Craft, Hawthorne, Packer & Dobson 2008).

Severe disease epidemics such as canine distemper virus and rabies can have a serious effect on survival probabilities of animals (Henderson 1982; Roelke-Parker, Munson, Packer, Kock, Cleaveland, Carpenter, O' Brien, Pospischil, Hoffmann-Lehmann, Lutz, Mwamengele, Mgasa, Machange, Summers & Appel 1996; Packer *et al*. 1999; Kissui & Packer 2004). The Serengeti lions lost 30% of the population during a serious outbreak of canine distemper virus in 1994. Serious disease outbreaks have been speculated to occur every 20 years in Namibia, with a reduction on 20 to 35%

Table 1: Survival probabilities (percentages) of lions in varying age groups under various environmental conditions. Good conditions occur when mean annual rainfall exceeds 237 mm. Average environmental conditions occur when the mean annual rainfall is from 237 to 165 mm. Poor environmental conditions occur when the mean annual rainfall < 165 mm.

Age (years)	**Good**	**Average**	**Poor**
0-1^{-}	0.60	0.50	0.10
1-2^{-}	0.90	0.75	0.30
2-3^{-}	0.95	0.90	0.60
3-4^{-}	0.97	0.95	0.85
4 and older (adult)	0.97	0.97	0.95

1^{-} = up to 1 but excluding 1

of the population (Berry, Bush, Davidson, Forge, Fox, Grisham, Howe, Hurlbut, Marker-Kraus, Martenson, Munson, Nowell, Schumann, Shille, Stander, Venzke, Wagener, Wildt, Ellis & Seal 1997). A 5 % chance of a serious disease outbreak every 100 years was therefore modelled in the present study, along with a 30% reduction in survival, but with no effect on the reproduction (Killian 2003).

Drought was not included as a catastrophe because water is available throughout the year and supplementary feeding is provided in harsh environmental conditions. Drought has also been shown to boost lion condition and food consumption because of the abundance of food and carcasses (Kissui & Packer 2004).

Initial population size

A specified age distribution of the lion population was utilized in the model (see Chapter 1 for the ages and sexes of the lions).

Ecological capacity

The ecological capacity is the maximum number of individuals that an environment can sustain over time, without that population having a detrimental effect on the environment (Miller & Lacy 2005). The ecological capacity of Lekgaba in terms of lion numbers was calculated by using the following method of Hayward *et al*. (2007b), which is:

Y = - 2.158 + 0.377X (data log transformed)

Where Y is the ecological capacity and X is the prey biomass based on the prey densities (Chapter 4). Van Orsdol *et al*. (1985) also used prey biomass based on prey densities to obtain an ecological capacity for a lion population. Their method was:

Y = 0.0870 + 0.0001X (data not log transformed)

Where *Y* is the ecological capacity and *X* is the prey biomass based on the prey densities (Chapter 4). However, the values from Van Orsdol *et al*. (1985), overestimate ecological capacities in various areas, especially for lions (Hayward *et al*. 2007b). The edible biomass and standing crop biomass were therefore used here to determine the ecological capacity of the study area for lions.

VORTEX does not allow the population growth to be modelled above the ecological capacity, but in nature this practice is far from true. Populations fluctuate in size due to prevailing environmental and ecological conditions. Therefore the ecological capacity was modelled at an overpopulation and at the actual ecological capacity, to compensate for the variations known to occur in population growth.

Harvest and supplementation

No lions were removed during the study period, or will be removed by trophy hunting in Tswalu Kalahari Reserve. Nevertheless, reproducing males should be replaced after a certain time period to prevent inbreeding (Hunter 1998). Subadult males, who are displaced at about three years of age by older dominant males, will also have to be removed to prevent them from moving into surrounding lands and causing serious damage to livestock enterprises (Van Bommel *et al*. 2007). Removal of subadult animals will bring about the need to supplement the population with new breeding males to ensure the long-term survival of the population.

Models

Three environmental conditions were modelled at ecological capacity and at various time intervals (10, 20, 50 and 100 years). Mortality rates during good environmental conditions were used to model the effect of a catastrophe on the population. The good environmental condition mortalities were used because they more closely mimic the actual environmental conditions found on Lekgaba. They were also used to model various ecological capacities and their effect on population survivability.

A model was also run where all the males in the initial population were removed to be supplemented with a coalition of two and three males of breeding age. The young cubs were old enough to escape infanticide from the new incoming males. Only one coalition was modelled due to known space use by the Kalahari lion (Chapter 5).

Results

The ecological capacity of the lion population in the predator camp on Tswalu Kalahari Reserve was determined as 17 lions when using the available edible prey biomass, and 20 individuals when using the standing crop prey biomass. When using the Van Orsdol *et al*. (1985) equation the ecological capacity was calculated as 34 individuals for the edible prey biomass and 42 lions for the standing crop prey biomass.

The effect of environmental conditions on the survival of the population showed that in years of good environmental conditions the population was expected to be viable for all the years of modelling (Table 2). Under average environmental conditions the population also grew to ecological capacity and stayed viable for all modelled time intervals (Table 3). However, when rainfall was expected to be poor and the mortality rates of younger lions were high, the population would become extinct after 20 years (Table 4). The probabilities of extinctions for each mortality rate at each time interval are shown in Figure 1.

The effect of a catastrophe, such as disease, has little effect on the growth rate and ecological capacity of the population (Figure 2). With a catastrophic disease increasing the probability of extinction increases from 0.02 to 0.08, and decreases the stochastic growth rate of r = 0.195.

When higher ecological capacities are used (34 animals), the population reaches ecological capacity (N = 33) after only 10 years even when a serious disease outbreak was modelled. The probability of extinction is 0.00 with the population remaining at ecological capacity for over 100 years (Figure 3).

Table 2: VORTEX analyses projections of the lion population on Tswalu Kalahari Reserve for four time intervals, under good environmental conditions (mean annual rainfall > 237 mm), an ecological capacity of 17 lions and low mortality rates.

Years	**r**	**SD(r)**	**PE**	**N**	**H**
10	0.285	0.196	0.00	16	83
20	0.261	0.193	0.00	17	74
50	0.239	0.179	0.01	17	54
100	0.222	0.169	0.02	16	34

r = stochastic growth rate

SD(r) = standard deviation around r

PE = probability of extinction

N = mean number of lions in the population

H = mean heterozygosity of the population

Table 3: VORTEX analyses projection of the lion population on Tswalu Kalahari Reserve for four time intervals, under average environmental conditions (mean annual rainfall from 165 mm to 237 mm), an ecological capacity of 17 lions and average mortality rates.

Years	**r**	**SD(r)**	**PE**	**N**	**H**
10	0.223	0.193	0.00	16	84
20	0.203	0.184	0.01	16	76
50	0.179	0.177	0.01	16	57
100	0.162	0.168	0.03	16	37

r = stochastic growth rate

SD(r) = standard deviation around r

PE = probability of extinction

N = mean number of lions in the population

H = mean heterozygosity of the population

Table 4: VORTEX analysis projection of the lion population on Tswalu Kalahari Reserve for four time intervals, under poor environmental conditions (mean annual rainfall < 165 mm), an ecological capacity of 17 lions and a high mortality rate.

Years	r	SD(r)	PE	N	H
10	-0.091	0.266	0.34	5	80
20	-0.101	0.272	0.96	3	64
50	-0.101	0.271	1.00	0	0
100	-0.103	0.272	1.00	0	0

r = stochastic growth rate

SD(r) = standard deviation around r

PE = probability of extinction

N = mean number of lions in the population

H = mean heterozygosity of the population

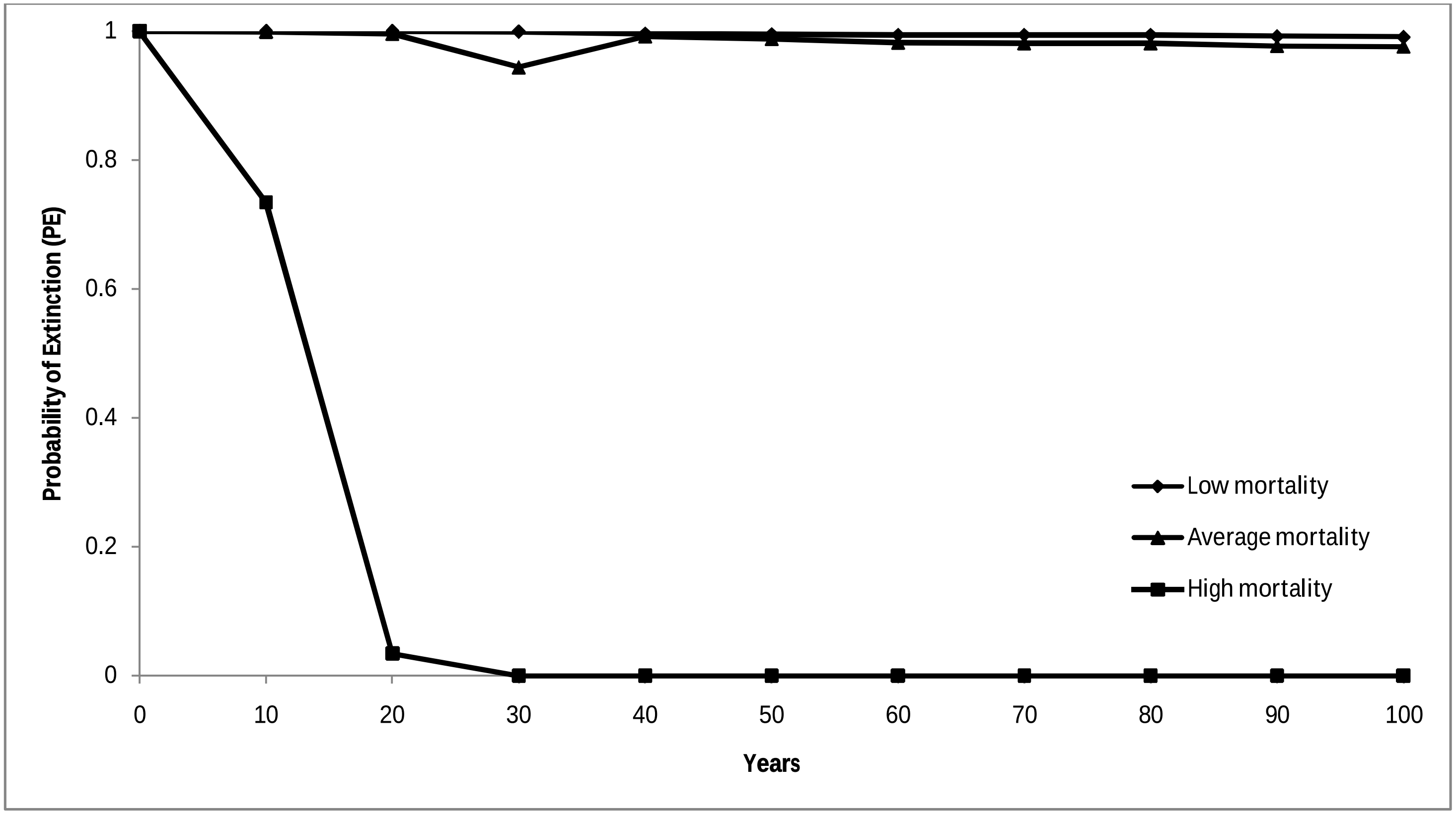

Figure 1: The probability of extinction of the lion population in the Lekgaba predator camp at Tswalu Kalahari Reserve for different levels of mortality, as projected by VORTEX analysis. A value of 1.0 indicates 100% survivability, while 0 indicates extinction.

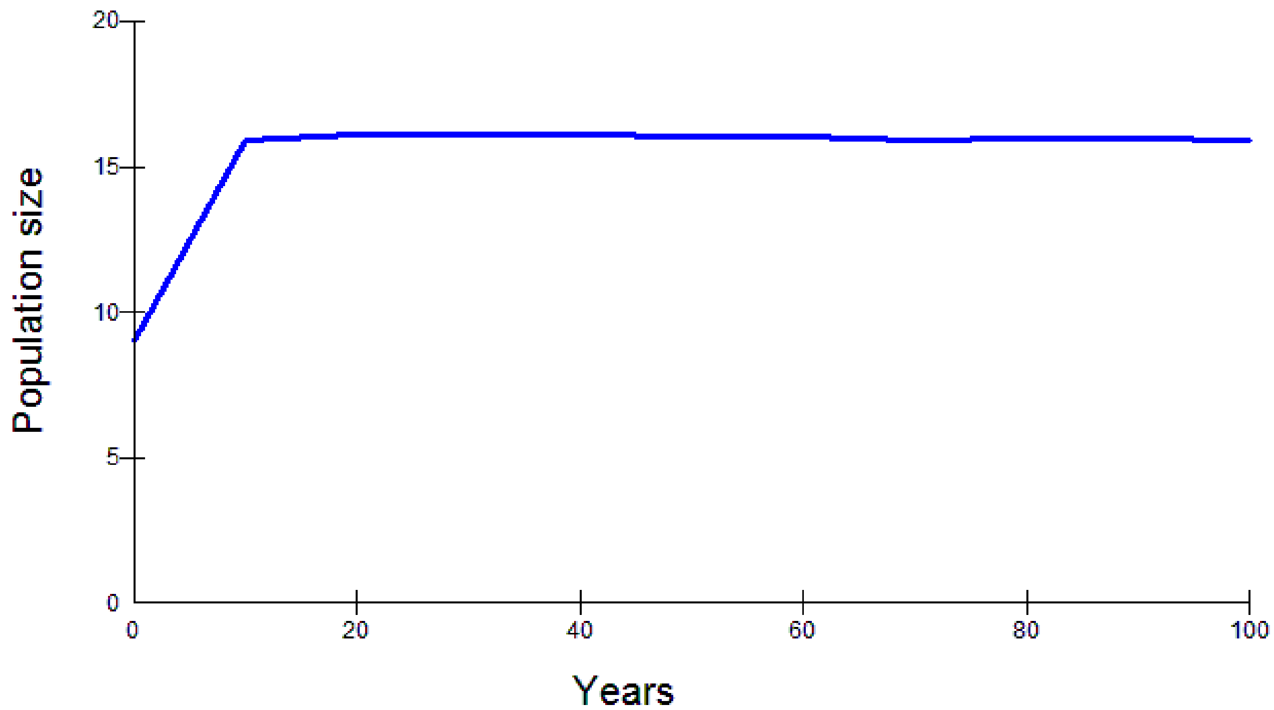

Figure 2: The increase in size of the lion population in the Lekgaba predator camp at Tswalu Kalahari Reserve to ecological capacity (17 lions) as modelled with a disease catastrophe affecting the population and projected by VORTEX analysis.

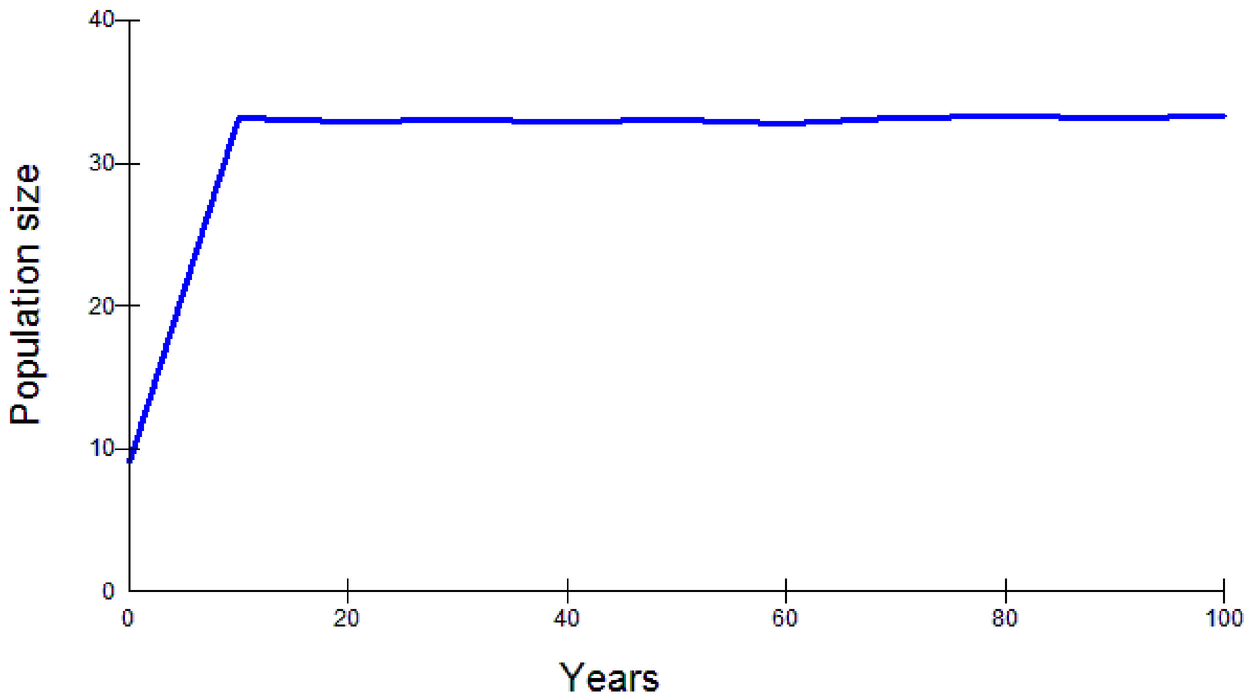

Figure 3: The increase in size of the lion population in the Lekgaba predator camp at Tswalu Kalahari Reserve when the ecological capacity of the lion population is doubled (34 lions) to compensate for fluctuations around the actual ecological capacity of 17 lions and projected by VORTEX analysis.

The harvesting of all the males in the population and replacement by a coalition of two breeding males yielded similar results to the original population, even when modelled after a disease catastrophe. The projected stochastic growth rate of r = 0.196 is similar to the stochastic growth rate of r = 0.195 for the initial population. When a coalition of three males of breeding age are supplemented the stochastic growth rate (r = 0.198) increased as expected and the probability of extinction (PE = 0.06) decreased as expected.

Discussion

The ecological persistence and survival of a small isolated lion population was determined by using a population viability analysis. However, the results of the VORTEX analysis should be treated with caution, as these software packages do not provide exact answers (Wilson 2006). Reintroduced small populations of lions differ markedly from populations in large self-containing systems (Hunter 1998). The reintroduced populations have a rapid stochastic growth rate and high survival probabilities of cubs and subadults (Hunter 1998).

Lekgaba is no exception, where a rapid population growth has led to the lion population reaching ecological capacity after less than ten years. Any reserve that hopes to reintroduce lions onto their property should note this rapid growth in the absence of socially limiting factors.

The ecological capacity of Lekgaba for lions was determined to be 17 individual animals, which is similar to the ecological capacity of Phinda Resource Reserve (17 animals), which has similar prey densities and is similar in size (170 km^2) to Lekgaba (Hunter 1998; Hayward *et al*. 2007b). The rapid growth rate of the lion population will place pressure on the prey population and managers should be aware of this rapid increase in the number of lions on the reserve. Calculating the ecological capacity for an enclosed reserve after every annual wildlife count (prey) allows managers to increase the available food resources or limit the number of predators that put pressure on the prey population (Hayward *et al*. 2007b). Using a more conservative estimate of ecological capacity reduces the likelihood of overpopulation occurring (Hayward *et al*. 2007b).

Environmental conditions play a large role in cub and subadult survival in lions (Van Vuuren *et al.* 2005). During high rainfall years (> 237 mm mean annual rainfall), cub and subadult mortality is low when compared to times of mean or low rainfall. At high cub and subadult mortality rates the population declines rapdily during the first ten years and becomes extinct soon after that. This is not foreseen to be a major problem for Tswalu where water provisioning, food supplementation and high prey densities are all being used as management options. Tswalu receives an annual rainfall of circa 250 mm, which indicate good environmental conditions and high lion and prey survival rates. Even after the addition of a disease catastrophe the lion population is expected to continue to grow to its ecological capacity. This could be due to the infrequent occurrence of disease and the relatively small effect that disease has on the reproductive potential and survivability of the lion population (Roelke-Parker *et al*. 1996). The lion population on Tswalu was also vaccinated against rabies after a bat-eared fox had died of a suspected rabies infection (*pers. obs.*). All domestic dogs in the surrounding areas were also vaccinated against disease in 2004.

The removal of reproducing males and supplementation of new males will have little effect on the growth rate of the population. New males will generally kill cubs less than nine months old (Whitman, Starfield, Quadling & Packer 2004), and stimulate females to come into oestrus soon after (Whitman *et al*. 2004). The rapid growth rate shown by the lions could mean a shorter interbirth interval for females, which may lead to inbreeding when breeding males mate with their daughters, or young males mate with sisters or mothers (Killian 2003). Males of breeding age should therefore be replaced when the threat of inbreeding occurs. Males should be exchanged with other males from different reserves or farms to enhance genetic diversity and minimise the risk of extinction. Few small enclosed populations are able to maintain genetic diversity and should be managed accordingly (Killian 2003).

Lions remain important for the ecotourism and hunting industries in South Africa. Lion populations in isolated areas have to be managed to ensure genetic diversity, economic efficiency and self-sustainability. Only through adequate research and correct management techniques and principles can this goal be achieved. Population viability analysis can provide insights into the population demographics of a population and the forces that act on the population over time. However, care should be taken in using the results of population viability analysis as an accurate and only tool to determine the extinction probabilities of a population. Populations should rather be modelled by using a variety of software packages and their data should be updated regularly (Ludwig 1999).

Conclusion

Reintroductions of large predators on small enclosed reserves can prove difficult and are rarely successful. However, when they are successful they can be a viable method of establishing populations of animals. The rapid growth in the study population is an indication that the population is viable over an extended period of time.

The predicted ecological capacity of the lion population is similar to other areas with similar prey densities and size. Different mortality rates will have an effect on the survivability of the lion population, with high mortality rates causing extinction. The current lion population grew to and persisted at ecological capacity when mortality rates where low. Disease did not have a major effect on the lion population because the breeding proportion of the population will not be severely affected by an outbreak of disease such as canine distemper virus or rabies.

Genetic diversity of the lion population must be maintained or improved by replacing individuals with unrelated individuals from other areas. This is easier to manage when replacing males, because young males are evicted from natal prides and become nomadic. They can then be used as replacement animals to ensure the maintenance of genetic diversity. The population dynamics of the lions should be frequently determined by performing population viability analyses.

CHAPTER 7

MANAGEMENT RECOMMENDATIONS

Introduction

The growth in popularity of eco-tourism and hunting in South Africa has seen a marked increase in the number of small game ranches that are being developed (Bothma 1997). Many of these ranches have a limited size and can create ecological and economic problems, particularly for larger carnivores (Bothma 1997). To solve these potential problems active adaptive management needs to be used to ensure the short- and long-term viability of animal populations on these small reserves (Helm 2006). Active management implies the manipulation of animal populations and the habitat in which they reside (Bothma 2002b). Active adaptive management involves a system of making management decisions by learning from previous experiences in order to manipulate the populations to obtain maximum benefit from those decisions (Bothma 2002b; Helm 2006).

No management decisions should be taken without adequate monitoring of animals and vegetation (Bothma 2002b). The monitoring of a population serves as an early warning system for managers, and provides an indication as to whether certain management decisions should be altered or improved upon (Bailey 1984; Helm 2006). The success of game ranches in South Africa is dependent on the determination of regular, repeatable ecological data (Bothma 2002b).

Knowledge of the exact ecological and economic role of larger carnivores on small enclosed reserves is limited (Killian 2003). Lions, in particular, are highly sought after by tourists and hunters (Van Dyk 1997), and as such provide economic benefits for conservation of the species. Lions can also affect the genetics and dynamics of prey populations by weeding out weak, sick and old animals (Cotterill 1997). However, there are also costs associated with introducing lions. Predation costs depend on the prey population and the number of rare and expensive prey types that occur in the area. Running and maintenance costs involved with providing photographic safaris, hunting safaris and fencing also contribute the negative impact that a lion population can have on the economic stability of a game ranch (Cotterill 1997). The regular monitoring of the population will also be costly in terms of fuel and man-power needed for adequate monitoring

This study aims to identify prey use, prey preferences and range use of the lion population on Tswalu Kalahari Reserve. The results these aims can play a role in determining the effect that the current lion population has on the ecological and economic stability of the Lekgaba predator camp of Tswalu Kalahari Reserve. Site-specific research and monitoring must be conducted on small enclosed reserves to provide managers with enough information to make decisions regarding the well-being of the lion population.

Site-specific management recommendations

The predator camp, Lekgaba, on Tswalu Kalahari Reserve, is one of very few small enclosed reserves in the Kalahari region. The lion population is popular for photographic safaris, while hunting is prohibited by E. Oppenheimer and Son, the owners of Tswalu. The lions are spoor-tracked by highly trained trackers and guides on a daily basis, making monitoring and research possible. All kills, social interactions, births and mortalities should be recorded by the staff and logged into a database. This database should be used to monitor the lion population and its effect on the prey base in the predator camp. There are several management recommendations that can be applied on Lekgaba in Tswalu Kalahari Reserve:

- Maximum visibility of the lion population should be maintained by having more than one pride and limiting the number of nomadic lions in the population. Having a large population will increase the number of sightings for the guests, as well as increasing the opportunity of finding lions in an area. Having more than one pride will also decrease pressure on the population by dispersing the amount of vehicles at each sighting (Anon 2008). Game drive traffic on Tswalu is not considered to be a problem. Larger prides will also allow the lions to kill larger prey types such as giraffe, eland and gemsbok more easily.

- Maintaining genetic diversity remains one of the most important management strategies on a small, enclosed reserve. Male lions should not be allowed to mate with their sisters, mothers or daughters, to prevent inbreeding and decrease the gene pool of lions in the region. New adult males should be introduced regularly to the population, while removing the reproducing males that are presently in the predator camp. A meta-population management strategy has been proposed, in which reserves exchange males to increase the size of the breeding pool (Anon 2008). It is essential that the new males which are being introduced are not related at all to the females or cubs residing in the area. Coalitions of male lions are ideal to introduce because they will more than likely not force each other out of the reserve onto neighbouring farms.

- The introduction of new lions into the population should be thoroughly researched and monitored. The new animals should be released into a holding boma for a period of six to eight weeks (Van Dyk 1997), where they acclimatise to the area. After the holding period, the lions should be released into a suitable area with abundant prey (Killian 2003). The new lions should be constantly monitored to ensure that they respect the electric fence and settle in to their new habitat.

- The ecological capacity of 17 lions (Chapter 6), in several prides will ensure optimal viewing of the lion population. However, constant monitoring and research are needed to maintain the ecological capacity and ensure that the lion population does not have a negative effect on the prey population. The ecological capacity must be updated regularly to achieve the management objectives of maintaining an adequate prey population for the long-term survival of the lion population

- Maintaining the lion population at ecological capacity can be achieved by controlling the growth and size of the population. Several management techniques can be applied for population control:

  - Translocation: any excess animals can be removed and transported to other nature reserves and game ranches. This is dependent on current legislation which governs the transport and housing of large predators on small, enclosed reserves.

  - The introduction of new males on a more regular basis can be used to control cub numbers through infanticide (Anon 2008). New males will destabilize the lion prides and kill any cubs that are not known to them. It should be ensured that any new male coalitions are not at all related to the cubs, which can increase the gene pool and increase the level of infanticide (Anon 2008). If it is not possible to introduce new males regularly the management staff can mimic infanticide by removing young cubs (> one year old) (Anon 2008). This should be considered as a last resort because of the public pressure and sentiment towards lion cubs.

  - Reproductive suppression can be achieved through contraception, sterilization and vasectomising the male lions (Anon 2008). The results from other studies have shown that these methods have a limited use and may lead to pride fragmentation, but that they can lead to effectively controlling the birth rate of the lion population (Anon 2008). Research is needed to obtain adequate information as to the effect that reproductive suppression methods have on lion populations.

    Artificial insemination is being considered as a possible management tool to introduce new genetic material into the population (Van Dyk 1997).

- Hunting of large trophy male lions is a highly controversial and sensitive subject (Killian 2003), however it does provide much needed income and allows for the replacement of adult male lions. Hunting is not permitted on Tswalu, but it can be considered as a management strategy if no other options are available to control and manipulate the adult male lion population. Euthanasia can also be practiced on the population but other avenues should be explored before considering this management option.

- The spread of disease through an isolated lion population can have a negative effect on the survival probability of that population. Regular disease monitoring and blood tests should be conducted to prevent the spread of disease, especially where new lions are introduced into the population.

- A management strategy for the prey population should be aimed at ensuring the long-term survival of both the lion and prey populations. The annual aerial wildlife census should be conducted as accurately and precisely as possible in order to determine the exact number of each prey type available on Lekgaba. The prey biomass (Chapter 4) should be maintained or enhanced by the regular reintroductions of prey types into the predator camp. However, reintroductions are costly and may lead to overgrazing by the enlarged prey population.

  Another consideration is whether or not to introduce prey types that are favoured by the lions. Introducing greater kudu, warthog and steenbok, may lead to the lions becoming dependent on these prey types and therefore further underutilizing the other prey types (Anon 2008). The lions should be encouraged to utilize gemsbok, blue wildebeest, red hartebeest and springbok as prey types. This can be achieved by not introducing the preferred prey types of the lion population.

Suitable habitat, especially for the smaller mammals, should be maintained and, where possible, enhanced through the use of burning regimes mechanical vegetation control methods.

- A genetic studbook should be created for the lion population. This studbook should include the age of the parents, the number and sex of all cubs born into the population. The studbook can be maintained by the guides, trackers, game scouts and management staff on Lekgaba.

The management staff of Tswalu Kalahari Reserve have expressed an interest in expanding the size of the Korannaberg section to incorporate the predator section and to fence off the main gravel road that runs between the two sections at present. The lion population will benefit from the increase in area size in a variety of ways. A higher prey biomass and increase in potential range will increase the ecological capacity of the lion population, and in so doing provide optimal game viewing experiences for tourists. Tswalu will be able to house a larger number of prides and therefore have more male lions for viewing purposes and increase the size of the genetic pool on Tswalu Kalahari Reserve. Less manipulation of the lion population will be needed as males will start their own pride takeovers and return the system to a more natural one. The prey base will now also have more space and higher numbers to escape predation pressure from an increase in the size of the lion population.

However, there are some negative aspects to introducing lions into the Korannaberg section of Tswalu Kalahari Reserve. The entire reserve will have to be fenced in wildlife-proof electric fencing at large expense to Tswalu Kalahari Reserve. The staff and guests will need to be educated about the danger posed by lions and all housing and facilities need to be fenced as well. Lions will also pose a serious threat to the horse-riding experience offered on Tswalu. Horse-riding will have to be conducted under controlled conditions especially where inexperienced riders are concerned.

Research topics

Regular monitoring of the prey use, range use and social behaviour of the lion population is important as an active adaptive management tool to determine the effect of various management strategies that are employed. Tswalu Kalahari Reserve can be used to conduct feeding trials on lions when new lions are introduced into the population (Chapter 4). The feeding trials will be used to ascertain the length of time that digesta remains in the gut of the lion. This can be conducted on animals in controlled circumstances on and those living in the wild. Scat samples can be collected by staff and analysed according to the methods provided in Chapter 4.

The prey population on Lekgaba needs to be analysed to ascertain if there is any negative predation pressure evident on the prey. The grazing and browsing capacity of Lekgaba should also be re-studied to determine the correct number of wildlife that Lekgaba can sustain. This will allow an accurate measure of available biomass and the calculation of the ecological capacity for lions on Lekgaba.

Conclusion

The current lion population residing in the predator camp of Tswalu Kalahari Reserve should be actively managed to prevent inbreeding depression of the population and the negative effect that a large lion population can have on the prey base within an enclosed reserve. The management objectives should ensure the long-term survival of both the lion and prey populations. This can be achieved by:

1. The regular removal and replacement of reproducing male lions.
2. The creation of a studbook to ensure that no lions become inbred.
3. Encouraging the lion population to prey on more abundant prey items such as gemsbok, eland, springbok and red hartebeest.
4. Determining the ecological capacity of Lekgaba in terms of prey numbers.
5. Accurate and precise annual game census techniques.
6. The regular monitoring of the lion population.

Prey and range use of lions on Tswalu Kalahari Reserve

By

David James Roxburgh

Supervisor: Prof. J. du P. Bothma

Centre for Wildlife Management
Department of Animal and Wildlife Sciences
Faculty of Natural and Agricultural Sciences
University of Pretoria

Magister Scientiae (Wildlife Management)

SUMMARY

The current tourism boom in South Africa has increased the number of small reserves that now house larger predators. These larger predators need to be intensively managed and regularly monitored so that their role on the nature reserve is clearly understood. The larger predator population, if not managed, can have a negative effect on the surrounding ecosystem in terms of predation pressure and conflict with neighbouring farms.

The prey use, range use and habitat selection of an isolated lion population were investigated. The study was conducted on Lekgaba, an 188 km^2 predator camp of Tswalu Kalahari Reserve. Tswalu Kalahari Reserve is situated in the south-eastern Kalahari region of the Northern Cape Province of the Republic of South Africa. The mean annual rainfall on Tswalu is 253.5 mm.

Four lions were introduced into Lekgaba from the Kgalagadi Transfrontier Park. The population has grown to nine individuals, three males and six females of varying ages. The two adult females split and established prides in the northern and southern part of the reserve respectively. The dominant male moved between both prides.

The prey use (Chapter 4) of the lion population was determined by locating kills and collecting lion scats. The kills and scats were analysed to obtain the prey selection of the lion population. 19 prey types were utilized by the lions, with the gemsbok and blue wildebeest being the most used of all prey types. The scat data was corrected for relative prey biomass, making smaller bodied prey types significantly more prominent than in kill or scat data. The prey selection list was then compared to the relative abundance of each prey type in Lekgaba. The greater kudu was overutilized when compared to its relative abundance while the Hartmann's mountain zebra was underutilized. Prey preference was calculated statistically and the results indicated that the warthog and steenbok were significantly preferred while there was significant lack of use of gemsbok and Burchell's zebra. A possible answer for the lack of use of gemsbok was that they were the most abundant prey type found on Lekgaba. The lion population used 13% of the edible biomass available to them. The daily consumption rate was 9.9 kg/Lion feeding Unit/day, which is high when compared to consumption rates of other lion populations. The high daily consumption rate can be attributed to the high density of prey available to the lions.

The range use (Chapter 5) and habitat selection were determined through a combination of indirect and direct observations, opportunistic observations and observations made by guides, game scouts and rangers. As was expected the range sizes of the male lions were larger than those of the females. Female range size is dependent on resource availability, while male range size is dependent on the availability of reproducing female lions.

The mean range size of the lion population on Lekgaba was smaller than range sizes of other lion populations in a semi-arid environment. The range size of the Lekgaba lion population was similar to lion range sizes in mesic savannas such as Welgevonden Private Game Reserve, the Associated Private Nature Reserves and Phinda Resource Reserve.

The lion population had clear habitat preferences (Chapter 5). Some of the habitat types did not meet the minimum habitat requirements for lions living in semi-arid environment. The mountains and hills were avoided, while the more open habitats, such as the plains and bushy plains, were favoured by the lion population.

The range size and habitat selection of the Lekgaba lion population seem to depend on the prey density and distribution, the hunting opportunities provided by the habitat types, the habitat selection of the prey and the location of the water sources.

A population viability analysis (Chapter 6) was conducted to determine the short- and long-term probability of survival of the lion population. The results indicated that the population was viable over the long-term. An ecological capacity for the lions was calculated. Differing environmental conditions resulted in differing mortality rates of lions. Poor environmental conditions, could lead to the extinction of the lion population in the short-term. Disease did not affect the population to a large degree. Regular monitoring and updating the Population Viability Analysis are needed.

Management recommendations (Chapter 7) were provided to ensure the long-term ecological and economic sustainability of an isolated lion population. Genetic replacement, prevention of inbreeding, predation pressure, ecological capacity and an increase in the area available to the lion population were deemed as the most important goals to achieve for the management staff of Tswalu Kalahari Reserve.

REFERENCES

ACOCKS, J.P.H. 1988. *Veld types of South Africa. Memoirs of the Botanical survey of South Africa* 57. Department of Agriculture and Water Supply, Government Printer, Pretoria, pp. 44-49.

ADMASU, E., THIRGOOD, S.J., BEKELE, A. & LAURENSON, M.K. 2004. Spatial ecology of white-tailed mongoose in farmland in the Ethiopian highlands. *African Journal of Ecology* 42: 153-159.

ALLDREDGE, J.R. & RATTI, J.T. 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 56: 1-9.

ANDERSON, J.L. 1981. The re-establishment and management of a lion *Panthera leo* population in Zululand, South Africa. *Biological Conservation* 19: 107-117.

ANDHERIA, A.P., KARANTH, K.U. & KUMAR, N.S. 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology, London* 273: 169-175.

ANON. 2008. Proceedings of the 1st lion workshop held at Ekuthuleni Game Lodge. Unpublished workshop report. Welgevonden Private Game Reserve, Waterberg.

APPS, P. 1992. *Wild ways: a field guide to the behaviour of southern African mammals.* Southern Book Publishers, Halfway House.

ARTHUR, S.M., MANLY, B.F.J., MCDONALD, L.L. & GARNER, G.W. 1996. Assessing habitat selection when availability changes. *Ecology* 77: 215-227.

ATTWOOD, T.C. & WEEKS, H.P. 2003. Spatial hone-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. *Canadian Journal of Zoology* 81: 1589-1598.

BAGCHI, S., GOYAL, S.P. & SANKAR, K. 2003. Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *Journal of Zoology, London* 260: 285-290.

BAILEY, J.A. 1984. *Principles of Wildlife Management.* John Wiley and Sons, New York.

BAUER, H. & VAN DER MERWE, S. 2002. *The African lion database*. Annual report, The African Lion Working Group.

BAUER, H., DE IONGH, H.H., PRINCEE, F.P.G. & NGONTOU, D. 2003. Research needs for lion conservation in west and central Africa. *Comples Rendus Biologies* 326: S112-S118.

BEISSINGER, S.R. & WESTPHAL, M.I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821-841.

BERRY, H., BUSH, M., DAVIDSON, B., FORGE, O., FOX, B., GRISHAM, J., HOWE, M., HURLBUT, S., MARKER-KRAUS, L., MARTENSON, J., MUNSON, L., NOWELL, K., SCHUMANN, M., SHILLE, T., STANDER, P.,

VENZKE, K., WAGENER, T., WILDT, D., ELLIS, S. & SEAL, U. 1997. Population and habitat assessment for the Namibian cheetah and lion. Workshop report. IUCN/SSC Conservation Breeding Specialist Group.

BERTRAM, B.C.R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology, London* 177: 463-482.

BIRÓ, Z., SZEMETHY, L. & HELTAI, M. 2004. Home range sizes of wildcats (*Felis silvestris*) and feral domestic cats (*Felis silvestris f. catus*) in a hilly region of Hungary. *Mammalian Biology* 69: 302-310.

BLACKWELL, P.G. 1997. Random diffusion models for animal movement. *Ecological Modelling* 100: 87-102.

BLUNDELL, G.M., MAIER, J.A.K. & DEBEVEC, E.M. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71: 469-489.

BÖRGER, L., FRANCONI, N., DE MICHELE, G., GANTZ, A., MESCHI, F., LOVARI, S. & COULSON, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75: 1393-1405.

BOTHMA, J. DU P. 1997. Larger carnivores on game ranches. In: J. van Heerden (Ed), *Proceedings of a symposium on lions and leopards as game ranch animals.* The Wildlife Group, South African Veterinary Association, Onderstepoort, pp. 58-74.

BOTHMA, J. DU P. 1998. *Carnivore ecology in arid lands*. Springer-Verlag, Berlin.

BOTHMA, J. DU P. 2002a. Counting wild animals. In J. du P. Bothma (Ed.) *Game Ranch Management*. Van Schaik Publishers, Pretoria, pp. 335-357.

BOTHMA, J. DU P. 2002b. Objectives. In J. du P. Bothma (Ed.) *Game Ranch Management*. Van Schaik Publishers, Pretoria, pp. 25-29.

BOTHMA, J. DU P. & LE RICHE, E.A.N. 1993. Disturbance bias when tracking Kalahari leopards (*Panthera pardus*) by spoor. *Koedoe* 36: 109-112.

BOTHMA, J. DU P. & LE RICHE, E.A.N. 1994a. Scat analysis and aspects of defecation in northern Cape leopards. *South African Journal of Wildlife Research* 24: 21-25.

BOTHMA, J. DU P. & LE RICHE, E.A.N. 1994b. Range use by an adult male caracal in the southern Kalahari. *Koedoe* 37: 105-108.

BOTHMA, J. DU P. & WALKER, C. 1999. *Larger carnivores of the African savannas*. J.L. Van Schaik Publishers, Pretoria.

BOTHMA, J. DU P., KNIGHT, M.H., LE RICHE, E.A.N. & VAN HENSBERGEN, H.J. 1997. Range size of southern Kalahari leopards. *South African Journal of Wildlife Research* 27: 94-99.

BOYCE, M.S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23: 481-506.

BRAIN, C., FORGE, O. & ERB, P. 1999. Lion predation on black rhinoceros (*Diceros bicornis)* in Etosha National Park. *African Journal of Ecology* 37: 107-109.

BRILLOUIN, L. 1956. *Scientific and information technology*. Academic Press, New York.

BRISCOE, B.K., LEWIS, M.A. & PARRISH, S.E. 2002. Home range formation in wolves due to scent marking. *Bulletin of Mathematical Biology* 64: 261-284.

BROOK, B.W., LIM, L., HARDEN, R. & FRANKHAM, R. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). *Biological Conservation* 82: 119-128.

BROOK, B.W., CANNON, J.R., LACY, R.C., MIRANDE, C. & FRANKHAM, R. 1999. Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*). *Animal Conservation* 2: 23-31.

BROOK, B.W., O' GRADY, J.J., CHAPMAN, A.P., BURGMAN, M.A., AKÇAKAYA, H.R. & FRANKHAM, R. 2000. Predictive accuracy of population viability anaylsis in conservation biology. *Nature* 404: 385-387.

BROOMHALL, L.S. 2001. Cheetah *Acinonyx jubatus* ecology in the Kruger National Park: a comparison with other studies across the grassland-woodland gradient. M.Sc Dissertation, University of Pretoria, Pretoria.

BRYDEN, B.R. 1978. The biology of the African lion (*Panthera leo*) Linnaeus, 1758) in the Kruger National Park. M.Sc Dissertation, University of Pretoria, Pretoria.

BURGMAN, M.A. & FOX, J.C. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation* 6: 19-28.

BUTLER, J.R.A. 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology* 38: 23-30.

BYERS, R.C., STEINHORST, R.K. & KRAUSMAN, P.R. 1984. Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* 48: 1050-1053.

BYGOTT, J.D., BERTRAM, B.C.R. & HANBY, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282: 839-841.

CARACO, T. & WOLF, L.L. 1975. Ecological determinants of group sizes of foraging lions. *American Naturalist* 109: 343-352.

CARO, T.M., PELKEY, N., BORNER, M., CAMPBELL, B.L., WOODWORTH, B.P., OLE KUWAI, J., HUISH, S.A. & SEVERRE, E.L.M. 1998. Consequences of different forms of conservation of large mammals in Tanzania: preliminary analyses. *African Journal of Ecology* 36: 303-320.

CARR, A.P. & RODGERS, A.R. 1998. *HRE: the home range extension for ArcView: users manual*. Centre for Northern Forest Ecosystem Research, Ohio.

CARROLL, C., NOSS, R.F., PAQUET, P.C. & SCHUMAKER, N.H. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation areas. *Ecological Applications* 13: 1773-1789.

CASTLEY, J.G., KNIGHT, M.H., MILLS, M.G.L. & THOULESS, C. 2002. Estimation of the lion (*Panthera leo*) population in the southwestern Kgalagadi Transfrontier Park in using a capture-recapture survey. *African Zoology* 37: 27-34.

CHARDONNET, PH. (ED.) 2002. *Conservation of the African lion: contribution to a status survey*. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA.

COCK, M.J.W. 1978. The assessment of preference. *Journal of Animal Ecology* 47: 805-816.

COOPER, S.M. 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyenas. *African Journal of Ecology* 29: 130-136.

COTTERILL, A. 1997. The economic viability of lions (*Panthera leo*) on a commercial wildlife ranch: examples and management implications from a Zimbabwean case study. In: J. van Heerden (Ed), *Proceedings of a symposium on lions and leopards as game ranch animals.* The Wildlife Group, South African Veterinary Association, Onderstepoort, pp. 189-197.

CRAFT, M.E., HAWTHORNE, P.L., PACKER, C. & DOBSON, A.P. 2008. Dynamics of a multihost pathogen in a carnivore community. *Journal of Animal Ecology* doi: 10.1111/j.1365-2656.2008.01410.x

CREEL, S. & CREEL, N.M. 1997. Lion density and population structure in the Selous Game Reserve; evaluation of hunting quotas and offtake. *African Journal of Ecology* 35: 83-93.

CROMHOUT, M. 2006. The ecology of the African buffalo in the eastern Kalahari region, South Africa. M.Sc Dissertation, University of Pretoria, Pretoria.

CUSHMAN, S.A., CHASE, M. & GRIFFIN, C. 2005. Elephants in space and time. *Oikos* 109: 331-341.

DAHLE, B. & SWENSON, J.E. 2003. Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology* 72: 660-667.

DAVIES, E.M. & DEE BOERSMA, P. 1984. Why lionesses copulate with more than one male. *American Naturalist* 123: 594-611.

DOUGLAS, R.M. 1989. A new method of cross-sectioning hair of large mammals. *South African Journal of Wildlife Research* 19: 73-76.

DRUCE, D., GENIS, H., BRAAK, J., GREATWOOD, S., DELSINK, A., KETTLES, R., HUNTER, L. & SLOTOW, R. 2004. Prey selection by a re-introduced lion population in the Greater Makalali Conservancy, South Africa. *African Zoology* 39: 273-284.

EBEDES, H. & BOTHMA, J. DU P. 2002. Ostriches. In: J. du P. Bothma (Ed.), *Game Ranch Management*. Van Schaik Publishers, Pretoria, pp. 220-226.

ELOFF, F.C. 1973a. Lion predation in the Kalahari Gemsbok National Park. *Journal of the South African Wildlife Management Association* 3: 59-63.

ELOFF, F.C. 1973b. Water use by the Kalahari lion *Panthera leo vernayi*. *Koedoe* 16: 149-154.

ELOFF, F.C. 2002. *Hunters of the dunes: the story of the Kalahari lion*. Sunbird Publishing, Cape Town.

ESRI INC. 1998. *Environmental Systems Research*. California, Redlands.

ESTES, R.D. 1997. *Behaviour guide to African mammals: including hoofed mammals, carnivores and primates.* Russel Friedman Books, Halfway House.

FELDHAMMER, G.A., DRICKAMER, L.C., VESSEY, S.H. & MERRITT, J.F. 1999. *Mammalogy: adaptation, diversity and ecology* (pp. 375-376). McGraw-Hill, Boston.

FERGUSON, S.H., TAYLOR, M.K., BORN, E.W. ROSING-ASVID, A. MESSIER, F. 1999. Determinants of home range size for polar bears *Ursus maritimus. Ecology Letters* 2: 311-318.

FISHER, D.O. & OWENS, I.P.F. 2000. Female home range size and the evolution of social organization in macropod marsupials. *Journal of Animal Ecology* 69: 1083-1098.

FLOYD, T.J., MECH, L.D. & JORDAN, P.A. 1978. Relating wolf scat to prey consumed. *Journal of Wildlife Management* 42: 528-532.

FRYXELL, J.M., GREEVER, J. & SINCLAIR, A.R.E. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131: 781-798.

FUNSTON, P.J. 1999. *Predator-prey relationships between lions and large ungulates in the Kruger National Park*. Ph.D Thesis, University of Pretoria, Pretoria.

FUNSTON, P.J., MILLS, M.G.L. & BIGGS, H.C. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology, London* 253: 419-431.

FUNSTON, P.J., MILLS, M.G.L., BIGGS, H.C. & RICHARDSON, P.R.K. 1998. Hunting by male lions: ecological influences and socioecological implications. *Animal Behaviour* 56: 1333-1345.

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, London* 259: 131-142.

GALLERANI LAWSON, E.J. & RODGERS, A.R. 1997. Differences in home-range size computed in commonly used software programs. *Wildlife Society Bulletin* 25: 721-729.

GAUTESTAD, A.O. & MYSTERUD, I. 1995. The home range ghost. *Oikos* 74: 195-204.

GEHRT, S.D. & FRITZELL, E.K. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Animal Behaviour* 55: 1211-1227.

GLEN, A.S. & DICKMAN, C.R. 2006. Diet of the spotted-tailed qoull (*Dasyurus maculates*) in eastern Australia: effects of season, sex and size. *Journal of Zoology, London* 269: 241-248.

GRAHAM, K., BECKERMAN, A.P. & THIRGOOD, S. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159-171.

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

GUASP, A.C., DE TORRES CURTH, M.I. & GONZÁLEZ, D.E. 1996. Areography 2.0. A program to delimit distributional areas of species. *Environmental Software* 11: 271-275.

HAMILTON, S. & MOLLER, H. 1995. Can PVA models using computer packages offer useful conservation advice? Sooty shearwaters *Puffinus griseus* in New Zeland as a case study. *Biological Conservation* 73: 107-117.

HANBY, J.P. & BYGOTT, J.D. 1987. Emigration of sub-adult lions. *Animal Behaviour* 35: 161-169.

HANBY, J.P., BYGOTT, J.D. & PACKER, C. 1995. Ecology, demography and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In: A.R.E. Sinclair & P. Arceses (Eds), *Serengeti II: Dynamics, management and conservation of an ecosystem*. University of Chicago Press, Chicago, pp. 315-331.

HARRIS, R.B., MAGUIRE, L.A. & SHAFFER, M.L. 1987. Sample sizes for minimum viable population estimation. *Conservation Biology* 1: 72-76.

HARRIS, S., CRESWELL, W.J., FORDE, P.G., TREWHELLA, W.J. WOOLLARD, T. & WRAY, S. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20: 97-123.

HAYWARD, M.W. & KERLEY, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology, London* 267: 309-322.

HAYWARD, M.W., HENSCHEL, P., O'BRIEN, J., HOFMEYR, M., BALME, G. & KERLEY, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology, London* 270: 298-313.

HAYWARD, M.W., O'BRIEN, J., HOFMEYR, M. & KERLEY, G.I.H. 2007a. Testing the predictions of prey of lion (*Panthera leo*) derived from modelled prey preferences. *Journal Wildlife Management* 71: 1567-1575.

HAYWARD, M.W., O' BRIEN, J. & KERLEY, G.I.H. 2007b. Carrying capacity of large African predators: predictions and tests. *Biological Conservation* 139: 219-229.

HAYWARD, M.W., ADENDORFF, J., O'BRIEN, J., SHOLTO-DOUGLAS, A., BISSETT, C., MOOLMAN, L.C., BEAN, P., FOGARTY, A., SLATER, R. & KERLEY, G.I.H. 2007c. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* 41: 205-214.

HEINSOHN, R. 1997. Group territoriality in two populations of African lions. *Animal Behaviour* 53: 1143-1147.

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

HELM, C.V. 2006. Ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the Highveld grasslands of South Africa. M.Sc Dissertation, University of Pretoria, Pretoria.

HEMSON, G., JOHNSON, P., SOUTH, A., KENWARD, R., RIPLEY, R. & MACDONALD, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74: 455-463.

HENDERSON, W.M. 1982. The control of disease in wildlife when a threat to man and farm livestock. *Symposium of the Zoological Society of London* 50: 287-297.

HILDYARD, C.J. 1983. The identification of mammals using hair samples. B.Sc. (Hons) (Wildlife Management) Project Report, University of Pretoria, Pretoria.

HOOGE, P.N. 1999. *Animal movement analysis ArcView extension*. USGS-BRD, Alaska Biological Science Centre, Glacier Bay Field Station, Gustavus.

HOOGE, P.N. & EICHENLAUB, B. 2000. *Animal movement extension to ArcView. Version 2.0*. Alaska Science Centre – Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.

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

HORNE, J.S. & GARTON, E.O. Selecting the best home range model: an information-theoretic approach. *Ecology* 87: 1146-1152.

HUNTER, L.T.B. 1998. *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa*. Ph.D Thesis, University of Pretoria, Pretoria.

JACOBS, J. 1974. Quantitative measurement of food selection. *Oecologia* 14: 413-417.

JANSEN, R., LITTLE, R.M. & CROWE, T.M. 2000. Habitat utilization and home range of the redwing francolin, *Francolinus levaillantii*, in highland grassland, Mpumalanga province, South Africa. *African Journal of Ecology* 38: 329-338.

JOUBERT, D. 2006. Hunting behaviour of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park. *African Journal of Ecology* 44: 279-281.

KARANTH, K.U. & SUNQUIST, M.E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* 64: 439-450.

KAYS, R.W. & PATTERSON, B.D. 2002. Mane variation in African lions and its social correlates. *Canadian Journal of Zoology, London* 80: 471-478.

KEOGH, H.J. 1979. An atlas of hair from southern African mammal species, with references to its taxonomic and ecological significance. D.Sc. Dissertation, University of Pretoria, Pretoria.

KEOGH, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research* 13: 89-94.

KERNOHAN, B.J., MILLSPAUGH, J.J., JENKS, J.A. & NAUGLE, D.E. 1998. Use of an adaptive kernel home-range estimator in a GIS environment to calculate habitat use. *Journal of Environmental Management* 53: 83-89.

KILLIAN, P.J. 2003. The ecology of re-introduced lions on the Welgevonden Private Nature Reserve, Waterberg. M.Sc Dissertation, University of Pretoria, Pretoria.

KISSUI, B.M. & PACKER, C. 2004. Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London, B series* 271: 1867-1874.

LACY, R.C. 1993. VORTEX: A computer simulation model for population viability analysis. *Widllife Research* 20:45-65.

LACY, R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins* 48: 191-203.

LACY, R.C., BORBAT, M. & POLLAK, J.P. 2005. *VORTEX: a stochastic simulation of the extinction process. Version 9.50*. Chicago Zoological Society, Brookfield.

LANDMAN, M., KERLEY, G.I.H. & SCHOEMAN, D.S. 2008. Relevance of elephant herbivory as a threat to important plants in the Addo Elephant National Park, South Africa. *Journal of Zoology, London* 274: 51-58.

LEHMANN, M.B., FUNSTON, P.J., OWEN, C.R. & SLOTOW, R. 2008. Feeding behaviour of lions (*Panthera leo*) on a small reserve. *South African Journal of Wildlife Research* 38: 66-78.

LEIMGRUBER, P., SENIOR, B., UGA, MYINT AUNG, SANGER, M.A., MUELLER, T., WEMMER, C. & BALLOU, J.D. 2008. Modeling population viability of captive elephants in Myanmar (Burma): implications for wild populations. *Animal Conservation* 11: 198-205.

LENT, P.C. & FIKE, B. 2003. Home-ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *South African Journal of Wildlife Research* 33: 109-118.

LINDENMAYER, D.B., BURGMAN, M.A., AKÇAKAYA, H.R., LACY, R.C. & POSSINGHAM, H.P. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modeling the viability of wildlife metapopulations. *Ecological modelling* 82: 161-174.

LINDSTEDT, S.L., MILLER, B.J. & BUSKIRK, S.W. 1986. Home range, time, and body size in mammals. *Ecology* 67: 413-418.

LOMBARDI, L., FERNANDEZ, N., MORENO, S. & VILLAFUERTE, R. 2003. Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. *Journal of Mammalogy* 84: 26-36.

LOVERIDGE, A.J., SEARLE, A.W., MURINDAGOMO, F. & MACDONALD, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* 134: 548-558.

LOW, A.B. & REBELO, A.G. 1998. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Government Printer, Pretoria.

LUDWIG, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80: 298-310.

MACDONALD, D.W. 1983. The ecology of carnivore social behaviour. *Nature* 301: 379-384.

MAHER, C.R. & LOTT, D.F. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* 49: 1581-1597.

MARCUM, L.C. & LOFTSGAARDEN, D.O. 1980. A nonmapping technique for studying habitat preferences. *Journal of Wildlife Management* 44: 963-968.

MARKER, L.L., MUNTIFERING, J.R., DICKMAN, A.J., MILLS, M.G.L. & MACDONALD, D.W. 2003. Quantifying prey preferences of free-ranging Namibian cheetahs. *South African Journal of Wildlife Research* 33: 43-53.

MARUCCO, F., PLETSCHER, D.H. & BOITANI, L. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the alps as a case study. *Journal of Mammalogy* 89: 665-673.

MARZLUFF, J.M., MILLSPAUGH, J.J., HURVITZ, P. & HANDCOCK, M.S. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85: 1411-1427.

MCBRIDE, C. 1990. *Liontide*. Jonathan Ball, Johannesburg.

MCCLEAN, S.A., RUMBLE, M.A., KING, R.M. & BAKER, W.L. 1998. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* 62: 793-801.

MCNAUGHTON, S.J. & GEORGIADES, N.J. 1986. Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics* 17: 39-65.

MCPHEE, M.E. & SILVERMAN, E.D. 2004. Increased behavioural variation and the calculation of release numbers for re-introduction programs. *Conservation Biology* 18: 705-715.

MELVILLE, H.I.A.S., BOTHMA, J DU P. & MILLS, M.G.L. 2004. Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research* 34: 67-75.

MILLER, P.S. & LACY, R.C. 2005. *VORTEX: a stochastic simulation of the extinction process. Version 9.50 user's manual*. Conservation Breeding Specialist Group, Apple Valley.

MILLS, M.G.L. 1992. A comparison of methods used to study food habits of large African carnivores. In: D.R. McCullough & R.H. Barrett (Eds.), *Wildlife 2001: Populations*. Elsevier, London, pp. 1112-1124.

MILLS, M.G.L. & BIGGS, H.C. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symposium of the Zoological Society of London* 65: 253-268.

MILLS, M.G.L & GORMAN, M.L. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology* 11: 1397-1406.

MILLS, M.G.L & SCHENK, T.M. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* 61: 693-702.

MILLSPAUGH, J.J., NIELSON, R.M., MCDONALD, L., MARZLUFF, J.M., GITZEN. R.A., RITTENHOUSE, C.D., HUBBARD, M.W. & SHERIFF, S.L. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70: 384-395.

MITCHELL, M.S. & POWELL, R.A. 2004. A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling* 177: 209-232.

MIZUTANI, F. & JEWELL, P.A. 1998. Home range and movements of leopards on a livestock ranch in Kenya. *Journal of Zoology, London* 244: 269-286.

MUKHERJEE, S., GOYAL, S.P. & CHELLAM, R. 1994. Standardisation of scat analysis techniques for leopard (*Panthera pardus*) in Gir National Park, Western India. *Mammalia* 58: 139-143.

MÜNZBERGOVÁ, Z. & EHRLÉN, J. 2005. How best to collect demographic data for population viability analysis. *Journal of Applied Ecology* 42: 1115-1120.

NELSON, D. 2004. *Dictionary of statistics*. Penguin Books, London.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38: 541-545.

NILSEN, E.B., PEDERSEN, S. & LINNELL, J.D.C. 2008. Can minimum convex polygon home ranges be used to draw biological meaningful conclusions? *Ecological Research* 23: 635-639.

NORTON, T.W. 1993. Introduction. *Biological Conservation* 73: 91.

NOWELL, K. & JACKSON, P. 1996. *Wild cats: a status survey and conservation action plan*. IUCN, Gland, Switzerland.

OGUTU, J.O. & DUBLIN, H.T. 1998. The response of lions and hyenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology* 36: 83-95.

OGUTU, J.O. & DUBLIN, H.T. 2002. Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology* 40: 120-129.

OGUTU, J.O. & DUBLIN, H.T. 2004. Spatial dynamics of lions and their prey along an environmental gradient. *African Journal of Ecology* 42: 8-22.

OWENS, M.J. & OWENS, D.D. 1984. *Cry of the Kalahari*. Houghton Mufflin, Boston.

OWEN-SMITH, N. & MASON, D.R. 2005. Comparative changes in adult vs. juvenile survival affecting population trends in African ungulates. *Journal of Animal Ecology* 74: 762-773.

PACKER, C. 1996. Who rules the park? Africa's lions fight disease and displacement. *Wildlife Conservation* June: 36-39.

PACKER, C. & PUSEY, A.E. 1983. Adaptations of females to infanticide by incoming males. *American Naturalist* 121: 716-728.

PACKER, C. & RUTTON, L. 1988. The evolution of cooperative hunting. *American Naturalist* 132: 159-198.

PACKER, C., PUSEY, A.E. & EBERLY, L.E. 2001. Egalitarianism in female African lions. *Science* 293: 690-693.

PACKER, C., SCHEEL, D. & PUSEY, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist* 136: 1-19.

PACKER, C., GILBERT, D.A., PUSEY, A.E. & O'BRIEN, S.J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351: 562-565.

PACKER, C, ALTIZER, S., APPEL, M., BROWN, E., MARTENSON, J., O'BRIEN, S.J., ROELKE-PARKER, M., HOFFMAN-LEHMANN, R. & LUTZ, H. 1999. Viruses of the Serengeti: patterns of infection and mortality in African lions. *Journal of Animal Ecology* 68: 1161-1178.

PERRIN, M.R. & BODBIJL, T. 2001. Habitat selection and small mammal prey availability of the gaboon adder in Zululand (KwaZulu-Natal), South Africa. *South African Journal of Wildlife Research* 31: 115-126.

PERRIN, M.R. & CAMPBELL, B.S. 1980. Key to the mammals of the Andries Vosloo Kudu Reserve (Eastern Cape),based on their hair morphology, for use in predator scat analysis. *South African Journal of Wildlife Research* 10: 1-14.

PIENAAR, D.J., BOTHMA, J. DU P. & THERON, G.K. 1992. Landscape preference of the white rhinoceros in the southern Kruger National Park. *Koedoe* 35: 1-17.

POWER, R.J. 2002. Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe* 45: 67-75.

POWER, R.J. 2003. Evaluation of how many lions a small reserve can sustain. *South African Journal of Wildlife Research* 33: 3-11.

PUTMAN, R.J. 1984. Facts from faeces. *Mammal Review* 14: 79-97.

QUINN, G.P. & KEOUGH, M.J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.

R DEVELOPMENT CORE TEAM. 2008. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org

RADLOFF, F.G.T. & DU TOIT, J.T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology* 73: 410-423.

RAPSON, J.A. & BERNARD, R.T.F. 2007. Interpreting the diet of lions (*Panthera leo*); a comparison of various methods of analysis. *South African Journal of Wildlife Research* 37: 179-187.

REED, J.M., MILLS, L.S., DUNNING, J.B., MENGES, E.S., MCKELVEY, K.S., FRYE, R., BEISSINGER, S.R., ANSLETT, M.C. & MILLER, P. 2002.

Emerging issues in population viability analysis. *Conservation Biology* 16: 7-19.

REYNOLDS, T.D. & LAUNDRE, J.W. 1990. Time intervals for estimating pronghorn and coyote home ranges and daily movements. *Journal of Wildlife Management* 54: 316-322.

ROELKE-PARKER, M.E., MUNSON, L., PACKER, C., KOCK, R., CLEAVELAND, S., CARPENTER, M., O' BRIEN, S.J., POSPISCHIL, A., HOFFMANN-LEHMANN, R., LUTZ, H., MWAMENGELE, G.L.M., MGASA, M.N., MACHANGE, G.A., SUMMERS, B.A. & APPEL, M.J.G. 1996. A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature* 379: 441-445.

ROWLANDS, I.W. & SADLEIR, R.M.F.S. 1968. Induction of ovulation in the lion, *Panthera leo. Journal of Reproduction and Fertility* 16: 105-111.

SALVATORI, V., SKIDMORE, A.K., CORSI, F. & VAN DER MEER, F. 1999. Estimating temporal independence of radio-telemetry data on animal activity. *Journal of Theoretical Biology* 198: 567-574.

SAMUEL, M.D., PIERCE, D.J. & GARTON, O. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* 54: 711-719.

SAMUELS, M.L. 1989. *Statistics for the life sciences*. Prentice Hall, New Jersey.

SCHALLER, G.B.1972. *The Serengeti lion*. The University of Chicago Press, Chicago.

SCHEEL, D. 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Animal Behaviour* 46: 695-704.

SCHOOLEY, R.L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *Journal of Wildlife Management* 58: 367-374.

SEAMAN, D.E., MILLSPAUGH, J.J., KERNOHAN, B.J., BRUNDIGE, G.C., RAEDEKE, K.J. & GITZEN, R.A. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63: 739-747.

SEAMAN, D.E. & POWELL, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home-range analysis. *Ecology* 77: 2075-2085.

SKINNER, J.D. & CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press, Cape Town.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the southern African subregion*. 2nd edition. University of Pretoria, Pretoria.

SMUTS, G.L. 1978. Interrelations between predators, prey and their environment. *Bioscience* 28: 316-320.

SMUTS, G.L. 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe* 19: 153-164.

SMUTS, G.L. 1982. *Lion.* Macmillan, London.

SOMERS, M.J. 1997. The sustainability of harvesting a warthog population: assessment of management options using simulation modeling. *South African Journal of Wildlife Research* 27: 37-43.

SONG, Y-L. 1996. Population viability analysis for two isolated populations of Hainan eld's deer. *Conservation Biology* 10: 1467-1472.

SOUTH, A. 1999. Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. *Ecological Modelling* 117: 343-360.

SPONG, G. 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology* 52: 303-330.

SPONG, G. & CREEL, S. 2004. Effects of kinship on territorial conflicts amoung groups of lions, *Panthera leo*. *Behavioural Ecology and Sociobiology* 55: 325-331.

STANDER, P.E. 1991. Demography of lions in Etosha National Park. *Madoqua* 18: 1-9.

STANDER, P.E. 1997. The ecology of lions and conflict with people in north-eastern Namibia. In: J. van Heerden (Ed), *Proceedings of a symposium on lions and leopards as game ranch animals.* The Wildlife Group, South African Veterinary Association, Onderstepoort, pp. 10-17.

STANDER, P.E. 1998. Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology* 35: 378-385.

STANDER, P.E. & ALBON, S.D. 1993. Hunting success of lions in a semi-arid environment. *Symposium of the Zoological Society of London* 65: 127-143.

STANDER, P.E., GHAU, //., TSISABA, D., □OMA, //. & I UI, I. 1997. Tracking and the interpretation of spoor: a scientifically sound method in ecology. *Journal of Zoology, London* 242: 329-341.

SUNQUIST, M.E. & SUNQUIST, F.C. 2002. *Wild cats of the world*. University of Chicago Press, Chicago.

SWIHART, R.K. & SLADE, N.A. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management* 49: 1019-1025.

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.

TAYLOR, B.L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* 9: 551-558.

TREVES, A. & KARANTH, K.U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491-1499.

TURNER, J. 2005. The impact of lion predation on the large ungulates of the Associated Private Nature Reserves, South Africa. M.Sc Dissertation, University of Pretoria, Pretoria.

TYSON, P.D. & CRIMP, S.J. 1998. The climate of the Kalahari transect. *Transactions of the Royal Society of South Africa* 53: 93-113.

VAN BOMMEL, L., BIJ DE VAATE, M.D. DE BOER, W.F. & DE IONGH, H.H. 2007. Factors affecting livestock predation by lions in Cameroon. *African Journal of Ecology* 45: 490-498.

VAN DYK, G. 1997. Re-introduction techniques for lion (*Panthera leo*). In: J. van Heerden (Ed), *Proceedings of a symposium on lions and leopards as game ranch animals.* The Wildlife Group, South African Veterinary Association, Onderstepoort, pp. 82-91.

VAN HEEZIK, Y.M. & SEDDON, P.J. 1998. Range size and habitat use of an adult male caracal in northern Saudi Arabia. *Journal of Arid Environments* 40: 109-112.

VAN ORSDOL, K.G. 1981. *Lion predation in Rwenzori National Park, Uganda*. Ph.D. Thesis, University of Cambridge, Cambridge.

VAN ORSDOL, K.G., HANBY, J.P. & BYGOTT, J.D. 1985. Ecological correlates of lion social organization. *Journal of Zoology, London* 206: 97-112.

VAN ROOYEN, N. 1999. The vegetation types and veld condition of Tswalu Private Desert Reserve. Unpublished report to the management of Tswalu Kalahari Reserve. University of Pretoria, Pretoria.

VAN ROOYEN, N., THERON, G.K. & BREDENKAMP, G.J. 1991. Kalahari vegetation: veld condition trends and status of species. *Koedoe* 34: 61-72.

VAN SCHALKWYK, A.G. 1994. Riglyne vir die bestuur van leeus (Panthera leo) in ingeperkte gebiede in Suid-Afrika*.* M.Sc Dissertation, University of Pretoria, Pretoria.

VAN VUUREN, J.H., HERRMANN, E. & FUNSTON, P.J. 2005. Lions in the Kgalagadi Transfrontier Park: modelling the effect of human-caused mortality. *International Transaction in Operational Research* 12: 145-171.

VAN WINKLE, W. 1975. Comparison of several probabilistic home-range models. *Journal of Wildlife Management* 39: 118-123.

VILJOEN, P.C. 1997. Ecology of lions in northern Botswana. In: J. van Heerden (Ed), *Proceedings of a symposium on lions and leopards as game ranch animals* The Wildlife Group, South African Veterinary Association,Onderstepoort, pp. 37-46.

VILJOEN, P.C. 2002. Lions. In: J. du P. Bothma (Ed), *Game Ranch Management*. 4th edition. Van Schaik Publishers, Pretoria, pp. 213-219.

VILJOEN, P.J. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib desert, Namibia. *African Journal of Ecology* 27: 227-240.

WATSON, L.H. & CHADWICK, P. 2007. Management of Cape mountain zebra in the Kammanassie Nature Reserve, South Africa. *South African Journal of Wildlife Research* 37: 31-39.

WATSON, L.H., ODENDAAL, H.E., BARRY, T.J. & PIETERSEN, J. 2005. Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. *Biological Conservation* 122: 173-180.

WEST, P.M. & PACKER, C. 2002. Sexual selection, temperature, and the lion's mane. *Science* 297: 1339-1343.

WHITMAN, K., STARFIELD, A.M., QUADLING, H.S. & PACKER, C. 2004. Sustainable trophy hunting of African lions. *Nature* 428: 175-178.

WILSON, K.A. 2006. Status and distribution of cheetahs outside formal conservation areas in the Thabazimbi district, Limpopo Province. M.Sc. Dissertation. University of Pretoria, Pretoria.

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

WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164-168.

YAMAZAKI, K. 1996. Social variation of lions in a male-depopulated area in Zambia. *Journal of Wildlife Management* 60: 490-497.

ZAR, J.H. 1999. Biostatistical analysis. Prentice-Hall, New Jersey.