Demographic characteristics of lion (*Panthera leo*) in the Kalahari Gemsbok National Park

by

Barend Otto Beukes

Thesis submitted in partial fulfilment of the requirements for the degree

Master of Technology: Nature Conservation

in the Faculty of Applied Sciences

at the Cape Peninsula University of Technology

Supervisor: Dr F.G.T. Radloff
Co-supervisor: Dr S.M. Ferreira

Cape Town
August 2016

DECLARATION

I, Barend Otto Beukes, declare that the contents of this thesis represent my own unaided work, and that the thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

14 August 2016

Signed **Date**

ABSTRACT

Lions are threatened across their natural range. The Kgalagadi Transfrontier Park (KTP), comprising the Kalahari Gemsbok National Park (KGNP; South Africa) and Gemsbok National Park (GNP; Botswana), is a stronghold for the species. Population size and demography of lions in the KGNP has been addressed in four historic studies. Studies in mid-1970 and 1990 reported a female biased population whereas in 2010 the sex structure was skewed towards males (56%). The bias in sex ratios towards males was first observed in cubs and sub-adults in 2001 and later, in 2010, throughout the population. Furthermore, in the 2010 assessment of the lion population, a smaller proportion of cubs (< 2 yrs) were observed in comparisons to the preceding studies (10% vs. ≥ 23%). The skew in age and sex structures that were observed in the KGNP led to concerns over the long-term sustainability of the greater KTP lion population. The lion population carries further risks associated with the stochastic, arid environment, in which the KTP lion population persists. Human-lion conflict on the borders of the KTP and anthropogenic alterations of the environment further threaten lion demographic stability.

In response to the potential threat to lions, an intensive study was conducted between 2013 and 2015 in the KGNP and a buffer area immediately to the east thereof in the GNP, with the aim of deriving robust estimates of lion population characteristics. Within the study area (14 250 km^2), 49 784 km were driven over 317 sampling days, which resulted 1162 lion sightings. Morphological features, primarily whisker spot patterns, were used to identify 261 unique individuals. Registering the population through individual identification provided for a non-invasive marking technique from which mark-recapture and minimum-known-alive estimates could be calculated. The population size of lions in the study area was defined using open-population mark-recapture analysis. The model POPAN in the Programme MARK provided the most precise estimate of population size (N = 246; 95%CI: 237-256). Track indices (N = 242; 95%CI: 176-307) in the current study provided a similar best estimate, but were imprecise and could not be used to detect robust trends in the KGNP lion population size between studies. Minimum-known-alive calculations (n = 145; December 2014) provided a gross underestimate in comparison with other techniques, and required more effort than mark-recapture or track indices. All the methods used in this study seem to indicate an increase in the lion population size from previous estimates (± 140). More prides were observed in the current study (n = 14) than observed in 1998-2001 (n = 11) and the average pride size was significantly larger in the current study (n = 16.07; ±8.7 SD) than in 1998-2001 (n = 7.55; ± 3.3 SD). Despite the apparent population increase, the variability in techniques used between the various studies, restricted the ability to define the amount of change in population size over time. Some of the discrepancies between population size estimates in the various studies could be attributed to methodological variability, differing definitions of the extent of the study area and in one case, the exclusion of small cubs (< 1 yr) from the estimates. Many of the methods used have inherently large margins of error, which inhibits the ability to detect trends in population size.

The sex ratio that was observed in this study (n = 261) showed a 1♂:1♀ ratio in all age classes and was comprised of 33% cubs (< 2 yrs), 12% sub-adults (2-4 yrs) and 55% adults (> 4 yrs) at the end of the study period. The ratio between males and females in the KGNP lion population has fluctuated between 1♂:1♀ to 1♂:2♀ ratio over a 38 year period (1977-2015). The ability to detect trends in the change of age and sex structure of lion in the KGNP over time was limited by low sample sizes in some historic studies. Nonetheless, the lion population in the KGNP are exhibiting uncharacteristically large proportions of males (49%). The largest measurable difference in the proportion of males in the populations is between the current study, where there was ±25% more males in comparison with observations in 1996-1997 (♂ = 24%; 95% CI: ±11%). Birth rates were lower in the current study (0.57 cubs per female per year) than observed between 1998 and 2001 (0.69 cubs per female per year). Apparent survival probability derived from Cormack-Jolly-Seber models were 82% (95% CI: 78-86) for the population per annum. The average survival probability was greater for females (± 93%) than for males (± 85%) in all age classes.

The current study provides the most comprehensive assessment of the KGNP lion population characteristics to date. The changes in demographic signals remain a concern for the future persistence of the KGNP lion population. Deriving robust estimates of demographic parameters and population size in the near future, from which accurate and precise trends can be observed, is of utmost importance. The potential drivers of demographic change in the KTP lion population requires further investigation to gain insight into potential conservation actions that may secure the persistence of the KTP lion population and associated ecological processes.

ACKNOWLEDGEMENTS

- I would like to thank my supervisor, Dr Frans Radloff for his boundless guidance, patience and dedication to this project. His efforts far surpassed what could be expected.
- I would also like to thank my co-supervisor, Dr Sam Ferreira for sharing his knowledge and for his support throughout the project.
- I am forever grateful to the primary sponsors of the project, for their significant financial contributions or material support. The primary sponsors include (in alphabetical order):
    - The Cape Peninsula University of Technology, Post Graduate Bursary, for financial contributions.
    - The Fehlmann family, Switzerland for their endless love and support and all those who made such generous financial contributions in response to the 'Fehlmann Brief'.
    - Land Rover and Jaguar, South Africa, in association with the SATIB Conservation Trust, for the sponsorship of a Land Rover Defender for use in project data collection and logistics. Particular gratitude goes to Mr Brian Courtney for his incredible contributions and support of the project.
    - The Peace Parks Foundation, for the donation of five GPS/VHF collars and travel expenses. Particular thanks to Mr Paul Bewsher, Mr Craig Beach and Ms Heloise de Villiers.
    - The University Research Fund, for financial contributions towards travel expenses.
- I would like to thank the Cape Peninsula University of Technology for their support. In particular, I would like to thank, Ms Lillian Bingo, Dr Joseph Kioko and Ms Michelle Slabber for their unending support of the research as well as Dr Corrie Uys for her statistical advice and assistance.
- I would like to thank South African National Parks (SANParks) for allowing this research to be conducted in the Kalahari Gemsbok National Park (KGNP) and to all those who contributed to the success of this research. Several individuals within SANParks require a special word of gratitude including:
    - Managerial staff in the Kalahari Gemsbok National Park including, Mr Lucius Moolman (Regional Manager) and Mr Steven Smith (Park Manager). Many thanks to the KGNP Section Rangers including, Mr Micho Ferreira, Mr Kennet Makondo and Mr Brent Whittington, and their respective teams. Mr Johan Kruger (Technical Manager) and his team for providing assistance with the many vehicle problems. Mr Ben van Eeden (Tourism Manager), and Johan and Corri Pretorius (Shop Managers) who always positively supported the project.
    - From SANParks Scientific Services, I would like to thank Dr Charlene Bissett, Mr Ernest Daemane, Mr Lourens de Lange, Mr Greame Ellis, Ms Khosi Mathebula and Mr Pauli Viljoen who contributed significantly in their support of the project.
    - From SANParks Veterinary Wildlife Services, my gratitude goes to, Dr Markus Hoffmeyr and Dr Dave Zimmerman, for coordinating and implementing the collaring and de-collaring of lions in the KGNP during the study.
- I would like to thank the Republic of Botswana, Ministry of Environment, Wildlife and Tourism for allowing the research to be conducted in the Gemsbok National Park. In particular, I would like to thank Mr L. Boutshese, Dr M.V. Flyman and Mr B.S. Mokara for their support of the research.
- Thank you to all of the corporate sponsors who supported the research though the supply of equipment and services including (in alphabetical order):
    - Axiom Systems Africa, in particular Mr Mark Auer, for the supply of photographic and computer equipment.

    - AEW Auto in association with the 4x4 Hilux Forum and Repcom, in particular Mr Allan Venter, for mechanical services and two way radios.
    - Bantam Custom Trailers, in particular Mr Johann Botha, for the use of a 4x4 trailer.
    - Bundutec, in particular Mr Abri Hoffman and Mr Martin Rautenbach for the supply of a BunduTop vehicle roof top tent and BunduAwn vehicle awning.
    - Camp Master and Mass Mart, in particular, Mr Grant Eeckhoven and Mr Craige Pershouse for the sponsorship of outdoor camping equipment.
    - Columbia, in particular Jackie Badenhorst, for the supply of outdoor clothing and sleeping bags.
    - Due South, for winter apparel.
    - Escape Gear, in particular Mr Murray Thomas for 4x4 seat covers.
    - First Alignment Centre, in particular Mr Johann Viljoen for the supply of off-road tyres.
    - Gomad 4x4 in association with A-Z Branding, in particular Mr Ciske van Gijsen, for the supply of an aluminium canopy and modifications of a long range water tank.
    - Greensport, in particular Mr Wouter Hattingh, for sponsoring off-road equipment.
    - Ibenstein and Kuwuki, in particular Rene and Loni Kraft, for logistical support.
    - Idea Wild, in particular Ms Ann Marie Gage, for photographic equipment.
    - Prime Labels, in particular Tanya Lotz, for vehicle vinyl branding.
    - SATIB Conservation Trust, in particular Mr Brian Courtney, Gavin Courtney and Julian Friedmond for logistical support.
    - State Veterinary Services, Northern Cape, in particular, to Dr Bertus Nel for veterinary assistance.
    - Walkers Midas, Upington, for logistical support.
    - !Xaus Lodge, in particular Richard and Nola and all staff members for their support.
- Immense gratitude to Mrs Brenda Stauch for her editorial assistance and endless love and support.
- Mrs Adri Beukes-Harnett and Mr Tom Harnett are thanked for their generous logistical assistance and for their love and support.
- Ulla, Jody and Thandi Paulus (Belgium) provided generous logistic and financial support throughout the duration of the project.
- Numerous individuals and families supported the research in a significant ways and I would like to especially thank the following people:
    - Beukes, Mr R and Mrs A; South Africa
    - Brock, Ms J; South Africa
    - Cooper, Mr J and Mrs B; South Africa
    - Daly, Mr R; United Kingdom
    - Du Toit, Mr C and Mrs L; South Africa
    - Gastner family; South Africa
    - Gibbs family; South Africa
    - Haigh, Ms S; South Africa
    - Higson, Mr J and Mrs H; South Africa
    - Hinrichsen family; South Africa
    - Hinton, Mr D; United States of America
    - Kitching Mr D and Mrs A; South Africa
    - Kohne, Mr N; South Africa

    - Selby, Ms D; United Kingdom
    - Stauch, Mr B and Mrs C; South Africa
    - Stauch, Mr T and Mrs F; South Africa
    - Webster, Ms R; United Kingdom
    - Wessels, Mrs C; South Africa
    - Whittington, Mrs M; South Africa
    - Winterton, Ms D; South Africa
    - Streicher, Mr J Mrs G; South Africa
    - Zeiher family; Germany
- I would also like to express my gratitude to all those who made financial contributions, or supported the project in other ways, that are not listed above.

DEDICATION

I dedicate this thesis to my wife Maya
and our daughter Leia

one love

TABLE OF CONTENTS

Chapter 1: General Introduction

Chapter 2: Study Area

Chapter 3: Effective estimation of abundance and demography: Lions (*Panthera leo*) in the Kalahari Gemsbok National Park

LIST OF FIGURES

LIST OF TABLES

GLOSSARY

AIC	Akaike’s Information Criterion
ANOVA	Analysis of variance
CJS	Cormack-Jolly-Seber
DNA	Deoxyribonucleic acid
GIS	Geographic Information System
GNP	Gemsbok National Park
GPS	Global Positioning System
IUCN	World Conservation Union
KGNP	Kalahari Gemsbok National Park
KTP	Kgalagadi Transfrontier Park
LRT	Likelihood Ratio Test
MLE	Model Likelihood Estimator
QGIS	Quantum GIS
SANParks	South African National Parks
VHF	Very High Frequency (30-300 MHz; 10-1m)
WMA	Wildlife Management Areas

Chapter 1:
General Introduction

1.1. Rationale

The Kgalagadi Transfrontier Park (KTP) has been identified as one of only ten localities within which lions (*Panthera leo verneyi*; Linnaeus, 1758) are appropriately protected across their natural geographic range (Bauer *et al*., 2015). In South Africa, the lions of the KTP are one of only two sustainable, free roaming lion populations with more than 500 lions present, the other being Kruger National Park (Bauer *et al*., 2005; Riggio *et al*. 2013; Bauer *et al*. 2015). Lions in the KTP are highly vulnerable to environmental fluctuations and human impact due to their low density, relative isolation and the arid, resource poor environment in which they occur (Bauer *et al*., 2005; van Vuuren *et al*., 2005; Ferreira *et al*., 2013). A study conducted in the Kalahari Gemsbok National Park, the section of the KTP situated in the Republic of South Africa, in response to a distemper pandemic (Zimmerman *et al*., 2009), identified a sex skew in the population towards a greater proportion of males (56%) (Ferreira *et al*., 2013). Prior to the study conducted in 2010 (Ferreira *et al*., 2013), the population exhibited a female biased sex structure (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011). However, although the total sample observed in 2001 (n = 228; Funston, 2011) displayed female bias, cubs (< 2 yrs) and sub-adults (2-4 yrs) were skewed toward a greater proportion of males, with 67% and 61% observed respectively (Funston, 2011).

An equal or greater proportion of males are uncommon among lion populations, which raised concerns of pending declines in lion numbers and increased susceptibility to extinction risks (Ferreira *et al*., 2013). In the KTP, a potential threat of localised extinction of lions exists where a male-biased population persists, particularly in the presence of poor ecological conditions (van Vuuren *et al*., 2005). A shift in sex ratios trending towards a greater proportion of males, observed first in young age classes (Funston, 2011) and later throughout the population (Ferreira *et al*., 2013) could influence other demographic parameters such as survival, fecundity and social dynamics (van Orsdol, 1985; Packer & Pusey, 1987; Yamazaki, 1996). Using modelled extinction risk parameters, female survivability was found to be the most important factor in the sustainability of the KTP lion population (van Vuuren *et al*., 2005). This is particularly so in the presence of the anthropogenic persecution that is experienced on the boundaries of the park (van Vuuren *et al*., 2005). Concerns over the sustainability of the lion population of the KGNP prompted further investigations in the form of the current study, to accurately describe lion demographic characteristics and define precise population size estimates from which trends can be described.

1.2. The natural history, biology and ecology of lions

Lion are the largest of all African carnivores and are described as a tawny colored cat, with males weighing approximately 190 kg and females 126 kg (Smuts *et al*., 1980; Bauer *et al*., 2015). Sexual dimorphism is presented in the form of dominant hair growth around the face and head in males known as a mane (Skinner & Chimimba, 2005; Blanchard, 2010). Males and females are of notable size difference with shoulder heights reaching an asymptote at two years of age at 95 cm and 107 cm for females and males respectively (Smuts *et al*., 1980; Ferreira & Funston, 2010). Females become reproductively mature between 46 and 57 months of age, and may start mating immediately, producing litters of between two and five cubs (Funston *et al*., 2003; Lehmann *et al*., 2008). Females remain reproductively active until approximately nine years of age (Bekoff *et al*., 1984) and intervals between births are approximately two years (Packer *et al*., 2001; Funston *et al*., 2003). Females may exhibit synchronous oestrus cycles, giving birth simultaneously to large groups of cubs known as cohorts (van Orsdol *et al*., 1985). Cubs born into large cohorts experience better health and higher survival rates (Pusey & Packer, 1987). Males also become reproductively mature at 3-4 years of age although they are limited in their procreative ability through social hierarchical structure and may only become reproductively active from approximately five years of age. Males remain reproductively capable throughout the remainder of their lives but may only be sexually active for the duration of pride tenure (Orford *et al*., 1988; Packer *et al*., 1998; Skinner & Chimimba, 2005; Daigle *et al*., 2015).

The only truly social felid are lions, with “prides” being made up of adult females (1-18 individuals) and their adolescents (Pusey & Packer, 1987; Abell *et al*., 2013) in a fission-fusion relationship with between one to three males (collectively a coalition) (Packer & Pusey, 1987). Males may be dominant and territorial over a pride and their home range for approximately three years after which immigrating males may displace them (Bygot *et al*., 1979). Female offspring generally remain resident within a pride. However; approximately 30% of females may emigrate depending on resource restraints (Smuts, 1978; Pusey & Packer, 1987; Mosser & Packer, 2009). All male offspring emigrate from their natal pride at an age of between two and five years with young males forming bachelor coalitions until they gain enough experience and fitness to assert dominance over a pride and displace resident males (Funston *et al*., 2003; Skinner & Chimimba, 2005; Mosser & Packer, 2009; Abell *et al*., 2013).

Lions are territorial, protecting their resources aggressively against rival prides and individuals (Bertram, 1978). Pride home range size varies significantly between populations depending on resource availability, from 50km² in the Kruger National Park to 4532 km² in the Kgalagadi Transfrontier Park (KTP) (Funston, 2011). Home range size decreases with increased prey availability but does not seem to be correlated to pride size (Loveridge *et al*., 2009)

Lions are considered apex predators and keystone ecological drivers in the ecosystems in which they occur. A decline in lion numbers may have numerous deleterious effects to both their prey species and other sympatric predators (Mills *et al*., 1978; Loveridge *et al*., 2007; Mills, 2015). Where lions occur as apex predators, they have the ability to regulate prey species abundance (Funston & Mills, 2006; Grange & Duncan, 2006; Salo *et al*., 2010). Although lions are generalist predators they may be selective, depending on prey availability, and often may have a major impact on a few preferred species (Radloff & Toit, 2004; Kissui & Packer, 2004; Grange & Duncan, 2006; Vanak *et al*., 2013; Mills, 2015). Their introduction or removal from systems prompt trophic cascades in which entire ecosystems alter their state, most often negatively in respect to biodiversity conservation objectives and ecosystem functioning (Kissui & Packer, 2004; Schuette *et al*., 2013; Ripple *et al*., 2014).

1.3. The conservation of lions

Although the most resent IUCN Red Data List status classifies the species overall as vulnerable, sub-populations in West and Central Africa are thought to warrant Critically Endangered status (Bauer *et al*., 2015; Henschel *et al*., 2015). However, in South Africa lions will most likely be classified as Least Concern on the next National Red List assessment (Bauer *et al*., 2015). The threat to lion persistence is evident through a decline in numbers of 42% globally and a decrease in distribution in excess of 80% over the past 21 years (IUCN SSC Cat Specialist Group, 2006; Bauer *et al*., 2015). Furthermore, major declines in free ranging lion are expected over the next 40 years (Packer *et al*., 2013). Lion status has remained Vulnerable since the first IUCN Red List assessment in 1996 (Nowell & Jackson, 1996; Bauer *et al*., 2015). Lions are classified as a protected species under CITES Appendix II with restricted harvesting and trading limitation (IUCN SSC Cat Specialist Group, 2006; Bauer *et al*., 2015). Of the greatest contributors to lion declines are unregulated hunting, human-lion conflict and persecution, habitat degradation and destruction, prey base depletion, disease and poaching (Packer *et al*., 1999; Björklund, 2003; Bauer *et al*., 2005; Packer *et al*., 2009; Riggio *et al*., 2013; Bauer *et al*., 2015).

Lions were once distributed throughout Sub-Sahara Africa and Northern Africa excluding the Sahara Desert region, Southern Europe, and South West Asia. Currently, lion are extinct in Europe and occur in only one location in India (Gir Forest National Park). They are extinct in the rest of Asia (Bauer *et al*., 2005; Bauer *et al*., 2015). One of the primary concerns in lion conservation is the availability of suitable rangeland on which lions may persist (Packer *et al*., 2013; Schuette *et al*., 2013; Ripple *et al*., 2014). Between eight and 17% of lion's historic range remains inhabited by lions, with an estimated 1.8 million km² of historic lion habitat currently without lions (Riggio *et al*., 2013; Bauer *et al*., 2015). Urban and agricultural development is projected to more than double in Africa over the next 40 years (Riggio *et al*., 2013). Human population size in Africa is expected to grow from 1.1 billion people in 2013 to 1.735 billion people in 2050 (Riggio *et al*., 2013). Many protected areas are under pressure of development as they constitute large productive tracts of land. Protected areas may thus become preferable for agricultural and urban development as anthropogenic resource requirements grow (Balmford *et al*., 2001; Bjorklund, 2003).

With the boundaries between human and lion habitat becoming increasingly contiguous, conflict between humans and lions continues to intensify (Patterson *et al*., 2004; van Vuuren *et al*., 2005; Mogensen *et al*., 2011; Schuette *et al*., 2013; Ripple *et al*., 2014; Henschel *et al*., 2014; Trinkel, 2015). Human-wildlife conflict is rapidly becoming one of the prime issues in species conservation (Lamarque *et al*., 2008; Dickman, 2010; Packer *et al*., 2013). A decrease in prey availability to lions can increase livestock losses and pose a potential threat to humans (Mills *et al*., 1978; Patterson *et al*., 2004; Bauer & de Iongh, 2005; van Vuuren *et al*., 2005; Lagendijk & Gusset, 2008; Woodroffe, 2011; Trinkel, 2015). Lions incur major losses due to retribution killing, which poses a significant threat to the persistence of lion populations (Woodroffe & Ginsberg, 1998; van Vuuren *et al*., 2005).

Lions have not only been identified as a threat, but also as a resource. Hunting has been identified as a critical application of resource utilization, aiding the wildlife industry as a whole and placing value on species and habitats not otherwise commercially viable under natural conditions (Whitman *et al*., 2007; Lindsey *et al*., 2012a; Lindsey *et al*., 2012b). Much research done on the commercial hunting of lions suggests that the responsible and scientifically guided, sustainable practice thereof is often preferable to the removal of hunting altogether (Whitman *et al*., 2007; Packer *et al*., 2009; Lindsey *et al*., 2012b; Lindsey *et al*., 2012b; Funston *et al*., 2013; Lindsey *et al*., 2013). However, the unsustainable practice of sports hunting will negatively impact population demographics, genetic integrity and viability of the affected populations (Loveridge *et al*., 2007; Marealle *et al*., 2010; Packer *et al*., 2010; Davidson *et al*., 2011; Becker *et al*., 2012; Lindsey *et al*., 2013; Snyman *et al*., 2014). This along with illegal poaching, lion bone and bush meat trade could have devastating effects on lion populations (Lindsey *et al*., 2012a; Everatt *et al*., 2014). In addition lions are also considered a major driver of non-consumptive eco-tourism (Macdonald & Sillero-zubiri, 2002), which is fundamental to the persistence of lion populations and the habitats in which they exist (Kerley & Boshoff, 1997; Hayward *et al*., 2007; Cousins *et al*., 2008; Cousins *et al*., 2010; Dickman *et al*., 2011; Minin *et al*., 2012).

With increased fragmentation of lion populations, inbreeding of small isolated populations are becoming more apparent and the genetic sustainability of isolated populations has become questionable (Bjorklund, 2003; Dubach *et al*., 2005; Miller *et al*., 2013; Dolrenry *et al*., 2014). Inbreeding in small populations may alter fecundity and survival rates, particularly under environmental stress (Bjorklund, 2003; Dolrenry *et al*., 2014). Inbreeding significantly increases the risk of local population extinction (Benson *et al*., 2011; Riggio *et al*., 2013). Out of four known sub-species of lion, only two remain extant, *Panthera leo verneyi* from Southern and Eastern Africa (Dubach *et al*., 2005) and *Panthera leo persica* from one location in Southern India (Banerjee *et al*., 2010). A third potential sub-species has been identified in a captive zoo population in Ethiopia (Bruche *et al*., 2013) and lions from West and Central Africa are genetically distinct from those of South and East Africa (Barnett *et al*., 2006b; Bertola *et al*., 2011; Barnett *et al*., 2014). Genetically, the lions of the KTP are considered indispensable for the long-term persistence of meta-populations in South Africa (Barnett *et al*., 2006a; Dolrenry *et al*., 2014). Lions from the KTP have been used for reintroduction of the species into several National Parks and private conservation areas in South Africa and Botswana, making it an important source population for meta-populations elsewhere (Antunes *et al*., 2008; Miller *et al*., 2013).

Diseases have varying effects on demographic parameters such as fecundity and mortality rates (Macdonald, 1993; Packer *et al*., 1999; Funk *et al*., 2001; Cleaveland *et al*., 2002; Dybas, 2009; Ferreira & Funston, 2010). Lions have evolved concurrently with many of the diseases for which they act as a host or vector. Some of these include Bovine Tuberculosis (BTb), Canine Distemper Virus (CDV), Feline Immunodeficiency Virus (FIV), Feline Coronavirus (FCoV), Feline Herpesvirus, (FHV-1), Feline Calicivirus (FCV), Feline Panleukopenia virus (FPLV) and Rotavirus (RV) (Alexander *et al*., 2010; Adams *et al*., 2009; Munson *et al*., 2008; Packer *et al*., 1999; Young, 1975). Some of the diseases such as FIV, FHV-1, FCV and CDV have been detected in the KTP lion population but have not been cause for major concern (Funston, 2002). Lions in general appear to be resilient to the presence of these diseases. Symptoms of disease appear to be relatively benign and most host populations show little effect on population viability, with no recorded mass deaths in Southern Africa due to disease (Alexander *et al*., 2010; Ferreira & Funston, 2010). However, in East Africa major population declines were experienced in the Serengeti and Masai Mara regions due to distemper (Roelke-Parker *et al*., 1996; Packer *et al*., 1999; Munson *et al*., 2008). Lion resilience for many of these diseases is rapidly becoming undermined through fragmentation and genetic introgression, particularly in small, isolated populations (Kissui & Packer, 2004; Adams *et al*., 2009; Ferreira & Funston, 2010; Benson *et al*., 2011).

In Sub-Sahara Africa, lions are conserved in 67 locations, in 27 countries that provide some form of statutory protection (Bauer *et al*., 2015) (Figure 1). However, lions are known to be extinct in 27 countries and thought to be extinct in a further seven countries where they occurred historically (Bauer *et al*., 2015). Only 10 of the 67 protected locations support sustainable populations of lions. These 10 locations or “Strongholds” support an estimated 24,000 out of a possible 35,000 free ranging lions that remain in Sub-Sahara Africa (Riggio *et al*., 2013; Bauer *et al*., 2015). The area within which lion currently occur naturally is only 17% (3.4 million km^2) of their historic range (Riggio *et al*., 2013). These strongholds are also restricted to the Southern and Eastern parts of Sub-Sahara Africa with few potential strongholds in the Central and Western African regions (Riggio *et al*., 2013; Bauer *et al*., 2015). The most conservative estimate of the number of lions in southern Africa was 22 000 lions, in 2002 (Chardonnet, 2002).

In the KTP, lions are an iconic species and key to tourism experiences and expectations, which increase their conservation value (Maciejewski & Kerley, 2014; Ferreira *et al*., 2013; Kerley *et al*., 2003). Lions are the apex predator in the Kalahari ecosystem and have significant effects on the ecology (Kissui & Packer, 2004; Grange & Duncan, 2006; Bauer *et al*., 2014; Mills, 2015). Hence, describing the demographic characteristics of lions in the KGNP, and identifying further trends in the demographic characteristics are important to understand the implications for lion persistence in the KGNP and greater KTP region.

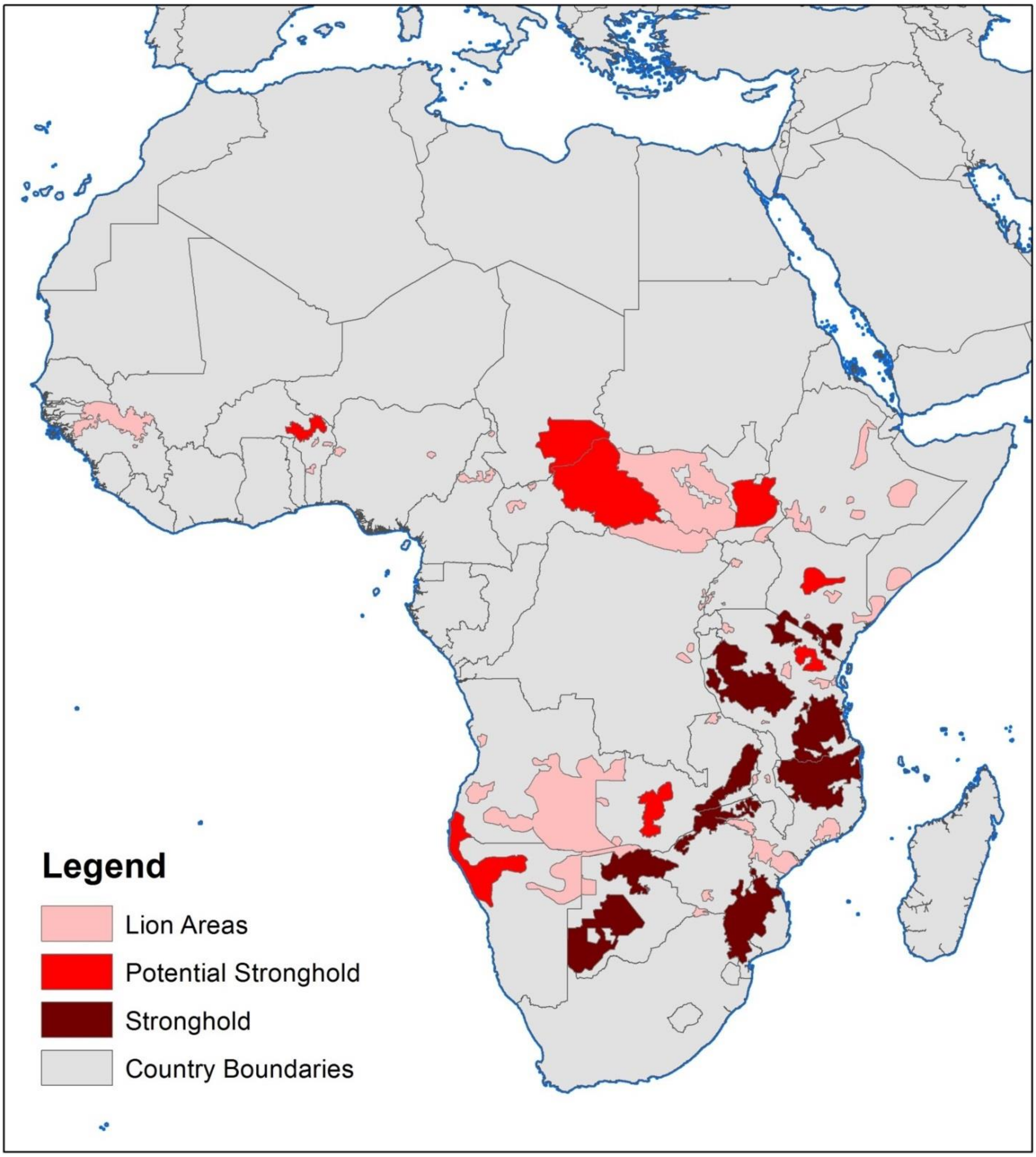

Figure 1.1 Current distribution, Lion Areas, Potential Strongholds and Strongholds for lion persistence in Africa (Bauer *et al*., 2015).

1.4. Lion demographic characteristics

A critical lack of current demographic information on the lion population of the KTP exists (Ferreira *et al*., 2013). The shift in sex structure throughout the lion population in the KTP from a female biased (Mills *et al*., 1978; Castley *et al*., 2002), to a male bias population (Funston, 2011; Ferreira *et al*., 2013), can have numerous intraspecific effects detrimental to their persistence (Ferreira *et al*., 2013). Effects such as a decline in population growth, increased resource competition among males, higher rates of coalition changeover and increased emigration of males, may exacerbate the sex skew observed in the KGNP (Packer & Pusey, 1983; van Vuuren *et al*., 2005; Funston, 2011; Ferreira *et al*., 2013). Demographic characteristics such as survival rates and fecundity are negatively impacted by an increased male presence in the population through increased competition (Woodroffe & Frank, 2005). Decreased survival rates and fecundity could lead to a decline in lion abundance in the KTP (van Vuuren *et al*., 2005).

Demographic parameters such as sex ratio, age distribution, fecundity, litter size, survivorship and mortality, as well as abundance, are fundamental to understanding populations (Ferreira & Funston, 2010; Barnett *et al*., 2014). From these, we may determine the likelihood of reproductive success and population survival (Bertram, 1975; Bertram, 1978; Ferreira & Funston, 2010; Becker *et al*., 2012). Survival and mortality are two measures by which we may discern population turnover or trends (Trimble *et al*., 2009; Ferreira *et al*., 2013). These along with fecundity are largely regulated by ecological conditions and resource restraints, which in turn are driven by rainfall (Hanby *et al*., 1995; Frank *et al*., 1998; Celesia *et al*., 2010; Trimble *et al*., 2009). Social aspects such as coalition tenure, social structure, immigration and emigration may also affect vital rates (Ferreira & Funston, 2010; Barnett *et al*., 2014).

Population growth rate and the probability of survival are dependent on female reproductive success, age, individual fitness, resource availability, competition and stochastic environmental events (Packer & Pusey, 1983; van Vuuren, *et al*., 2005; Celesia *et al*., 2010; Balme *et al*., 2012). Survivorship is expected to be lower in younger age classes, with the probability of survivorship increasing with age (Funston, 2011; Elliot *et al*., 2014). Demographic parameters determine population growth rates and their response, or resistance, to stochastic environmental events (Bjorklund, 2003; van Vuuren *et al*., 2005). Although demographic variability has a large range, certain parameters, such as adult sex ratios, fecundity and mortality rates are important to population recovery in cases of stochastic events, where numbers rapidly decline or fecundity is limited (Bjorklund, 2003; van Vuuren *et al*., 2005). Skewed sex ratios may thus have deleterious effects on local population persistence (Woodroffe & Ginsberg, 1998; Ferreira *et al*., 2013). Demographic change along with stochastic environmental effects pose a significant threat to the persistence of the small, isolated lion populations (Kissui & Packer, 2004; Hayward *et al*., 2007; Ferreira *et al*., 2013; Miller *et al*., 2013).

Despite the fact that the lion population in the KTP has access to an immense area (± 72,000 km^2) (Funston, 2002; Mudongo & Dipotso, 2011) they occur at low density, ± 1.4/100 km^2 (Ferreira *et al*., 2013). Compared to other lion populations (Table 1.1), lion density is relatively low and the KTP lion population may face many of the challenges faced by small populations (Castley *et al*., 2002). Population size is expected to change because of demographic processes such as survival rates and fecundity (Michod & Anderson, 1980). In the KGNP, four population size estimates (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2002; Ferreira *et al*., 2013) have identified a population of approximately 140 individuals. However, the four population size estimates were made using different techniques with varying accuracy and precision, which can limit comparisons (Gerrodette, 1978).

Female fecundity over a two and a half year period showed a recruitment rate of 0.67 cubs per female per year (Funston, 2011). This is somewhat lower than the birth rates in other populations, which can be as high as 2.3 cubs per female per year (Table 1.2). No conclusive survival rates dependent on age class or sex have been calculated for the lion population in the KTP. However, simulated survival parameters suggest probable survival rates during good ecological conditions to be 90% for cubs between one and two years, 95%-97% for sub-adults and 97% for adults in the KTP (van Vuuren *et al*., 2005). Observed survival rates for cubs in the KTP were 60% (Funston, 2011). However, actual survival rates are expected to be higher as this estimate was based on visual observations and many cubs may simply not have been observed, rather than have succumbed during the study period (Funston 2002; 2011).

Table 1.1 Density estimates of lion populations across several studies conducted in Africa. Density estimates were extracted from publications and presented in order of density. In some cases only the range of density estimates or approximate estimates are presented (±). 95% confidence intervals (95%CI) are presented where available. The year of estimate are also shown.

Location	Lion/100km²	95% CI	Year	Source
Masai Steppe	±0.33	--	1963	Lamprey, 1964
Kgalagadi Wildlife Management Areas	0.79	0.43-1.15	2010	Mudongo & Dipotso, 2011.
Kalahari Gemsbok National Park	1.34	1.082-1.59	1997	Kastley *et al.,* 2002
Kalahari Gemsbok National Park	1.35	0.95-1.76	2010	Ferreira *et al*., 2013
Kalahari Gemsbok National Park	1.36	1.14-1.89	1976	Mills *et al*., 1978
Kalahari Gemsbok National Park	1.41	1.15-1.34	2001	Funston, 2011
Khutse Game Resesrve	1.62-1.82	--	2008-2010	Schiess-Meier *et al*., 2014
Etosha National Park (Central)	2.5	2.1-4.4	1980-1996	Trinkel, 2013
Laikipia Game Reserve	5-6	--	2002	Woodroffe & Frank, 2005
Okavango Delta	±5.8	--	2011	Cozzi *et al*., 2013
Selous Game Reserve	±8	--	1967-1972	Rodgers, 1974
Serengeti National Park	7.9-9.4	--	1969	Schaller, 1972
Kafue National Park	±12.05	--	1963	Mitchel *et al*., 1965
Kruger National Park	±13	--	1985-1995	Funston *et al*., 2003
Kruger National Park	10.5-15.5	--	1975	Smuts, 1976
Nairobi National Park	±26.32	--	1972	Rudnai, 1973.
Ngorongoro Conservation Area	±27.03	--	1969	Schaller, 1972
Masai Mara National Reserve	20-40	--	1992	Ogutu & Dublin, 1998
Lake Manyara National Park	±40	--	1968	Makacha & Schaller, 1969

Table 1.2 Birth rates, as the number of cubs per reproductive female per year, observed across several studies of lion across their range. Birth rates are presented in descending order of the number of cubs born per reproductive female.

Location	Country	Birth Rate	Publication
Gir Bioregion	India	0.37	Banarjee & Yadvendradev, 2012
Kgalagadi Transfrontier Park	South Africa/Botswana	0.67	Funston, 2011
Etosha National Park	Namibia	0.77	Orford et al., 1988
Laikipia Game Reserve	Kenya	0.858	Woodroffe & Frank, 2005
Kruger National Park	South Africa	1	Funston *et al*., 2003
Korongwe Game Resesrve	South Africa	1.3	Lehmann *et al.,* 2008
Kgalagadi Transfrontier Park Boundary Prides	South Africa	1.33	van Vuuren *et al.,* 2005
Welgevonden Private Game Reserve	South Africa	1.9	Killian & Bothma, 2003
Makalali	South Africa	2.3	Druce *et al.,* 2004

Initial studies on lion population characteristics in the KTP were restricted to the South African Kalahari Gemsbok National Park (KGNP) (Eloff, 1980; Mills *et al*., 1978; Mills, 2015). The remaining Botswana section of the Transfrontier Park known as the Gemsbok National Park (GNP) remained un-studied until 1996, but even in that study sampling was also largely focused to the KGNP (Castley *et al*., 2002). More in depth ecological studies of lion in the broader KTP lion population was first conducted between 1998 and 2001 (Funston, 2011). Initial studies conducted were limited to certain sections of KGNP but gave some idea of sex and age structure as well as fecundity, survival and mortality rates (Mills, 1978; Eloff, 1980).

Initial observations of the KGNP lion population noted a normal relationship between males (♂) and females (♀) (1♂:1.8♀) (Mills *et al*., 1978) as determined from a subsample of 73 lions, and an extremely high mortality rate in cubs (95%) (Eloff, 1980). These studies were focused on the northern parts of the KGNP and in the case of cub survival, sample sizes were relatively low (n=16) (Eloff, 1980; Mills, 2015). Age class ratios, when considered as adult (A; > 4 years old), sub-adults (SA; 2-4 years old) and cubs (C; < 2 years old), were not excessively skewed to any age category at 1.6A:1SA:1.2C respectively (Mills *et al*., 1978). By 1996, the proportion of females increased to 1♂:2♀ as determined from a subsample of 79 lions. Females in the adult age category showed a marked increase to a ratio of 1♂:3.4♀ and adults showed majority at a ratio of 5.3A:1SA:2.1C (Castley *et al*., 2002).

In 2001 the overall sex ratio evened out somewhat to a ratio 1♂:1.2♀ (n = 216). However, the proportion of adult females stayed close to the 1:3.4 of 1996 at 1♂:3.3♀ and cub and sub-adult sex ratios skewed towards males at 2♂:1♀ and 1♂:0.8♀ respectively. This was determined to be similar to populations that experience selective adult mortality through commercial lion hunting (Yamazaki, 1996; Loveridge *et al*., 2007; Whitman *et al*., 2007; Funston, 2011). Age class structure during the same period saw a reduction in adult presence to a ratio of 3.6A:1SA:2.6C (Funston, 2011). The skew towards males in the younger age class in 2001 was attributed to high rates of coalition changeover (Funston, 2011). In 2010 sex ratios were equal in adults and skewed to males in the sub-adult age category at a ratio of 3♂:1♀ as determined from a subsample of 49 lions. However, cubs' sex ratios were undefined (Ferreira *et al*., 2013). Both adult and cub ratios showed an increase from 1996 to a ratio of 4.7A:1SA:2.7C. Survival probability of cubs showed a substantial increase from a perceived 5% survival in 1980 to 60% in 2001 (Eloff, 1980; Funston, 2011). However, this large discrepancy may well be a relic of small sample sizes and stochastic events in the 1980 study (Eloff, 1980).

Demographic variables of lions are expected to differ between prides and populations (Bauer & van der Merwe, 2004; Celesia *et al*., 2010; Ferreira *et al*., 2013). Although age and sex structures vary largely between different regions and populations the majority have sex ratios that favor females (Table 1.3). Age class structure in lions, from several populations, show greater proportions of adults (≥ 40 %) and variable proportions of sub-adults (Range: 11-31%) and cubs (Range: 10-44%) (Table 1.4).

Table 1.3 Sex ratios of lion populations from across their range presented in percentages. Overall figures are presented for the entire observed population including all age classes, whereas adult figures are presented for individuals older than four years.

	Overall		**Adult (> 4 yrs)**		
Location	**Male**	**Female**	**Male**	**Female**	**Source**
Etosha National Park	32	68	28	72	Trinkel, 2013
Gir bioregion	39	61	--	--	Banarjee & Yadvendradev, 2012
Kalahari Gemsbok National Park	37	63	32	67	Mills *et al.,* 1978
Kalahari Gemsbok National Park	24	76	23	77	Castley *et al*., 2002
Kalahari Gemsbok National Park	56	44	50	50	Ferreira *et al*., 2013
Kgalagadi Transfrontier Park	43	57	24	76	Funston, 2011
Kgalagadi Wildlife Management Areas	65	35	61	39	Mudongu & Dipotso, 2011.
Kruger National Park	40	60	33	67	Smuts, 1978
Kruger National Park (1989)	--	--	31	69	Mills, 1995
Kruger National Park (1993)	--	--	48	52	Mills, 1996
Kruger National Park	43	57	40	60	Funston *et al*., 2003
Luangwa Game Reserve	--	--	34	66	Yamazaki, 1996
Selous Game Reserve	18	82	43	57	Caro *et al.,* 2009

Table 1.4 Age class structure observed in several different studies. Observations are presented in percentages.

	Age Class Structure (%)			
Location	**Adult (> 4 yrs)**	**Sub-adult (2-4 yrs)**	**Cubs & Juvenile (< 2 yrs)**	**Source**
Etosha National Park (1985)	51	11	26	Trinkel, 2013
Etosha National Park (1996)	41	14	44	Trinkel, 2013
Gir Bioregion	55	19	25	Banarjee & Yadvendradev, 2012
Kalahari Gemsbok National Park	40	24	36	Mills *et al.,* 1978
Kalahari Gemsbok National Park	65	13	23	Castley *et al.,* 2002
Kalahari Gemsbok National Park	65	24	10	Ferreira *et al.,* 2013
Kgalagadi Transfrontier Park	49	23	27	Funston, 2011
Kgalagadi Game Management Areas	69	31	0	Mudongo & Dipotso, 2011.
Kruger National Park	58	19	24	Smuts, 1978
Kruger National Park	72	14	14	Mills, 1995
Kruger National Park	56	23	21	Funston et al., 2003

1.5. Possible causes of change in demographic signals

The study conducted in 2010 (Ferreira *et al*., 2013), which identified the sex skew toward a greater proportion of males, postulated that changes in prey dynamics in the KTP may influence sex ratios and age structure in the population. The Trivers and Willard hypothesis, which pertains to these interactions suggests, that females skew offspring sex ratios towards the offspring of a certain sex, which will in future procreate with maximum success (Trivers & Willard, 1973). Sex ratio bias of males has been observed when male cooperation increased the success of mate acquisition and mating success in lions of the Serengeti National Park and Ngorongoro National Park (Packer & Pusey, 1987; Yamazaki, 1996). Bias of sex ratios toward a greater proportion of males is found primarily in populations where high rates of coalition changeovers occur and where there is increased competition over limited females and resources (Packer & Pusey, 1987; Yamazaki, 1996; Díaz-muñoz *et al*., 2014). Although lions are social, fission-fusion among social groups may have a higher occurrence in regions with low prey biomass and low lion population densities (Schaller, 1972; Bertram, 1975; East, 1984; De Bie, 1991; Packer *et al*., 2005).

Improved body condition in vertebrates primarily promote an increase in male offspring (Trivers & Willard, 1973; Allainé *et al*., 2000; Burke & Birch, 1995; Brown & Silk, 2002; Sheldon & West, 2004; Navara *et al*., 2010; Sogbohossou *et al*., 2014) but may also skew to females such as the case in springbok (*Antidorcas marsupialis*) (Radford *et al*., 2005). Changes in prey abundance, prey residency and consequent habitat utilization have an effect on lion body condition and this can in turn influence sex ratios (Trivers and Willard, 1973; Hanby & Bygot, 1979; van Orsdol *et al*., 1985; Celesia *et al*., 2010; Ferreira & Funston, 2010). In the KTP, prey availability may not only change in response to natural environmental fluctuations, such as rainfall (Mills *et al*., 1995; Scheffer *et al*., 2001) but also in response to anthropogenic influences such as the supply of artificial water sources and fences (Suding *et al*., 2004). The artificial restrictions of fences (Hayward & Kerley, 2008) and the supplementation of water in the KTP could influence prey dynamics (Knight, 1995), which in turn could affect the body condition of lions (Mills, 1995; Ferreira & Funston, 2010) and consequently, demographic parameters (Trivers & Willard, 1973; Mills, 1995; Cameron, 2004)

Lion home ranges cover large areas in the KTP (2823 ± 498km^2) (Funston, 2011) which may facilitate loose territoriality and higher rates of male coalition takeover events (Packer & Pusey, 1983; Pusey & Packer, 1987; Bauer *et al*., 2003; Funston, 2011). Infanticide is a frequent occurrence after coalition takeover events (Bertram, 1975; Packer & Pusey, 1983; Packer *et al*., 2001; Lindsey *et al*., 2012a). Although the physiological mechanism remain poorly understood, where coalition changeover and subsequent infanticide occur, the majority of the first generation offspring sired by the new male occupants are biased toward males (Packer & Pusey, 1982; Packer & Pusey, 1987; Yamazaki, 1996). Subsequent generations were found to be closer to parity at birth (Packer and Pusey, 1987).

The association of poor resource availability and the fission-fusion nature of low-density lion populations may lead to high rates of coalition changeover, infanticide and consequentially an increased production of males (Bertram, 1975; Packer and Pusey, 1984; McComb *et al*., 1994; Packer *et al*., 2005; Packer *et al*., 2001; Funston, 2011). Similar effects have been observed in populations that experience commercial hunting. Where hunting occurs, adult males incur the greatest losses due to the trophy value of males, which exhibit greater size, display large manes as a dimorphic feature and are thus more desirable as a trophy specimen (Lindsey *et al*., 2012). In these populations, pride males removed through hunting allow new males to take over a pride, often killing cubs, and subsequently cub sex ratios favoured males (69%) (Woodroffe & Frank, 2005; Loveridge *et al*., 2007).

Increased survival rates of infants and juveniles have also shown to increase the proportion of males in a population (Allainé *et al*., 2000; Becker *et al*., 2012). It may be expected that males have lower survival rates from sub-adulthood where intra species conflict occurs (Elliot *et al*., 2014). Although there is less intra-species conflict in infants and juveniles, males may have higher energy requirements and their survival is more resource dependent (Ferreira & Funston, 2010). This may lead to higher rates of mortality in male cubs and juveniles under poor ecological conditions. Good ecological conditions or large cohorts of cubs may increase their survival and therefore their proportional ratios in a population (Pusey & Packer, 1987). Fission-fusion social structures may delay dispersal in male sub-adults which may also increase male survival (Elliot *et al*., 2014)

It was postulated that the disproportionate number of male cubs observed in the KTP between 1998 and 2001 might be a “compensation mechanism” for the higher mortality rate in dispersing males; however, the physiological mechanism is not described. Where individuals are born near the boundary of the park, males and females are equally probable to transgress (van Vuuren *et al*., 2005; Funston, 2011). However, females are philopatric and mostly remain in their natal prides, whereas all males emigrate from their natal prides (Pusey & Packer, 1984; Hanby & Bygott, 1987; Hanby *et al*., 1995; Elliot *et al*., 2014). Dispersing males may travel as far as 120 km before establishing their own territory (van Vuuren *et al*, 2005; Funston, 2011). In many instances males are forced to leave the park in search of a new territory and a sustainable resource supply, which may ultimately lead to their demise (van Vuuren *et al*, 2005; Funston, 2011).

Changes in parameters such as immigration, dispersal, coalition change and social interaction may also cause changes in age specific sex ratios (Packer and Pusey, 1987; Ferreira *et al*., 2013). Responses to human-lion conflict can change these parameters and may alter demographic composition and intra-species interactions (Mills *et al*., 1978; van Vuuren *et al*., 2005; Ferreira *et al*., 2013; Sogbohossou *et al*., 2014; Daigle *et al*., 2015).
Lions in KTP come into conflict with commercial livestock farmers on all the boundaries of the park, mostly in the south and south-west of the park where livestock farming are the primary commercial enterprises (van Vuuren *et al*., 2005). Lion demographic profiles may be altered through retribution killing and management actions in response to transgressing lions (van Vuuren *et al*., 2005; Funston, 2011; Ferreira *et al*., 2013; Everatt *et al*., 2014;). Management protocols often effect ecological interactions without appropriate cognisance of the repercussions (Funston, 2002; Sogbohossou *et al*., 2014; Daigle *et al*., 2015). These often have opposing results from conservation and biodiversity objectives (Chauvenet *et al*., 2011; Ferreira *et al*., 2013; Trinkel, 2013). Lions, which transgress the park boundary, whether fenced or unfenced, are often subject to retribution killing in response to livestock losses (Funston, 2002; Ferreira *et al*., 2013). Landowners not as prone to reprisals contact conservationists who, according to protocol, retrieve the lion or lions and translocate them back into the park interior (Funston, 2002).

Transgressing lions, which are relocated into the interior of the park, are often placed within the territories of non-associated prides (Pers. Obs. 2013-2015). The outcomes of interactions between resident and relocated lions in the KGNP have not been recorded, but may result in conflict, particularly between males. Such conflict may lead to coalition changeovers, infanticide and consequences in sex and age structures (Pusey & Packer, 1987; Yamazaki, 1996). Furthermore, there may be consequences for survival and dispersal (Massei *et al*., 2010). Lions have the ability to move over large distances and despite translocation have been known to relocate their prides, and become habitual transgressors (Funston, 2002; Pers. Obs. 2013-2015). Despite efforts by conservationists to mitigate human-lion conflict, translocations may not be successful, but rather influence not only the transgressing lion negatively, but also resident lions, which are exposed to transgressors (Massei *et al*., 2010).

Although several factors can cause changes in demographic parameters and population size, it is important to have robust estimates of population characteristics from which to measure change over time (Gerrodette, 1978; Woodroffe & Ginsberg, 1998). Accurate and precise estimates of population characteristics provide the basis from which inferences can be made with relation to potential drivers of lion demographics. Attaining robust estimates are a function of methodological ability to measure a representative sample from which conclusions can be derived

1.6. Methods used to determine demographic characteristics and population size

In cryptic carnivores, such as lions, individual registration (individual identification) is commonly used to determine demographic characteristics, where individuals are discerned from each other through the identification of unique marks on the animal (Pearl, 2000). These markers may be natural, such as spot patterning on leopard coats (*Panthera pardus*) (Balme *et al*., 2009), or may be more discrete and difficult to discern, such as whisker spot patterns in lion (Pennycuick & Rudnai, 1970), as well as scarring, ear knicks and nose pigmentation (Whitman & Packer, 2006). Discernible patterns brand marked onto individuals, by the use of heated iron brands (Stander, 1992; Castley *et al*., 2002), and genetic markers from DNA extracted from faecal samples (Tende *et al*., 2014) have also been used to identify individuals. Radio telemetry or Global Positioning System collars are used to track individual life histories of collared individuals and their associated prides (Woodroffe & Frank, 2005; Loveridge *et al*., 2007; Funston, 2011).

The total or mean population characteristics, such as age and sex structures, are determined from a sample of the population and described as point estimates in time at the end of a study period (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011; Ferreira *et al*., 2013). To derive other demographic characteristics such as fecundity, survival, mortality, immigration and emigration, observations of individuals are required over a longer period to capture life history patterns (Banerjee *et al*., 2010; Funston, 2011; Barthold *et al*., 2016). Life history patterns, such as survival probability, are often simulated in computer programs to identify variability between different age and sex structures (White & Burnham, 1997; Zheng *et al*., 2007; Grosbois *et al*., 2009). Factors such as birth rates and mortality rates are used to define population growth (Lebreton *et al*., 1993; Pradel, 1996), assess extinction risks (van Vuuren *et al*., 2005; Woodroffe & Frank, 2005) and define evolutionary processes (Cam, 2009).

Registration studies have been used to enumerate lion populations (Pennycuick & Rudnai, 1970; Stander, 1991; Mosser & Packer, 2009). However, results come at great expense, particularly when counting cryptic carnivores in vast areas (Balme *et al*., 2009). Registration studies often only describes the minimum-known-alive number in the population, which predominantly provides an underestimation (Efford, 1992), and are often used in conjunction with other methods (Owen-Smith, 1990; Woodroffe & Frank, 2005; Morley & van Aarde, 2007). Mark-recapture (or capture-mark-recapture) techniques are among the most common in determining population size estimates of wildlife (Cam, 2009), and are achieved by the registration of a portion of the sample population through either natural (Fearnbach *et al*., 2012; Bolger *et al*., 2012; Bonner & Holmberg, 2013) or unnatural (Mills *et al*., 1978; Castley *et al*., 2002) marking of individuals. The relative proportional difference between marked and unmarked individuals at discrete capture events are analysed statistically, as according to the Lincoln-Peterson index (Pollock, 1991), and an estimate of population size is derived. Mark-recapture techniques have developed into having very specific applications, depending on the objective, whether to derive estimates of population growth, survival, capture probability or abundance (Cooch & White, 2015). Abundance estimates no longer only account for proportional differences between marked and unmarked animals in a sampled population, but have evolved to account for detection and survival probability based on life history data (Barker & White, 2004; Morrison *et al*., 2011; Cooch & White, 2015). Mark-recapture techniques are considered as a reliable method when the correct models are applied and the assumptions, under which the method is applied, are not violated (Morley & van Aarde, 2007; Cooch & White, 2015) and can be very precise (Schwarz *et al*., 1999). In the KGNP, two population size estimates have been conducted using mark-recapture estimates, the first using the Lincoln Index (Mills *et al*., 1978) and the second, the Lincoln-Peterson estimator (Castley *et al*., 2002).

Indices of animal abundance or density have been used successfully to track changes over time (Stephens *et al*., 2006), particularly when direct observations are limited by resource constraints or the detection probability of the study subject (Balme *et al*., 2009). Track indices for instance, have been calculated as the relationship between known density of animals in an area and the relative density of tracks (spoor) along a transect (Stander, 1998). The concept of track indices relies on the probability that a fixed amount of effort will result in an expected retrieval of signs that are representative of the population (Schwarz *et al*., 1999). For lion populations, a strong relationship exists between the track density (n/100 km) and lion density (n/100 km^2) (Stander, 1998; Funston, 2002; Balme *et al*., 2009; Funston *et al*., 2010). The relationship between track and actual density has been calibrated in various environments, for various substrates (Funston *et al*., 2010) and for a variety of species (Stander, 1998; Funston, 2002; Balme *et al*., 2009; Funston *et al*., 2010). In the KTP and KGNP, track density has been directly calibrated to lion density derived from density estimates of registered individuals, in known prides, within known home ranges (Funston, 2002; Funston *et al*., 2010). Less commonly used indices, particularly in defining lion population variables, are of signs such as scat, den sites and overlaps in home ranges between territorial groups (Pearl, 2000).

Other indices based on occupancy, use camera trapping to identify the presence or absence of animals as the relative abundance of a species, or the presence or absence of unique individuals from which mark-recapture estimates can be derived (Maputla *et al*., 2013; Gutierrez-Gonzalez *et al*., 2012; Rowcliffe & Carbone, 2008). Camera trap base surveys often rely on individual identification to attain accurate and precise estimates of density or abundance, and in the case of lions, would require branding individuals to mark them, as features such as whisker spot patterns are not easily identifiable from camera traps (Cozzi *et al*., 2013; Kane *et al*., 2015). Camera trapping is capable of determining occupancy or species richness but the method is seldom used to determine population size estimates due to the challenges in individual identification (Everatt *et al*., 2014; Hatfield, 2014).

Call-up (or call-in/lure counts) stations are a relatively inexpensive method to determine lion density (Cozzi *et al*., 2013) and have been used to attain density estimates (Groom *et al*., 2014; Omoya *et al*., 2013; Ferreira & Funston, 2010b) through attracting lions to a sound stimulus of a distressing prey species or conspecific competitor (Cozzi *et al*., 2013). Call-ups have been used in previous studies in the KGNP for mark-recapture purposes, to derive age and sex structure (Ferreira *et al*., 2013; Funston, 2002) and to determine density in the Wildlife Management Areas (WMA) bordering the KTP to the east and north of the park. Density estimates in the WMA's have proved to be relatively inaccurate in comparison to other techniques (Mudongo & Dipotso, 2011). Call-ups in arid areas are limited by low lion density with a poor return rate except where call-ups are conducted at locations where fresh lion tracks have been found(Ferreira *et al*., 2013; Mudongo & Dipotso, 2011). Furthermore, call-up's are subject to high seasonal and spatial variability, have large margins of error in comparison to other methods (Mudongo & Dipotso, 2011; Cozzi *et al*., 2013) and require further development to account for some bias in the method (Young-Overton *et al*., 2014).

Several assumptions must be met when deriving estimates of population characteristics (Schwarz *et al*., 1999; Franklin & Walker, 2010). These assumptions may be related to behavioural responses, consistencies in capture or survival probabilities and may be related to resource restraints or environmental fluctuations (Schwarz *et al*., 1999; Pearl, 2000). These assumptions limit the different techniques in their abilities to accurately represent the population in their estimates, and limit the precision with which estimates may be derived (Krebs, 1999; Schwarz *et al*., 1999). To enable conservationists to respond to changes in species characteristics and in the environment, the methods that are applied to describe the population need to be robust (accurate and precise) in both design and analysis (Barker & White, 2004; Eberhardt, 2007) as well as cost effective (Midlane *et al.,* 2015). Robust estimates will detect changes over time (Gerrodette, 1978), which will guide conservationists in their decisions which will either benefit, or be to the detriment of their charge (Parrott, 2011; Cushman *et al*., 2015).

1.7. Objectives of this thesis

The primary aim of this thesis was to define lion population characteristics within the study area by determining the population size, as well as the age- and sex-structures, so that vital rates can be derived and changes in population characteristics over time can be determined. The four primary objectives were:

1. To determine the population size of lions in the KGNP.
2. To determine which methods are best suited to estimate lion abundances in the KGNP?
3. To determine the demographic characteristics of the lion population in the KGNP.
4. To determine whether the lion population size and demographic characteristics have changed over time.

1.8. Structure of the thesis

This thesis is comprised of five chapters. Chapters 3 and 4 have been compiled as independent manuscripts to facilitate publication in peer-reviewed journals.

Chapter 2 describes the study area with consideration of the attributes that determine lion presence, abundance and demographic characteristics.

Chapter 3 is focussed on determining the population size of lions in the KGNP by means of various methodological approaches. Here the relative accuracy and precision of various applied and indirect methods are measured, including the effort required to detect robust demographic characteristics.

Chapter 4 is concerned with defining the demographic characteristics of the lion population in the KGNP through direct observations and modelling techniques.

Chapter 5 is a combined data and synthesis chapter concerned with determining the change in demographic characteristics and population size over time. Historic studies and the current study are compared, and the ability to detect trends over time with the available information is analysed.

1.9. References

Abell, J., Kirzinger, M.W.B., Gordon, Y., Kirk, J., Kokeŝ, R., Lynas, K., Mandinyenya, B. & Youldon, D. 2013. A social network analysis of social cohesion in a constructed pride: Implications for ex situ reintroduction of the African Lion (*Panthera leo*). *PLoS ONE*, 8(12): 1–11.

Adams, H., van Vuuren, M., Bosman, a-M., Keet, D., New, J. & Kennedy, M. 2009. The epidemiology of lion lentivirus infection among a population of free-ranging lions (*Panthera leo*) in the Kruger National Park, South Africa. *Journal of the South African Veterinary Association*, 80(3): 151–156.

Alexander, K. a., McNutt, J.W., Briggs, M.B., Standers, P.E., Funston, P., Hemson, G., Keet, D. & van Vuuren, M. 2010. Multi-host pathogens and carnivore management in southern Africa. *Comparative Immunology, Microbiology and Infectious Diseases*, 33(3): 249–265.

Allainé, D., Brondex, F., Graziani, L. & Coulon, J. 2000. Male-biased sex ratio in litters of Alpine marmots supports the helper repayment hypothesis. *Behavioral Ecology*, 11(5): 507–514.

Antunes, A., Troyer, J.L., Roelke, M.E., Pecon-Slattery, J., Packer, C., Winterbach, C., Winterbach, H., Hemson, G., Frank, L., Stander, P., Siefert, L., Driciru, M., Funston, P.J., Alexander, K. a., Prager, K.C., Mills, G., Wildt, D., Bush, M., O'Brien, S.J. & Johnson, W.E. 2008. The evolutionary dynamics of the lion *Panthera leo* revealed by host and viral population genomics. *PLoS Genetics*, 4(11): 1–11.

Balme, G. a., Hunter, L.T.B. & Slotow, R. 2009. Evaluating Methods for Counting Cryptic Carnivores. *Journal of Wildlife Management*, 73(3): 433–441.

Balme, G.A., Batchelor, A., Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D.W. & Hunter, L.T., 2013. Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes.*Mammal Review*, *43*(3), pp.221-237.

Balmford, A., Moore, J.L. & Brooks, T. 2001. Conservation Conflicts Across Africa. *Science*, 291(1): 2616–2619.

Banerjee, K. and Jhala, Y.V., 2012. Demographic parameters of endangered Asiatic lions (*Panthera leo* persica) in Gir Forests, India. *Journal of Mammalogy*, 93(6): 1420-1430.

Banerjee, K., Jhala, Y. V. & Pathak, B. 2010. Demographic structure and abundance of Asiatic lions *Panthera leo persica* in Girnar Wildlife Sanctuary, Gujarat, India. *Oryx*, 44(2): 248.

Barker, R.J. & White, G.C. 2004. Towards the mother of all models : customised construction of the mark–recapture likelihood function. *Animal Biodiversity and Conservation*, 1(1): 177–185.

Barnett, R., Yamaguchi, N., Barnes, I. & Cooper, A., 2006a. Lost populations and preserving genetic diversity in the lion *Panthera leo*: Implications for its ex situ conservation. *Conservation Genetics*, *7*(4): 507-514.

Barnett, R., Yamaguchi, N., Barnes, I. & Cooper, A. 2006b. The origin, current diversity and future conservation of the modern lion (*Panthera leo*). *Proceedings of the Royal Society of London B, Biological Sciences*, 273(1598): 2119–2125.

Barnett, R., Yamaguchi, N., Shapiro, B., Ho, S.Y.W., Barnes, I., Sabin, R., Werdelin, L., Cuisin, J. & Larson, G. 2014. Revealing the maternal demographic history of *Panthera leo* using ancient DNA and a spatially explicit genealogical analysis. *Evolutionary Biology*, 14(1): 70.

Barthold, J.A., Loveridge, A.J., Macdonald, D.W., Packer, C. & Colchero, F. 2016. Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, 53: 295–304.

Bauer, D., Schiess-meier, M., Mills, D.R. & Gusset, M. 2014. Using spoor and prey counts to determine temporal and spatial variation in lion (*Panthera leo*) density. *Canadian Journal of Zoology*, 92: 97–104.

Bauer, H., Chardonnet, P. & Nowell, K. 2005. Status and distribution of lion (*Panthera leo*) in East and Southern Africa. *East and Southern African Lion Conservation Workshop, January 2006, Johannesburg, South Africa*: pp28.

Bauer, H. & Iongh, H.H. 2005. Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, 43(3): 208–214.

Bauer, H. & Merwe, S. Van Der. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, 38(1): 26–31.

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2015. *Panthera leo. The IUCN Red List of Threatened Species 2015: e.T15951A50658092.*

Becker, M.S., Watson, F.G., Droge, E., Leigh, K., Carlson, R.S. and Carlson, A.A., 2013. Estimating past and future male loss in three Zambian lion populations. *The Journal of Wildlife Management*, 77(1):128-142.

Bekoff, M., Daniels, T.J. & Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics*, 15(1984): 191–232.

Benson, J.F., Hostetler, J.A., Onorato, D.P., Johnson, W.E., Roelke, M.E., O'Brien, S.J., Jansen, D. & Oli, M.K., 2011. Intentional genetic introgression influences survival of adults and subadults in a small, inbred felid population. *Journal of Animal Ecology*, *80*(5): 958-967.

Bertola, L.D., Hooft, W.F. Van, Vrieling, K. & Weerd, D.R. Uit De. 2011. Genetic diversity , evolutionary history and implications for conservation of the lion (*Panthera leo*) in West and Central Africa. *Journal of Biogeography*, 38: 1356–1367.

Bertram BCR. 1978. Lion population regulation. *East African Wildlife Journal*, 11: 215–225.

Bjorklund, M. 2003. The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics*, 4: 515–523.

Blanchard, D.C. 2010. Of lion manes and human beards: Some unusual effects of the interaction between aggression and sociality. *Frontiers in behavioral neuroscience*, 3: 45–52.

Bolger, D.T., Morrison, T.A., Vance, B., Lee, D. & Farid, H. 2012. A computer-assisted system for photographic mark–recapture analysis. *Methods in Ecology and Evolution*, 3(5): 813–822.

Bonner, S. & Holmberg, J. 2013. Mark-Recapture with multiple non-invasive marks. *Biometrics,* 69(3): 766-775.

Brown, G.R. & Silk, J.B. 2002. Reconsidering the null hypothesis : Is maternal rank associated with birth sex ratios in primate groups? *PNAS*, 99(17): 11252–11255.

Bruche, S., Gusset, M., Lippold, S., Barnett, R., Eulenberger, K., Junhold, J., Driscoll, C.A. & Hofreiter, M. 2013. A genetically distinct lion (*Panthera leo*) population from Ethiopia. *European Journal of Wildlife Research*, 59(2): 215–225.

Burke, R.L. & Birch, J.M. 1995. White-tailed deer vary offspring sex-ratio according to maternal condition and age. *Ecological Research*, 10: 351–357.

Bygott, J.D., Bertram, B.C.R. & Hanby, J.P., 1979. 1979. Male lions in large coalitions gain reproductive advantages. *Nature*, 282: 839–841.

Cam, E. 2009. Contribution of capture-mark-recapture modeling to studies of evolution by natural selection, in D.L. Thomson *et al*. *(eds.), Modeling demographic processes in marked populations, Environmental and Ecological Statistics 3,* Springer US: 83-129.

Cameron, E.Z., 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271(1549):1723-1728.

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 using a capture–recapture survey. *African Zoology*, 37(1): 27–34.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48(1): 58–71.

Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA: pp21.

Chauvenet, A.L.M., Durant, S.M., Hilborn, R. & Pettorelli, N. 2011. Unintended consequences of conservation actions: Managing disease in complex ecosystems. *PLoS ONE*, 6(12): e28671.

Cleaveland, S., Hess, G.R., Dobson, A.P., Laurenson, M.K., McCallum, H.I., Roberts, M.G. & Woodroffe, R. 2002. The role of pathogens in biological conservation. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds). In The Ecology of Wildlife Diseases. Oxford University Press, Oxford, UK: 139–150.

Cooch, E.G. & White, G.C. 2015. Program MARK - A Gentle Introduction (14th edition). *University of Collorado and Cornell University,* USA: 1067.

Cousins, J.A., Sadler, J.P. & Evans, J. 2008. Exploring the Role of Private Wildlife Ranching as a Conservation Tool in South Africa : Stakeholder Perspectives. *Ecology and Society*, 13(2): 43.

Cousins, J.A., Sadler, J.P. & Evans, J., 2010. The challenge of regulating private wildlife ranches for conservation in South Africa. *Ecology and Society*, *15*(2): 28.

Cozzi, G., Broekhuis, F., Mcnutt, J.W. & Schmid, B. 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity Conservation*, 22(12): 2937–2956.

Cushman, S.A., Elliot, N.B., Macdonald, D.W. & Loveridge, A.J. 2015. A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecology*: 1-17

Daigle, C.L., Brown, J.L., Carlstead, K. & Pukazhenthi, B. 2015. Multi-institutional survey of social , management , husbandry and environmental factors for the SSP African lion *Panthera leo* population : examining the effects of a breeding moratorium in relation. *International Zoo Yearbook*, 49: 1–16.

Davidson, Z., Valeix, M., Loveridge, A.J., Madzikanda, H. & Macdonald, D.W. 2011. Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation*, 144(1): 114–121.

Díaz-muñoz, S.L., Duval, E.H., Krakauer, A.H. & Lacey, E.A. 2014. Cooperating to compete : altruism , sexual selection and causes of male reproductive cooperation. *Animal Behaviour*, 88(1): 67–78.

Dickman, A.J., 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal conservation*, *13*(5): 458-466.

Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. 2011. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *PNAS*, 108(34): 13937–13944.

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R.S. & Frank, L., 2014. A metapopulation approach to African lion (*Panthera leo*) conservation. *PloS one*, *9*(2): e88081.

Dubach, J., Patterson, B.D., Briggs, M.B., Venzke, K., Flamand, J., Stander, P., Scheepers, L. & Kays, R.W. 2005. Molecular genetic variation across the southern and eastern geographic ranges of the African lion , *Panthera leo*. *Conservation Genetics*, 6: 15–24.

Dybas, C.L. 2009. Infectious diseases subdue Serengeti lions. *Bioscience*, 59: 8–13.

Eberhardt, L.L. 2007. *A Course in Quantitative Ecology*.

Efford, M. 1992. Revised estimates of the bias in the 'minimum number alive' estimator. *Canadian Journal of Zoology*, 70(3): 628–631.

Elliot, N.B., Valeix, M., Macdonald, D.W. & Loveridge, A.J. 2014. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, 123(9): 1049–1056.

Eloff, F.C. 1980. Cub mortality in the Kalahari Lion *Panthera leo vernayi* (Roberts, 1948). *Koedoe*. 23(1): 163–170.

Eloff, F.C. 1998. The life of the Kalahari lion (*Panthera leo vernayi*). *Transactions of the Royal Society of South Africa*, 53: 267–269.

Everatt, K.T., Andresen, L. & Somers, M.J. 2014. Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PLoS ONE*, 9(6): p.e99389.

Fearnbach, H., Durban, J. & Parsons, K. 2012. Photographic mark–recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications*, 22(5): 1689–1700.

Ferreira, S. & Funston, P.J. 2010. Age assignment to individual African lions. *South African Journal of Wildlife Research*, 40(1): 1–9.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables : prey and disease effects in Kruger National Park , South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Frank, D.A., Mcnaughton, S.J. & Tracy, B.F. 1998. The ecology of the Earth's grazing ecosystems. *Bioscience*, 48(7): 513–521.

Franklin, S. & Walker, C. 2010. *Survey Methods and Practices* F.S. & W.C., (eds). Statistics Canada, Ottawa, Ontario, Canada K1A 0T6, (12): pp408.

Funk, S.M., Fiorello, C.V., Cleaveland, S. & Gompper, M.E. 2001. The role of disease in carnivore ecology and conservation. In: Gittleman JL, Funk SM, Macdonald DW,Wayne RK (*eds*) , Cambridge University Press, Cambridge, UK. In *Carnivore Conservation*. 443–466.

Funston, P.J. 2002. *Kalahari Transfrontier Lion Project: Executive Report*. Endangered Wildlife Trust, Upington. South Africa: pp236.

Funston, P.J. 2011. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41(1): 1–10.

Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A. & Ferreira, S.M. 2010. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281(1): 56–65.

Funston, P.J., Groom, R.J. & Lindsey, P.A. 2013. Insights into the Management of Large Carnivores for Profitable Wildlife-Based Land Uses in African Savannas. *PLoS ONE*, 8(3): e59044.

Funston, P.J. & Mills, M.G.L. 2006. The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *South African Journal of Wildlife Research*, 36(1): 9–22.

Funston, P.J., Mills, M.G.L., Richardson, P.R.K. & van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology*, 259(2): 131–142.

Grange, S. & Duncan, P. 2006. Bottom-up and top-down processes in African ungulate communities : resources and predation acting on the relative abundance of zebra and grazing bovids. *Ecography*, 29: 899–907.

Gerrodette, T.I.M. 1978. A power analysis for detecting trends. *Ecology*, 68(5): 1364–1372.

Grosbois, V., Harris, M.P., Anker Nilssen, T., McCleery, R.H., Shaw, D.N., Morgan, B.J.T. & Gimenez, O. 2009. Modeling survival at multi-population scales using mark–recapture data. *Ecology*, 90(10): 2922–2932.

Hanby, J.P., Bygott, J.D. & Packer, C. 1995. *Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro crater and the Serengeti plains*. A.R.E. Sinclair & P. Arcese, (eds). In Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. The University of Chicago Press: 315–331.

Hatfield, R. 2014. Population dynamics of the African lion (*Panthera leo*) within the Maasai Mara region of southern Kenya. *Kaleidoscope*, 11(1): 70.

Hayward, M.W., Adendorff, J., Brien, J.O., Sholto-Douglas, A., Bissett, C., Moolman, L.C., Bean, P., Fogarty, A., Howarth, D., Slater, R. & Kerley, G.I.H. 2007. The reintroduction of large carnivores to the Eastern Cape , South Africa : an assessment. *Oryx*, 41(2): 205–214.

Hayward, M.W. & Kerley, G.I.H. 2008. Fencing for conservation : Restriction of evolutionary potential or a riposte to threatening processes ? *Biological Conservation*, 142(1): 1–13.

Henschel, P., Bauer, H., Sogbohoussou, E. & Nowell, K. 2015. *Panthera leo* (West Africa subpopulation). *The IUCN Red List of Threatened Species 2015:e.T68933833A54067639.*

Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., MacDonald, D., Saidu, Y. & Hunter, L.T.B. 2014. The lion in West Africa is critically endangered. *PLoS ONE*, 9(1): e83500.

IUCN SSC Cat Specialist Group. 2006. *Regional Conservation Strategy for the Lion (Panthera leo) in Eastern and Southern Africa*.

Kane, M.D., Morin, D.J. & Kelly, M.J. 2015. Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation*, 24(14): 3527-3541

Kerley, G. & Boshoff, A. 1997. A proposal for Greater Addo National Park: A Regional and National Conservation and Development Opportunity. *Report No. 17. Terrestrial Ecology Research Unit, Department of Zoology, University of Port Elizabeth. South Africa. Pp. 61.*

Kerley, G.I.H., Pressey, R.L. & Cowling, R.M. 2003. Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot , South Africa. *Biological Conservation* 112(1): 169–190.

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*, *Biological Sciences*. 271(1550): 1867–1874.

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33(4): 377–394.

Krebs, C.J. 1999. *Ecological methodology* (Vol.620). Menlo Park, California: Benjamin/Cummings.

Lagendijk, D.D.G. & Gusset, M. 2008. Human–carnivore coexistence on communal land bordering the greater Kruger area , South Africa. *Environmental Management*, 42(6): 971–976.

Lamarque, F., Anderson, J., Chardonnet, P., Fergusson, R., Lagrange, M., Osei-Owusu, Y., Bakker, L., Belemsobgo, U., Beytell, B., Boulet, H., Soto, B. & Tabi Tako-Eta, P. 2008. Human-wildlife conflict in Africa: An overview of causes, consequences and management strategies. Working Paper. *International Foundation for the Conservation of Wildlife, Food and Agriculture Orginisation of the United Nations*, Rome (February 2008): Pp.81.

Lamprey, H.F., 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *African Journal of Ecology*, 2(1): 1-46.

Lebreton, J., Pradel, R. & Clobert, J. 1993. The statistical analysis of survival in animal populations. *Tree*, 8(3): 91–94.

Lehmann, M.B., Funston, P.J., Owen, C.R. & Slotow, R. 2008. Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, 43(2): 230–236.

Lindsey, P., Alexander, R., Balme, G., Midlane, N. & Craig, J. 2012. Possible relationships between the South African captive-bred lion hunting industry and the hunting and conservation of lions elsewhere. *South African Journal of Wildlife Research*, 42(1): 11–22.

Midlane, N., O’Riain, M.J., Balme, G.A. and Hunter, L.T., 2015. To track or to call: comparing methods for estimating population abundance of African lions Panthera leo in Kafue National Park. *Biodiversity and Conservation*, *24*(6): 1311-1327.

Lindsey, P.A., Balme, G.A., Booth, V.R. & Midlane, N. 2012. The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. *PLoS ONE*, 7(1): e29332.

Lindsey, P.A., Balme, G.A., Funston, P., Henschel, P., Hunter, L., Madzikanda, H., Midlane, N. & Nyirenda, V. 2013. The Trophy Hunting of African Lions: Scale, Current Management Practices and Factors Undermining Sustainability. *PLoS ONE*, 8(9): e73808.

Loveridge, A.J., Searle, A.W., Murindagomo, F. and 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*(4): 548-558.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F. & Macdonald, D.W. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, 32(6): 953–962.

Macdonald, D.W. 1993. Rabies & wildlife: a conservation problem? *Onderstepoort Journal of Veterinary Research*, 60: 351–355.

Macdonald, D.W. & Sillero-Zubiri, C., 2002. Large carnivores and conflict: lion conservation in context. In *Lion conservation research. Workshop* 2: 1-8.

Maciejewski, K. & Kerley, G.I.H. 2014. Understanding Tourists ' Preference for Mammal Species in Private Protected Areas : Is There a Case for Extralimital Species for Ecotourism? *PLoS ONE*, 9(2): e88192.

Makacha, S. and Schaller, G.B., 1969. Observations on lions in the lake Manyara National Park, Tanzania. *African Journal of Ecology*, 7(1): 99-103.

Maputla, N.W., Chimimba, C.T. & Ferreira, S.M. 2013. Calibrating a camera trap–based biased mark–recapture sampling design to survey the leopard population in the N'wanetsi concession , Kruger National Park , South Africa. *African Journal of Ecology*, 51: 422–430.

Marealle, W.N., Fossoy, F., Holmern, T., Stokke, B.G. & Roskaft, E. 2010. Does illegal hunting skew Serengeti wildlife sex ratios? *Wildlife Biology*, 16(4): 419–429.

Massei, G., Quy, R.J., Gurney, J. & Cowan, D.P. 2010. Can translocations be used to mitigate human–wildlife conflicts ? *Wildlife Research*, 37(5): 428–439.

McComb, K., Packer, C. & Pusey, A.E. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, 47(2): 379–387.

Michod, R.E. & Anderson, W.W. 1980. On Calculating Demographic Parameters from Age Frequency Data. *Ecology*, 61(2): 265–269.

Midlane, N., O'Riain, M.J., Balme, G.A., Robinson, H.S. & Hunter, L.T.B. 2014. On tracks : A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park , Zambia. *Biological Conservation*, 172: 101–108.

Midlane, N., O’Riain, M.J., Balme, G.A. and Hunter, L.T., 2015. To track or to call: comparing methods for estimating population abundance of African lions Panthera leo in Kafue National Park. *Biodiversity and Conservation*, *24*(6):1311-1327.

Miller, S.M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D.J., Ferreira, S., Funston, P.J., Hofmeyr, D., Kilian, P.J., Matthews, W., Naylor, S., Parker, D.M., Slotow, R., Toft, M. & Zimmermann, D. 2013. Management of reintroduced lions in small , fenced reserves in South Africa : an assessment and guidelines. *South African Journal of Wildlife Research*, 43(2): 138–154.

Mills, M.G.L. 1995. Notes on wild dog Lycaon pictus and lion *Panthera leo* population trends during a drought in the Kruger National Park. *Koedoe*, 38(1): 95–99.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 42(2): 127–137.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. 1995. The Relationship between Rainfall , Lion Predation and Population Trends in African Herbivores. *Wildlife Research,* 22(1): 75-87.

Mills, M.G.L., Wolff, P., le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion *Panthera leo* in the Kalahari Gemsbok National Park. *Koedoe*, 21(1): 163–171.

Minin, E. Di, Fraser, I., Slotow, R., Macmillan, D.C., Di Minin, E., Fraser, I., Slotow, R. & Macmillan, D.C. 2012. Understanding heterogeneous preference of tourists for big game species : implications for conservation and management. *Animal Conservation*, 16(3): 1–10.

Mitchell, B.L., Shenton, J.B. and Uys, J.C.M., 1965. Predation on large mammals in the Kafue National Park, Zambia. *Zoologica africana*, 1(2): 297-318.

Mogensen, N.L., Ogutu, J.O. & Dabelsteen, T. 2011. The Effects of Pastoralism and Protection on Lion Behaviour, Demography and Space use in the Mara Region of Kenya. *African Zoology*, 46(1): 78–87.

Morley, R.C. & van Aarde, R.J. 2007. Estimating abundance for a savanna elephant population using mark–resight methods : a case study for the Tembe Elephant Park , South Africa. *Journal of Zoology*, 271(4): 418–427.

Morrison, T.A., Yoshizaki, J., Nichols, J.D. & Bolger, D.T. 2011. Estimating survival in photographic capture–recapture studies : overcoming misidentification error. *Methods in Ecology and Evolution*, 2(5): 454–463.

Mosser, A. & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion , *Panthera leo*. *Animal Behaviour*, 78(2): 359–370.

Mudongo, E.I. & Dipotso, M.F. 2011. Predator population estimates in Kgalagadi wildlife management areas , through spoor counts and call-ups. Chapter 2 in: Kgalagadi District, District Biologists Reports. Wildlife populations and problem animal trends in Kgalagadi, southwestern Botswana. *Internal report, Department of Wildlife and National Parks, Tsabong, Botswan.*: pp28.

Munson, L., Terio, K.A., Kock, R., Mlengeya, T., Roelke, M.E., Dubovi, E., Summers, B., Sinclair, A.R.E. & Packer, C. 2008. Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. *PLoS ONE*, 3(6): e2545.

Navara, K.J., Workman, J.L., Oberdick, J. & Nelson, R.J. 2010. Short Day Lengths Skew Prenatal Sex Ratios Toward Males in Siberian Hamsters. *Physiochemical and Biophysical Zoology*, 83(1): 127-134.

Nowell, K. & Jackson, P. 1996. Wild cats: status survey and conservation action plan. Gland. IUCN. pp328.

Ogutu, J.O. and Dublin, H.T., 1998. The response of lions and spotted hyaenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology*, 36(1): 83-95.

Orford, H., Perrin, M. & Berry, H. 1988. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). *Journal of Zoology*, 216(4): 717–733.

Owen-Smith, N. 1990. Demography of a large herbivore, the greater kudu Tragelaphus strepsiceros, in relation to rainfall. *Journal of Animal Ecology*, 59(3): 893–913.

Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., Brien, S.J.O., Hofmann-lehmann, R. & Lutz, H. 1999. Viruses of the Serengeti : patterns of infection and mortality in African lions. *Journal of Animal Ecology*, 68(6): 1161–1178.

Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. 2010. Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conservation Biology*, 25(1): 142–153.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., Sinclair, A.R.E. & Journals, P.S. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science (New York, N.Y.)*, 307(5708): 390–393.

Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. 2009. Sport Hunting, Predator Control and Conservation of Large Carnivores. *PLoS ONE,* 4(6): e5941.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H. & Polasky, S. 2013. Conserving large carnivores : dollars and fence. *Ecology Letters*, 16(5): 635–641.

Packer, C. & Pusey, A.E. 1983. Adaptations of female lions to infanticide by incoming males. *The American naturalist*, 121(5): 716–728.

Packer, C. & Pusey, A.E. 1982. Cooperation and competition within coalitions of male lions kin selection or game theory. *Nature*, 296(5859): 740–742.

Packer, C. & Pusey, A.E. 1983. Male takeovers and female reproductive parameters: A simulation of oestrous synchrony in lions (*Panthera leo*). *Animal Behaviour*, 31(2): 334–340.

Packer, C. & Pusey, A.E. 1987. Retracing the history of the Ngorongoro lions. *Swara*, 10(4): 30–31.

Packer, C., Pusey, A.E. & Eberly, L.E., 2001. Egalitarianism in female African lions. *Science*, 293(5530): 690-693.

Packer, C., Tatar, M. & A. Collins. 1998. Reproductive cessation in female mammals. *Nature*, 392(6678): 807–881.

Parrott, L. 2011. Hybrid modelling of complex ecological systems for decision support : Recent successes and future perspectives. *Ecological Informatics*, 6(1): 44–49.

Patterson, B.D., Kasiki, S.M., Selempo, E. & Kays, R.W. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation*, 119(4): 507–516.

Pearl, M.C. 2000. *Research Techniques in Animal Ecology: Methods and Cases in Conservation Science*. L. B. & T. K. Fuller, ed. Columbia University Press, New York. pp. 442.

Pennycuick, C.J. & Rudnai, J. 1970. A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, 160(4): 497–508.

Pollock, K.H., 1991. Review papers: modelling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. *Journal of the American Statistical Association*, 86(413): 225-238.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, 52: 703–709.

Pusey, A.E. & Packer, C. 1987. Intrasexual cooperation and the sex ratio in African lions. *Amierican Naturalist*, 130(4): 636–642.

Radford, A.N., Anderson, C., Liversidge, R., Kru, O., Krüger, O., Radford, A.N., Anderson, C., Liversidge, R., B, P.R.S., Radford, A.N., Anderson, C. & Liversidge, R. 2005. Successful sons or superior daughters : sex-ratio variation in springbok. *Proceedings of the Royal Society of London B*, *Biological Sciencess,* 272(1561): 375–381.

Radloff, F.G.T. & Toit, J.T.D.U. 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(3): 410–423.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*, 22(1): 17–35.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science*, 343(6167): 1241484.

Rodgers, W.A., 1974. The lion (*Panthera leo*) population of the eastern Selous Game Reserve. *African Journal of Ecology*, 12(4):313-317.

Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofman Lehmann, R., Lutz, H., Mwamengele, G.L.M., Mgasa, M.N., Machange, G.A., Summers, B.A., Appel, M.J.G., Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofmann-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(6564): 441–445.

Salo, P., Banks, P.B., Dickman, C.R. & Korpimaki, E. 2010. Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, 80(4): 531–546.

Schaller, 1972. *The Serengeti Lion*. Chicago, University of Chicago Press.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature*, 413(6856): 591–596.

Schuette, P., Wagner, A.P., Wagner, M.E. & Creel, S., 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, 158(1): 301-312.

Schwarz, C.J., Seber, G.A.F., Schwarz, C.J. & Seber, G.A.F. 1999. Estimating Animal Abundance : Review III. *Statistical Science*, 14(4): 427–456.

Sheldon, B.C. & West, S.A. 2004. Maternal dominance, maternal condition , and offspring sex ratio in ungulate mammals. *The American Naturalist*, 163(1): 40–53.

Skinner, J.D. and Chimimba, C.T., 2005. *The mammals of the southern African sub-region*. Cambridge University Press.

Smuts, G.L. 1978. Reproduction and social organisation of lions from the Kruger National Park.pdf. *Carnivore*, 1(1): 17–28.

Smuts, G.L., Robinson, G.A. & Whyte, I.J. 1980. Comparative growth of wild male and female lions (*Panthera leo*). *Journal of Zoology*, 190(3): 365–373.

Snyman, A., Jackson, C.R. & Funston, P.J. 2014. The effect of alternative forms of hunting on the social organization of two small populations of lions *Panthera leo* in southern Africa. *Oryx* 49(4): 1–7.

Sogbohossou, E.A., Bauer, H., Loveridge, A., Funston, P.J., De Snoo, G.R., Sinsin, B. & De Iongh, H.H. 2014. Social structure of lions (*Panthera leo*) is affected by management in Pendjari Biosphere Reserve, Benin. *PLoS ONE*, 9(1): e846784

Smuts, G.L., 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe*, 19(1): 153-164.

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(3): 378–385.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua*, 18(1): 1–9.

Stander, P.E. 1992. Cooperative hunting in lions : the role of the individual. *Behavioral Ecology and Sociobiology*, 29(6): 445–454.

Stephens, P.A., Zaumyslova, O.Y., Miquelle, D.G., Myslenkov, A.I. & Hayward, G.D. 2006. Estimating population density from indirect sign : track counts and the Formozov – Malyshev – Pereleshin formula. *Animal Conservation*, 9(3): 339–348.

Suding, K.N., Gross, K.L. & Houseman, G.R. 2004. Alternative states and positive feedbacks in restoration ecology. , 19(1): 46–53.

Trimble, M.J., Ferreira, S.M. & Aarde, R.J. Van. 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. *Journal of Zoology*, 279(1980): 18–26.

Trinkel, M. 2013. Climate variability , human wildlife conflict and population dynamics of lions *Panthera leo*. *Naturwissenschaften*, 100(4): 345–353.

Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068): 90–92.

Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S. & Slotow, R. 2013. Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. *Ecology*, 94(11): 2619–2631.

van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organization (*Panthers, leo*). *Journal of Zoology*, 206(1): 97–112.

van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the kgalagadi transfrontier park: modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

White, G.C. & Burnham, K.P. 1997. Program MARK : Survival Estimation from Populations of Marked Animals. *Bird Study*, 46(S1): S120–S139.

Whitman, K.L. & Packer, C. 2006. A practical guide to aging African lions. *Conservation Force, USA*.

Whitman, K.L., Starfield, A.M., Quadling, H. & Packer, C. 2007. Modeling the Effects of Trophy Selection and Environmental Disturbance on a Simulated Population of African Lions. *Conservation Biology*, 21(3): 591–601.

Woodroffe, R. 2011. Ranging behaviour of African wild dog packs in a human-dominated landscape. *Journal of Zoology*, 283(2): 88–97.

Woodroffe, R. & Frank, L.G. 2005. Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation*, 8(1): 91–98.

Woodroffe, R. & Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science*, 280(5372): 2126–2128.

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

Young, E. 1975. Some important parasitic and other diseases of lion, *Panthera leo*, in the Kruger National Park. *Journal of the South African Veterinary Association*, 46(2): 181–183.

Young-overton, K.D., Funston, P.J. & Ferreira, S.M. 2014. Rainfall driven changes in behavioural responses confound measuring trends in lion population size. *Wildlife Biology*, 20(6): 344–355.

Zheng, C., Ovaskainen, O., Saastamoinen, M. & Hanski, I. 2007. Age-dependent survival analyzed with Bayesian models of mark-recapture data. *Ecology*, 88(8): 1970–1976.

Zimmerman, D., Govender, D. & Mills, G. 2009. Canine Distemper Virus (cdv): Clinical Disease and Mortalities in Lions (*Panthera leo*) of the Kgalagadi Transfrontier Park. *Scientific report 01/ 2009, South African National Parks, Skukuza.*

Chapter 2:
Study Area

2.1. Introduction

In 1931, the Kalahari Gemsbok National Park (KGNP) was proclaimed as a protected area in response to an onslaught of poaching and bush-meat hunting, which was alleged to have a large impact on wildlife abundance in the south-western Kalahari region (Anonymous, 2008). Shortly thereafter, in 1939, a game reserve extending approximately 40 km to the east of KGNP, now known as the Gemsbok National Park (GNP) in the then Bechuanaland (Botswana) was proclaimed by the British ruling government (Anonymous, 2008). The GNP of Botswana was further extended in 1971 to include the Mabuasehube Game Reserve. On the 7 April 1999 the presidents of South Africa and Botswana signed a treaty that declared the Kgalagadi Transfrontier Park as the first Transfrontier Conservation Area in Africa and it was formally proclaimed on 20 May 2000 (Anonymous, 2008) (Figure 2.1).

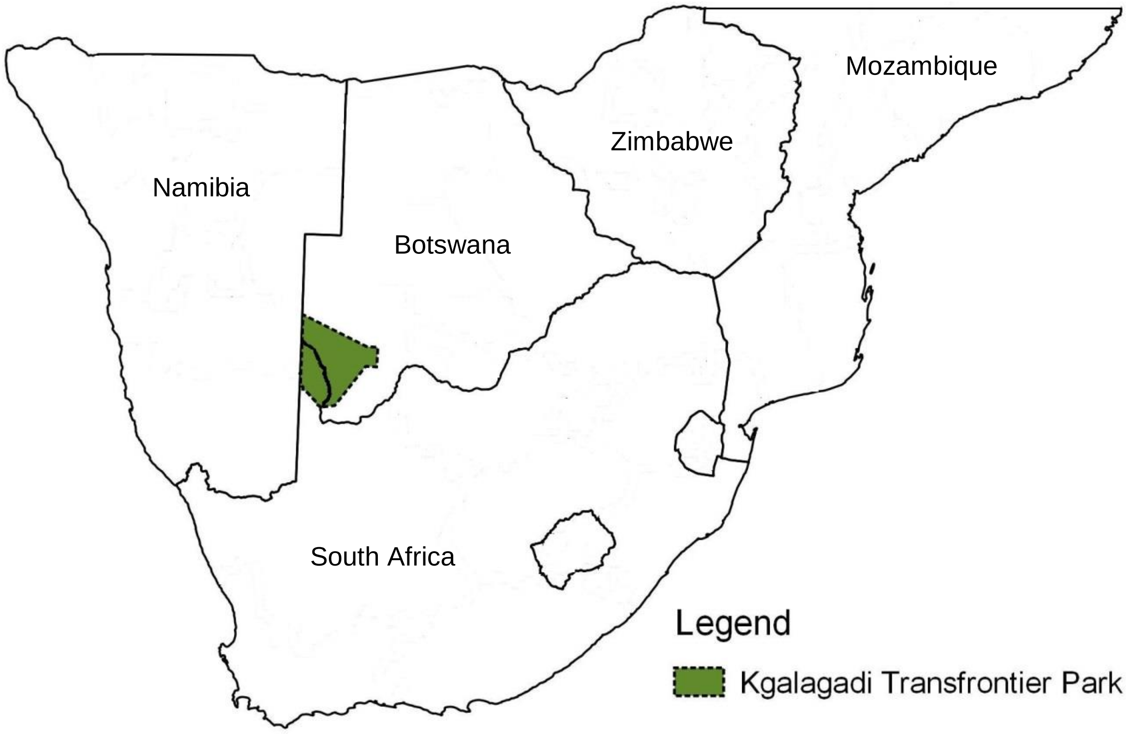

Figure 2.1 The location of the Kgalagadi Transfrontier Park (KTP) delineating the Kalahari Gemsbok National Park (South Africa) to the southwest of the KTP and the Gemsbok National Park (Botswana) to the east of the Nossob River, which demarcates the boundary between South Africa and Botswana within the KTP.

The KGNP is currently gazetted under the National Environmental Management: Protected Areas Act (NEM:PAA) 57 of 2003 (South Africa). The NEM:PAA was amended in the National Environmental Management: Protected Areas Amendment Bill No. 31239 (GN 5/85) in 2008, after a 25 000 ha section of the KGNP to the west of the Auob river, was awarded to the indigenous community through a lands claim (NEM:PAA, 2008). The community owned section is still included into the management of the KGNP and remains a part of the protected area (Anonymous, 2008). The Kgalagadi Transfrontier Park is managed under a joint management committee, which includes the South African National Parks (SANParks), and the Republic of Botswana's Department of Wildlife and National Parks (DWNP).

To the south, east and north of the KTP in Botswana, vast areas are proclaimed as Wildlife Management Areas (WMA) (Funston, 2002; Mudongo & Dipotso, 2011). These WMA's serve as buffers between agricultural land and the GNP in Botswana and allow for movement of migratory species between the KTP and the Central Kalahari Game Reserve (Verlinden, 1998; Funston, 2002). These areas are restricted in their activities, and although communities in Botswana are allowed to utilize the natural resources in the WMA's, no agricultural or industrial activities are permitted (Mudongo & Dipotso, 2011). The WMA's bordering the KTP contribute a further 36,822 km² to wildlife habitat and together with the KTP cover a contiguous area of approximately 80 000 km², rendering it one of the largest conservation areas in the world (Herholdt & Anderson, 2006; Funston, 2002; Mudongo & Dipotso, 2011). The vast extent of the KTP in an arid Savanna environment and its buffering WMA's enables the conservation of lions (*Panthera leo*) in one of southern Africa's most important lion conservation areas (Riggio *et al*., 2013).

2.2. The study area

The study area includes the KGNP and a 17 km buffer to the east of the Nossob River into the Gemsbok National Park (GNP), Botswana. The study area is 14 250 km², of which 9710 km² comprises the KGNP (Figure 2.2). The extent of the study area has been defined by fenced boundaries to the south, southwest and west, bordering agricultural areas, used predominantly for the cultivation of cattle as well as sheep and goat (Funston, 2002; van Vuuren *et al*., 2005; Mudongo & Dipotso, 2011). The area to the East of the Nossob River is unfenced and forms part of the KTP. The area considered as the study area was defined by the home range extension of five collared lionesses that formed part of this study, and which were known to reside in the KGNP, but also extended their home ranges approximately 17 km (± SD = 6 km) into the GNP (Figure 2.2). The study area lies entirely within the KTP (36 000 km²) in the extreme Southwest of the Arid Kalahari Region (Leistner, 1959b; Rooyen *et al*., 2008).

Gravel or sand roads run along the entire extent of two ephemeral riverbeds within the KTP, namely the Auob and the Nossob Rivers, as well as several roads, which transect the dunes within the study area (Figure 2.3). Several artificial water sources exist across the study area which are fed by either solar or wind driven pumps (Mills & Retief, 1984; Knight, 1995) at a density of 0.57 water holes per 100 km² (Funston, 2011) (Figure 2.3). In the riverbeds, 41 artificial water holes exist, 17 situated in the Auob and 24 in the Nossob riverbeds (Mills & Retief, 1984; Knight, 1995). Twenty-three water holes are found in the dunes, two of which were not operational for the majority of the study period (Pers. Obs. 2013-2015). Some boreholes were drilled in the KGNP before the 1900's but the majority of the boreholes were sunk during the prior to the Second World War (Knight *et al.*, 1988; Anonymous, 2008). Eleven tourist camps are distributed across the study area, predominantly on the perimeter of the Nossob and Auob Rivers.

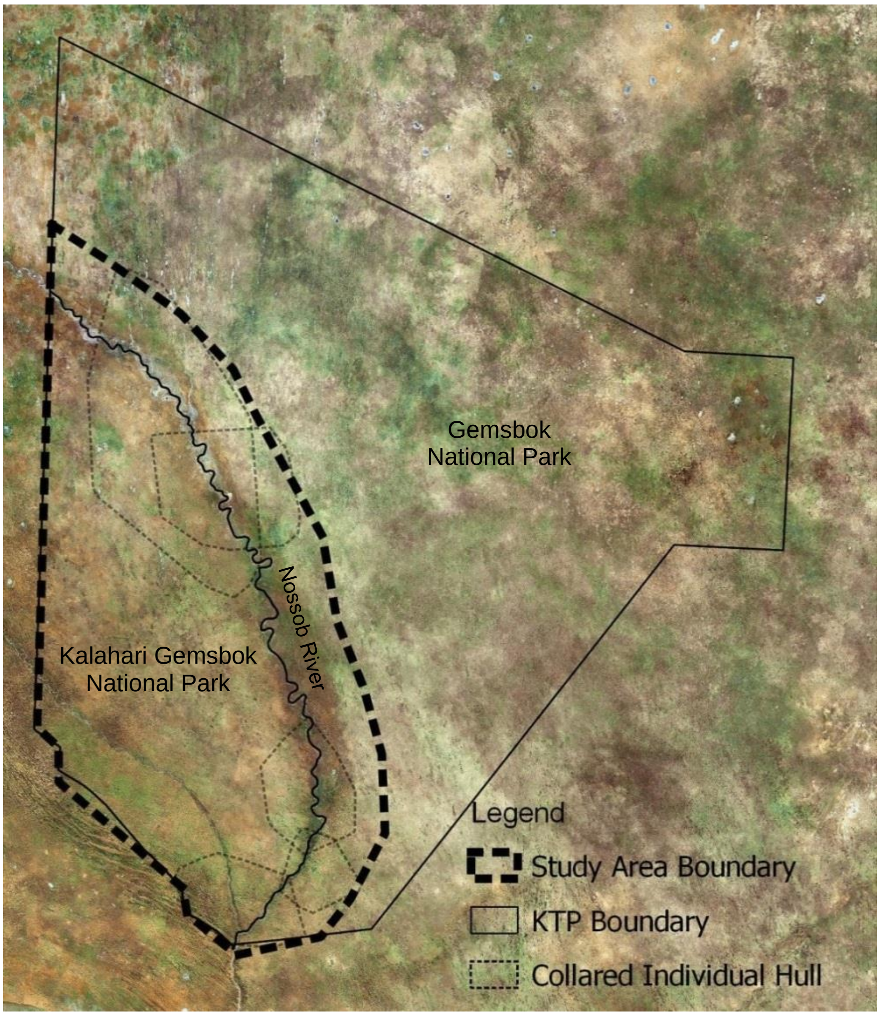

Figure 2.2 Study area (14,250 km²) within the Kgalagadi Transfrontier Park (KTP), defined by the extent of five collared lionesses' home-range east of the Nossob River. The study area covers the entire KGNP, South Africa, west of the Nossob River and a 17 km buffer into the GNP, Botswana, to the east of the Nossob River.

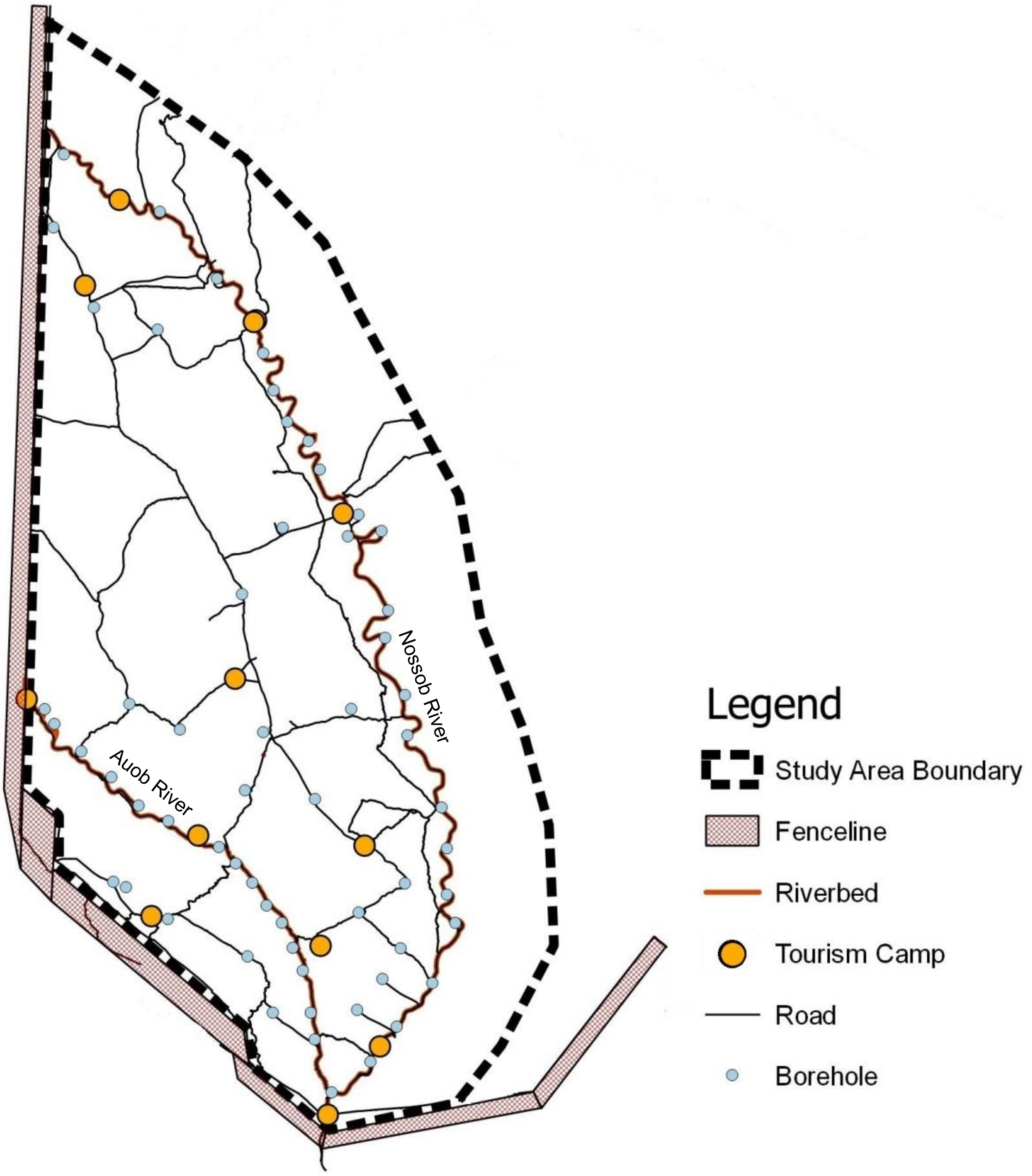

Figure 2.3 The study area within the KTP is delineated with particular reference to manmade features. Gravel and sand roads run along the entire length of the Auob and Nossob River, and several roads transect the dunes. Along the Auob and Nossob Rivers, as well as in the dunes, several waterholes influence animal ecology and provide water to tourism camps that are distributed across the KGNP. The southern, south-western and western boundaries of the study area are fenced to separate wildlife from livestock, and deter human-lion conflict.

2.3. Climate

The KTP, in the southwest of the arid Kalahari, maintains climatic conditions that can be classified as a desert environment (Laity, 2008; Durant *et al*., 2014). These conditions include high summer temperatures, evaporation which exceeds precipitation (<250 mm) and high rainfall variability, prominent winds, clear skies over 70% of the time and low (< 30%) humidity (Laity, 2008). The south-western region of the Kalahari ecosystem is dominated by anti-cyclonic low-pressure systems characterized by infrequent rain events, a generally cloudless atmosphere punctuated by erratic cumulus convection and strong seasonal definition (Tyson & Crimp, 1998).

The KGNP receives approximately 220 mm of highly erratic precipitation between November and April (Knight, 1995; Bergstrom & Skarpe, 1999; van Rooyen *et al*., 2008). Variance in localized rainfall ranges between averages of 180 mm in the southwest to 230 mm in the North of the KGNP per annum (Grist *et al*., 1997). Rainfall shows extreme variation across the KGNP and most of the rain falls over short bursts as isolated thunderstorms across the landscape, with greater variability in the southwest of the KGNP (Tyson & Crimp, 1998; Anonymous, 2008; van Rooyen *et al*., 2008). The mean rainfall in the south-western Kalahari, calculated from measurements at Nossob, Mata-Mata and Twee Rivieren rest camps in the KGNP, and the town of Van Zylsrus to the southeast of the KGNP, was 180.4 mm between 1980 to 2005 (Stapelberg *et al*., 2008). Between 1972 and 1989, the average precipitation in the KGNP was 225 mm (Knight, 1995). During the three years within which the study occurred (2013 to 2015), the annual rainfall across the KGNP ranged between 129 mm and 266 mm per annum (pers. comm. M. Ferreira, 2016[1]), which is below the long-term average (Knight, 1995). Evapotranspiration rates are high (> 3 000 mm per annum) (Mucina & Rutherford, 2006), and natural surface water occurs only for short periods after heavy rain, in ephemeral riverbeds and pans scattered across the dune habitats (Nagy & Knight, 2008).

Temperature can range from extremes of -10°C in winter to 45°C in summer (Mills, 2015). Average summer (November – April) maximum temperature exceeds 35°C and the winter (May – October) mean maximum temperature is 29°C Anonymous, 2008). Average monthly minimum temperatures during winter are approximately 4°C but in summer, minimum temperature rarely falls below 15°C (Anonymous, 2008). Annual mean temperatures fluctuate between 11°C and 32°C (Herholdt, 2006).

---

[1] Micho Ferreira, Section Ranger, Twee Rivieren, Kalahari Gemsbok National Park, Northern Cape, South Africa. 8800.

Seasonality has been defined by distinctions in temperature and precipitation. Taking into account only temperature, a hot (October to March) and a cold (April to September) season has been defined (Bothma & Bothma, 2006; Melville & Bothma, 2006; Bothma & le Riche, 1994). Taking into account only precipitation, a dry (May to October) and wet (November to April) season has been identified (van Rooyen *et al*., 2006; Bergstrom & Skarpe 1999). Further definitions of climatic variability in the arid Kalahari have been made taking into consideration both precipitation and temperature simultaneously. Three seasons have been defined in this manner namely hot and dry (September to December), hot and wet (January-April) and cold and dry (May to August) seasons (van Vuuren *et al*., 2005; Mills & Retief, 1984). Although several seasonal definitions have been identified, precipitation is by far the most important to ecosystem interaction (Stapelberg *et al*., 2008).

Ecological conditions can be defined in relation to rainfall (van Vuuren *et al*., 2005; Bergstrom & Skarpe, 1999; Jeltsch *et al*., 1999). Ecosystems have a measured response to rainfall, such as primary productivity and, relevant to the study of lions, prey biomass (Mills *et al*., 1995; Celesia *et al*., 2010). Ecological conditions have been described in the KTP by relative bi-annual rates of precipitation (van Vuuren *et al*., 2005). Good ecological conditions persist when the average rainfall over a two-year period equals or exceeds 237 mm, average ecological conditions persist when the two-year average rainfall is between 235 mm and 165 mm and poor ecological conditions persist when the average rainfall over a two-year period is below 165 mm (van Vuuren *et al*., 2005). Although this is not representative of the entire study area, this does indicate that the study was commenced during poor ecological conditions. However, during the study period, the average rainfall was equal to the long-term average between 1980 and 2005, with the two-year average exceeding 185 mm in Twee Rivieren throughout the study period (2013-2015) (pers. comm. M. Ferreira, 2016).

2.4. Topography

The KGNP lies at an altitude between 800 m and 1,100 m above sea level with a gradual south-westerly slope (Anonymous, 2008; Stapelberg *et al*., 2008). The topology is characterized by sand dunes, ranging from flat sand plains in the north and east, gently undulating dunes in the north-west, steep parallel dunes in south, and steep irregular dunes predominantly in the centre and to the west of the study area (Mills & Retief, 1984; Anonymous, 2008; van Vuuren *et al*., 2008). Dunes range in height between 6 m and 20 m high, with some very tall dunes (maximum 40m), extending out of the riverbeds in the northern half of the Auob River (Leistner, 1967; Mills & Retief, 1984). The dune structure remains relatively stable only shifting after large disturbance events such as fire (Haddon & McCarthy, 2005). Dunes in the northwest of the study area are shaped predominantly by northerly winds, whereas in the south, westerly winds are the dominant cause of dune formation (Heine, 1989). The central areas of the KGNP receive a mixture of these prevailing winds, causing more irregular dune formations (Heine, 1989). Bare dunes, which resulted from fire, drought or grazing, are subject to three times more soil movement from wind than vegetated dunes (Wiggs *et al*., 1994). The dune fields are interspersed with one hundred and twenty six large pans in the KGNP (Mucina & Rutherford, 2006) at a density of approximately 0.17 pans per 100 km² (Funston, 2011). Two types of pans are discerned in the KGNP, sparsely vegetated pans and saltpans with no plant growth (Leistner, 1967; van Rooyen & van Rooyen, 1998; Mucina & Rutherford, 2006).

The dunes cover approximately 86% of the study area, dissected by two ephemeral riverbeds. The riverbeds account for approximately 2% of the study area (van Rooyen *et al*., 2008). A 2.5 km buffer on either sides of the river beds are considered riparian zones (±2000 km²) (van Rooyen *et al*., 2008; Ferreira *et al*., 2013) where animal densities are expected to be higher (van Rooyen *et al*., 2008). The riparian zone occupies approximately 14% of the study area. The Auob River and the Nossob River cross the study area in a north west to southerly direction until their confluence in the very south of the study area named Samevloeing. The Auob River is characterised by steep calcrete and dune slopes from the riverbed into the dune fields, with a span of between 100 m and 500 m (Bothma & De Graaff, 1973; Mills & Retief, 1984). The Auob River has its source in Stampriet, Namibia, which is approximately 360 km to the north west of the point where the river enters the KGNP and ends at its confluence with the Nossob River. Within the park boundaries, the Auob River flows approximately once every decade and the Nossob, approximately twice a century (Mills & Mills, 2013). The Nossob river is similar in structure to the Auob in the southern region of the study area, whereas in the northern reaches of the Nossob the riverbed is wide (100-1000 m) and comparatively shallow, with dunes extending gradually from the riverbed (Bothma & De Graaff, 1973; Mills & Retief, 1984). The Nossob River originates out of the Anas mountains near Windhoek, Namibia, and enters the study area in the northwest and forms the political boundary between Botswana and South Africa (Anonymous, 2008).

2.5. Geology

The Kalahari basin, or the area commonly referred to as the Kalahari Desert was formed because of tectonic uplifts during the Pliocene era (Thomas & Shaw, 1991). The current extent of the sands which lie within the basin cover an area approximately 2.5 million km², spanning across seven countries including South Africa, Namibia, Botswana, Angola, Zambia, Zimbabwe and the Democratic Republic of Congo (Thomas & Shaw, 1991). The study area lies to the extreme southwest of the Kalahari basin (Stapelberg *et al*., 2008).

The study area is underlain by the Kalahari Group basal formation, which lies on top of the Karoo Sequence (Malherbe, 1984). Sands formed predominantly through aeolian and some fluvial erosion (Heine, 1989), derived from the Gordonia Formation, are the most common of the soil types, comprising most of the dune habitat (Malherbe, 1984). Other Kalahari Groups can be classified into brown to white fine grained sands from the Goeboe Goeboe Formation, gravels belonging to the Wessels Formation, red clay from the Budin Formation, sandstones from the Eden Formation, calcrete from the Mokalanen Formation and clayey limestone from the Lonely Formation (Malherbe, 1984).

The sands in the Kalahari are considered deep (±40m) and poorly structured with little organic composition (Dougill & Thomas, 2004). The soils are generally nutrient poor and low in exchangeable cations, lacking in many micronutrients, and exhibiting large variability in concentrations of major nutrients such as phosphorous, nitrogen, potassium and carbon (Dougill & Thomas, 2004; Scholes, 2011). The sand can be classified into two types, firstly sandy soils, which are divided into red, pink and white sand. The colour of these sands is because of iron oxide bonded to the soil particles. The other classifications are of fine sand structures, which are sub-divided into river, alluvial and pan soils.

2.6. Habitat structure and vegetation

The study area falls within one of the least productive environments in the world with an annual primary production rate of between zero and five tons of net primary production per annum (Lieth, 1975; Knight, 1991; Schultz, 2005). Although the region falls within an area with optimal temperature (24-30ºC) and sunlight for optimal photosynthetic production (Schultz, 2005), plant growth is limited by a lack of nutrients and water (Scholes, 2011). Not only is the general nutrient content in the KGNP poor, decomposition and nutrient turnover is also slow in such a xeric environment (Lieth, 1975; Scholes, 2011).

The study area and the broader KTP fall within the Savanna Biome (van Rooyen *et al*., 1988) and has been classified as Kalahari Thornveld (Acocks, 1988) and more recently as Thorn Savanna (Schultz, 2005). The vegetation types within the KTP have been classified on numerous accounts (Pole-Evans, 1936; Brynard, 1958; Leistner, 1959a; Leistner, 1959c; Giess, 1971; Bothma & De Graaff, 1973; Leistner & Werger, 1973; Coetzee & Werger, 1975; Wergner, 1986; Acocks, 1988; van Rooyen *et al*., 1988; van Rooyen & van Rooyen, 1998; Low & Rebelo, 1998; van Rooyen *et al*., 2008). However, the first study of lions in the broader KTP, differentiated between two distinct units of vegetation in the dune habitats, based on structural differences, which had implications for lion population characteristics (Funston, 2002). A Tree Savanna habitat in the northeast of the park and found solely in the GNP was described as a sparse to open Tree Savanna, with large grassy plains (van

Rooyen, 2000). The south-western area of the KTP, and occupying the majority of the KGNP, was classified as Dune Savanna (15 633 km²), characterized by shrubby grassland with few large trees on parallel dunes (Leistner, 1967; Funston, 2002). The current study took place within the Dune Savanna habitat (Funston, 2002) and is described as being homogenous and belonging to the Kalahari Duneveld Bioregion, which is characterized by three primary plant species, namely *Vachelia erioloba, Rhigozum trichotomum* and *Schmidtia kalahariensis* representing trees, shrubs and grasses respectively (Mucina & Rutherford, 2006).

Further detailed distinctions have been made between landscapes based on terrain morphology, soil and vegetation structure in the KGNP (van Rooyen *et al*., 2008). However, the greatest and most relevant distinctions in the study area are between the riverbeds (Figure 2.4 & 2.5), pans (Figure 2.6) and dune habitats (Figure 2.7) (van Rooyen *et al*., 2008), which show differences in prey and lion density (Mills, 1984; Funston, 2002; Ferreira *et al*., 2013). When referring to riverbeds, these include a 2.5 km buffer of plains and terraces along riverbeds and grass pans, on compact whitish sand to either side of the riverbed (van Rooyen *et al*., 2008; Ferreira *et al*., 2013). The riverbeds, although ephemeral, have greater water retention qualities and hold surface water for short periods after rains (Knight, 1995). Nutrients are generally more abundant in the riverbeds with some leaching of nutrients from the dunes to the lower lying areas of the riverbeds and pans (Berkeley *et al*., 2005). Soils in the riverbeds are of a finer texture, are more adherent to nutrients and have a greater content of organic matter and clay content than the soils in the dunes (Berkeley *et al*., 2005). The riverbeds thus have a greater capacity for primary production and this is particularly observed in plant growth and the herbivore aggregations in the riverbeds during the rainy season (Bergstrom & Skarpe, 1999).

The riverbeds and pans hold a greater diversity of plants, but are characteristically composed of short steppe like grasslands (Knight, 1995). The primary grass species found in the riverbeds and pans include S*chmidtia spp, Stipagrostis spp, Centropodia spp* and *Eragrostis spp.* Shrubs such as *Grewia flava*, *Cersia tenuinervis* and *Rhigozum trichotomum* (Knight, 1995; van Rooyen *et al*., 2008). Conspicuous trees of former genera *Acacia*, now known as *Vachellia erioloba* and *V. haemotoxylon* (Dyer, 2014) are prominent in the river habitats. However, the riverbeds represent less than 15% of the study area (Knight, 1995; van Rooyen *et al*., 2008)

The remainder of the study area consists of the dune landscapes and make up the vast majority of habitat available to lions and their prey. The dunes can be sparsely vegetated with trees, shrubs and grasses, bare dunes, flat grasslands and tree savannahs (Bothma &

De Graaff, 1973). The dominant vegetation includes grasses (*Schmidtia kalahariensis, Stipagrostis amabilis, S. uniplumis, S. ciliata*, *Eragrostis lehmanniana, Centrapodia glauca*), scattered trees, that often grow in a shrub form (*Vachellia erioloba, V. haematoxylon* and *Boscia albitrunca*), and shrubs (*Rhigozum trichotomum* and *Senegalia mellifera*) (van Rooyen *et al*., 2008). The sandy aeolian sand of the dunes, is low in nutrients, has poor water retention qualities, and is poor in organic matter (Berkeley *et al*., 2005). These qualities make it a less productive environment than the riverbed habitat.

Figure 2.4 The ephemeral Nossob River can be relatively narrow (100m) in its southern reaches and 1000m wide towards the north. The riverbeds, particularly the northern reaches of the Nossob River have a higher rate of primary productivity. The Nossob River may flow twice a century.

Figure 2.5 The Auob river is mostly narrow (100-500m) with high dunes (left of image) or calcrete ridges (right of image) rising from the riverbed. The Auob flows approximately once a decade but as with the Nossob River, can hold puddled surface water for several days after rains and has a greater abundance and higher quality food per area than the dune environment

Figure 2.6 Within the dune habitat, one hundred and twenty six large pans have been identified and mapped in the KGNP. These pans can be sparsely vegetated pans or salt pans with no plant growth. Animals are lured to the pans where they attain nutrients from natural licks, in some cases nutritious forbs and graze, and surface water, for short periods after rains.

Figure 2.7 The dunes comprise more than 85% of the available habitat to animals in the KTP. Dune topography may vary greatly across the study area from parallel dunes in the southwest as shown in the image above, gently undulating or vast plains in the northeast or irregular high dunes in the west of the study area. However, primary production is consistently lower in the dunes than in the riverbeds and animal densities are correspondingly low.

2.7. Prey prevalence and conspecific competitors

The riverbeds and pans, which are subject to higher primary production, are the most intensively used due to the higher biomass of edible nutritious plant matter (Bergstrom & Skarpe, 1999). Densities of game in the riverbeds are also accentuated by the presence of artificial water holes in the riverbeds and in the dunes, where they are often located at pans (Mills & Retief, 1984; Knight, 1995). Another attraction of herbivores to the riverbeds and pans are areas of compressed clay soils, which serve as natural licks by herbivores to supplement their nutritional and salt intake (Stapelberg *et al*., 2008). However, herbivore numbers fluctuate seasonally in the KGNP (Mills, 1984). Animals congregate in the KGNP during the wet summer months, particularly in the riverbeds, and disperse again in the dry winter season (Mills & Retief, 1984b; Bergstrom & Skarpe, 1999). The extreme and inconsistent climatic conditions in the KTP limit ungulate abundance and biomass (Mills, 2015), and animals which are adapted to erratic arid conditions, such as gemsbok, *Oryx gazelle* and springbok, *Antidorcas marsupialis,* are dominant in the landscape (Stapelberg *et al*., 2001). Species that are dependent on water and high quality graze, such as blue wildebeest, *Connochaetes taurinus*, are less common across the KTP and mostly restricted to riverine areas (Williamson & Williamson, 1988; Spinage, 1992; Knight, 1995). Other ungulate species, which occur at lower densities including red hartebeest, *Alcelaphus buselaphus,* eland, *Tragelaphus oryx,* steenbok, *Raphicerus campestris,* and common duiker, *Sylvicapra grimmia* (Mills & Retief, 1984b). Other common resident species include ostrich, *Struthio camelus*, porcupine, *Hystrix africaaustralis*, springhare, *Pedetes capensis* andhare, *Lepus spp*. (Mills, 1984).

Seasonal and stochastic migrations are typical in arid landscapes where animals, particularly large ungulate species, have to move over large areas in search of food and surface water (Verlinden, 1998; Cain *et al*., 2005). The greater Kalahari once epitomized some of the largest migrations across vast landscapes, and more localized migrations persist in the KTP and adjoining WMA’s (Verlinden, 1998). Mass migrations as recorded historically no longer occur (Child & Le Richie, 1969; Verlinden, 1998). Large scale seasonal migrations of springbok (Eloff, 1961) and wildebeest (Spinage, 1992) through the KTP were historically recorded (Verlinden, 1998). Blue wildebeest used to be highly migratory, driven by water dependence and a requirement for high quality graze (Williamson & Williamson, 1988; Knight, 1995; Verlined, 1998). Springbok and wildebeest have since established resident herds in the KGNP (Knight, 1995; Owen-Smith, 1996) and now occur mostly within the riverbed areas (Eloff, 1966; Knight, 1995), close to waterholes (Mills & Retief, 1984b) at lower densities (Spinage, 1992). Eland are also migratory and are known to move between the Central Kalahari Game Reserve in Botswana into the KGNP during dry seasons

(Verlinden, 1998). Red hartebeest appear to have localized seasonal migrations within the greater KTP region and occur at lower densities in the Auob riverbed than in the Nossob riverbed (Mills & Retief, 1984b; Knight, 1995). Gemsbok, the most abundant large ungulate (Ellis & Herbst, 2013; Mills, 2015), and the largest contributor to lion diet (Eloff, 1984; Mills, 1984; Beukes *et al*., unpublished data 2016), are sedentary in the KTP (Mills, 2015).

Lion diet in the KGNP consists predominantly of large ungulates (>80 kg), such as gemsbok, wildebeest, hartebeest, eland, and kudu, as well as smaller prey items such as ostrich, steenbok, *Raphicerus campestris,* and common duiker, *Sylvicapra grimmia* (Eloff, 1984; Mills & Retief, 1984). In the KGNP, porcupine, *Hystrix africaaustralis,* constitutes a larger portion of lion diet than elsewhere, but their biomass contribution is negligible (Eloff, 1984; Mills & Retief, 1984). Warthog have been recorded in the KTP (Mills & Mills, 2013) but have not been recorded in lion diet (Eloff, 1984; Mills, 1984). Giraffe were introduced to the KGNP in 1990 and currently occur only in the Auob River and adjoining dune areas (Hall-Martin & De Graaf, 1978; Kruger, 1994; Bezuidenhout *et al*., 2010) but have not been recorded as constituting any part of lion diet in the KGNP (Eloff, 1984; Mills 1984, Beukes *et al*., unpublished data 2016). The abundance of available prey species are predominantly limited by rainfall, which is positively correlated to primary production (Coe *et al*., 1976; Sinclair, 1979; East, 1984; Mills & Retief, 1984; Walker *et al*., 1987). Game numbers have fluctuated over time in the KGNP (Mills 1984) (Table 2.1). Wildebeest and eland appear to be the most susceptible to drought conditions and their abundance shows the greatest variability over time, whereas gemsbok and hartebeest show comparatively less susceptibility to drought conditions and have not shown large fluctuations over time (Knight, 1995).

Table 2.1 Population size estimates of six prey species commonly consumed by lions in the KGNP. The years in which the aerial surveys were conducted are presented in brackets when different from the year of publication. Confidence intervals (95%) are presented where available and where information is not available (NA), it is indicated.

Species	Knight, 1995 (1978-1984)	Knight, 1995 (1985)	Funston, 2002 (1998-2001)	Ellis & Herbst, 2013
Gemsbok	7998 (±2665)	8948 (±2541)	13988	8120
Red hartebeest	1581 (±820)	1002 (±660)	1588	1110
Eland	2604 (±2114)	3209 (±859)	1588	1100
Blue wildebeest	1290 (±250)	5496 (±2363)	141	1440
Springbok	5411 (±899)	5022 (±1765)	360	2790
Ostrich	1695 (±428)	2406 (±747)	NA	1550

The WMA's connect the KTP with the Central Kalahari Game Reserve, which allows migratory ungulates to move between and within these areas (Verlinden, 1998). However, fences and human settlements restrict much of the original migratory routes and destinations (Verlinden, 1998). Changes in the migratory habits of particularly wildebeest and springbok have caused structural changes in the potential prey composition (Mills, 1984; Knight, 1991; Castley *et al*., 2002). Furthermore, declines of large ungulates and ostrich have been observed across the southern Kalahari ecosystem (Spinage & Matlhare, 1992; Verlinden, 1998). Changes in the composition of prey, and responding lion diet may ultimately lead to changes in lion population characteristics (Castley *et al*., 2002; Ferreira *et al*., 2013). Apart from the natural prey species of lion present in the KTP, lions that live on the periphery of the KTP have access to livestock, predominantly sheep, goats and cattle, as an alternate source of food (Mills, *et al*., 1978; van Vuuren *et al*., 2005). Lion predation on livestock has been a major source of human-lion conflict over several decades in the KGNP and KTP (Mills *et al*., 1978) and remains a primary concern of lion persistence (van Vuuren *et al*., 2005; Ferreira *et al*., 2013) and a potential driver of demographic change (Woodroffe & Frank, 2005).

Large Carnivores (> 20 kg) are characteristic of Africa Savanna ecosystems (Mills, 2015) and several conspecifics co-occur with lion in the study area. Apart from lion, the order Carnivora are represented by large carnivores such as spotted hyaena, *Crocuta crocuta*, cheetah, *Acinonyx jubatus*, leopard, *Panthera pardus* and brown hyaena, *Hyaena brunnea* (Mills, 1984; Mills, 2015). Smaller carnivore species found in the KTP include black backed jackal, *Canis mesomelas*, Cape Fox, *Vulpes chama*, bat eared fox, *Octocyon megalotis*, African wild cat, *Felis lybica*, caracal, *Caracal caracal*, and honey badger, *Mellivora capensis* (Kruuk & Mills, 1983; Melville *et al*., 2004; Herbst & Mills, 2006; Blaum *et al*., 2008).

In the KTP, carnivores prevail in more equal proportions than those of more mesic areas, where the largest carnivores often dominate the tertiary trophic level (Mills, 2015). Furthermore, brown hyenas are abundant in the KGNP (N = 172; Mills, 1990), whereas lion often numerically dominate spotted hyena where they co-occur (Mills, 2015). In the KGNP, lions are abundant (N = 130; 95% CI: 91-169; Ferreira *et al*., 2013) and spotted hyaena are uncommon (N = 84; Mills, 1984). African wild dog, *Lycaon pictus*, historically occurred in the northern reaches of the KTP, but have disappeared from the ecosystem in recent history (Mills, 2015). Cheetahs and leopards are the least abundant of the large predators (Mills, 2015), with approximately 204 and 151 individuals in the KTP respectively (Funston, 2002). Negative interactions between different large carnivore species are also less common due to the low densities in the KGNP, and food loss to lions through scavenging by species such as spotted hyaena's, is rare (Mills, 2015).

2.8. References

Acocks, J.P.H. 1988. Veld types of South Africa. , 57(3).

Anonymous. 2008. Kalahari Gemsbok National Park management plan. *South African National Parks, Pretoria, South Africa*.

Bergstrom, R. & Skarpe, C. 1999. The abundance of large wild herbivores in a semi-arid savanna inrelation to seasons, pan and livestock. *African Journal of Ecology*, 37(1): 12-26.

Berkeley, A., Thomas, A.D. & Dougill, A.J. 2005. Cyanobacterial soil crusts and woody shrub canopies in Kalahari rangelands. *African Journal of Ecology*, 43(2): 137–145.

Beukes, M. 2016. Unpublished Master's Thesis. Cape Peninsula University of Technology, Cape Town, South Africa.

Bezuidenhout, H., Ferreira, S.M. & Herbst, M. 2010. *An assessment of the proposed giraffe translocation from the Mata Mata section to Unions End in the Kalahari Gemsbok National Park*. Internal Report, SANParks, Kimperly. South Africa.

Bothma, J. du P. & le Riche, E.A.N. 1994. The relationship between minimum air temperature and daily distances moves by Kalahari leopards. *South African Journal of Wildlife Research*, 24(1 & 2): 18–20.

Bothma, J.D.P., van Hoven, S. & Le Riche, E.A.N. 1993. GPS-corrected and GIS-based remapping of the Kalahari Gemsbok National Park and the adjacent area in Botswana. *Koedoe*, 36(2): 105–108.

Bothma, J.P. & Bothma, M.D. 2006. Activity patterns in southern Kalahari leopards. *African Zoology*, 41(1): 150–152.

Bothma, J.P. & De Graaff, G. 1973. A habitat map of the kalahari Gemsbok National Park. *Koedoe*, 16(1): 181–188.

Brynard, A.M. 1958. Verslag insake voorlopige ondersoek rakende toestande in die Nasionale Kalahari-Gemsbokpark. *Koedoe*, 1(1): 162–183.

Cain, J.W., Krausman, P.R., Rosenstock, S.S. and Turner, J.C., 2005.*Literature review and annotated bibliography: Water requirements of desert ungulates* (No. 2005-1141). Geological Survey, USA.

Caro, T.M. & Stoner, C.J. 2003. The potential for interspecific competition among African carnivores. *Biological Conservation*, 110(1): 67–75.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48(1): 58–71.

Coetzee, B.J. & Werger, M.J. a. 1975. A west-east vegetation transect through Africa south of the Tropic of Capricorn. *Bothalia*, 11(4): 539–560.

Dougill, A.J. & Thomas, A.D., 2004. Kalahari sand soils: spatial heterogeneity, biological soil crusts and land degradation. *Land Degradation & Development*, 15(3): 233-242.

Durant, S.M., Wacher, T., Bashir, S., Woodroffe, R., Ornellas, P., Ransom, C., Newby, J., Abáigar, T., Abdelgadir, M., El Alqamy, H. and Baillie, J., 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. *Diversity and Distributions*, 20(1): 114-122.

Dyer, C. 2014. New names for the African Acacia species Vachellia and Senegalia. *Southern Forests: a Journal of Forest Science*, 76(4): iii-iii.

Ellis, G. & Herbst, M. 2013. *Kalahari Gemsbok National Park aerial census report*. Unpublished report to South African National Parks. Pretoria. South Africa.

Eloff, F.C. 1961. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park, Part III. *Koedoe*, 4(1): 18–30.

Eloff, F.C. 1966. Range extension of the blue wildebeest. *Koedoe*, 9: 34–36.

Eloff, F.C. 1984. The Kalahari ecosystem. *Koedoe*, 27(2): 11–20.

Eloff, P. 1962. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. part IV. *Koedoe*, 5(1): 128–136.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Funston, P.J. 2002. *Kalahari Transfrontier Lion Project: Executive Report*. Endangered Wildlife Trust, Upington. South Africa: pp236.

Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria*, 4: 5–114.

Haddon, I.J. & McCarthy, T.S. 2005. Mesozoic–Cenozoic interior sag basins of central Africa: The Late-Cretaceous–Cenozoic Kalahari and Okavango basins. *Journal of African Earth Sciences*, 43(1): 316–333.

Hall-Martin, A.J. & De Graaf, G. 1978. A note on the feasability of introducing giraffe to the Kalahari Gemsbok National Park. *Koedoe*, 21(1): 191–193.

Heine, K. 1989. Some observations concerning the age of the dunes in the western Kalahari and palaeoclimatic implications. *Palaeoecology of Africa and the surrounding islands*, 21: 161–178.

Herholdt, J.J. & Anderson, M.D. 2006. Observations on the population and breeding status of the African white-backed vulture, the black-chested snake eagle, and the secretarybird in the Kgalagadi Transfrontier Park. *Ostrich*, 77(3&4): 127–135.

Jeltsch, F., Moloney, K. & Milton, S.J. 1999. Detecting process from snapshot pattern : lessons from tree spacing in the southern Kalahari. *Oikos*, 85: 451–466.

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33(4): 377–394.

Knight, M.H. 1991. 241 pp. 1991. Ecology of gemsbok Oryx gazella gazella (Linnaeus) and blue wildebeest Connochaetes taurinus (Burchell) in the southern Kalahari. *Ph.D. dissert., University of Pretoria, Pretoria, South Africa.*

Knight, M.H. 1995. Draught-related mortality of wildlife in the outhern Kalahari and the role of man. *African Journal of Ecology*, 33(4): 377–394.

Knight, M.H., Knight-Eloff, A. & Bornman, J.J., 1988. The importance of borehole water and lick sites to Kalahari ungulates. *Journal of Arid Environments*, 15(3): 269-281.

Kruger, J.W., 1994. *The feeding ecology and behaviour of re-introduced giraffe (Giraffa camelopardalis) in the Kalahari Gemsbok National Park.* Ph.D. dissert., University of Pretoria, Pretoria, South Africa.

Laity, J.J. 2008. *Deserts and desert environments, Vol. 3*. Wiley-Blackwell Publishes House, UK.

Leistner, O.A. & Werger, M.J.A., 1973. Southern Kalahari phytosociology.*Vegetatio*, 28(5-6): 353-399.

Leistner, O.A. 1959a. Notes on the vegetation of the Kalahari Gemsbok National Park with special reference to its influence on the distribution of antelopes. *Koedoe*, 2(1): 128–151.

Leistner, O.A. 1959b. Notes on the vegitation of the Kalahari Gemsbok National Park. *Koedoe*, 2: 128–151.

Leistner, O.A. 1959c. Preliminary list of plants found in the Kalahari Gemsbok National Park. *Koedoe*, 2: 152–172.

Leistner, O.A., 1967. The plant ecology of the southern Kalahari. *Botanical. Survey Memoirs. 38. Pretoria: Dep. Agric. Tech. Serv., Bot. Res. Inst.*

Lieth, H. 1975. Primary production of the major vegetation units of the world. In Primary productivity of the biosphere. *Springer Berlin Heidelberg.* 203–215.

Low, A.B. & Rebelo, A.G. 1998. *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: Department of Environmental Affairs and Tourism.

Malherbe. 1984. The Geology of the Kalahari Gemsbok National Park. *Koedoe* 27(2): 33–44.

Melville, H.I.A.S. & Bothma, J.R. 2006. Possible optimal foraging for Brants ' s whistling rats by caracals in the Kgalagadi Transfrontier Park. *African Zoology*, 41(1): 134–136.

Mills, M.G.L. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe,* 27(2): 281–294.

Mills. 1984. The comparative behavioural ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Koedoe*, 27(1): 237–247.

Mills, M.G.L. 1990. *Kalahari hyaenas: The comparative behavioural ecology of two species*. Unwin Hyman, London.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 42(2): 127–137.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. 1995. The Relationship between rainfall , lion predation and population trends in African herbivores. *Wildlife Research*, 22: 75–88.

Mills, G. & Mills, M. 2013. *A natural history guide to the arid Kalahari*. Black Eagle Media (Pty) Ltd. Cape Town.

Mills, M.G.L. & Retief, P.F. 1984. The response of ungulates to rainfall along the riverbeds of the Southern Kalahari 1972-1982. *Koedoe*, 27(2): 129–141.

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

Mudongo, E.I. & Dipotso, M.F. 2011. Predator population estimates in Kgalagadi wildlife management areas , through spoor counts and call-ups.Chapter 2 in 2011 Kgalagadi District, District Biologists Reports. Wildlife populations and problem animal trends in Kgalagadi, southwestern Botswana. *Internal report, Department of Wildlife and National Parks,Tsabong, Botswana*: pp28.

Nagy, K.A. & Knight, M.H. 2008. Energy, water, and food use by springbok antelope (*Antidorcas* marsupialis) in the Kalahari desert. *Journal of Mammalogy*, 75(4): 860–872.

Périquet, S., Fritz, H. & Revilla, E. 2014. The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, 90(4): 1197–1214.

Pole-Evans, I.B. 1936. A vegetation map of South Africa. *Memoirs of the Botanical Survey of South Africa*: 1–23.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*, 22(1): 17–35.

Scholes, R.J. 2011. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography*, 17(4): 415–419.

Schultz, J. 2005. The ecozones of the world. *Berlin: Springer.*

Spinage, C.A. 1992. The decline of the Kalahari wildebeest. *Oryx*, 26(3): 147–150.

Spinage, C.A. & Matlhare, J.M. 1992. Is the Kalahari cornucopia fact or fiction? Journal of Applied Ecology, 29: 605-610.

Stapelberg, F.H., van Rooyen, M.W. & Bothma, J.Du P. 2008. Seasonal nutrient fluctuation in selected plant species in the Kalahari. *African Journal of Range and Forage Science*, 25(3): 111–119.

Steenkamp, C.J., Vogel, J.C., Fuls, A., van Rooyen, N., van Rooyen, M.W. 2008. Age determination of Acacia erioloba trees in the Kalahari. *Journal of Arid Environments*, 72(4): 302–313.

Thomas, D. & Shaw, P.A. 1991. The Kalahari Environment. *Cambridge University Press*.

Tyson, P.D. & Crimp, S.J. 1998. The climate of the Kalahari transect. *Transactions of the Royal Society of South Africa*, 53(2): 93-112

van Rooyen, A.F. 2000. *Rangeland degradation in the southern Kalahari.* Doctoral dissertation, University of Natal, Pietermaritzburg, South Africa.

van Rooyen, M.W., van Rooyen, N. & van den Berg, H.M.. 2008. Landscapes in the Kalahari Gemsbok National Park , South Africa. *Koedoe*, 50(1): 99–112.

van Rooyen, N., van Rensburg, D.J., Theron, G.K. & Bothma, J.D.P. 1988. A check list of flowering plants of the Kalahari Gemsbok National Park. *Koedoe*, 31(1): 115–135.

van Rooyen, N. & Van Rooyen, M. 1998. Vegetation of the southwestern arid Kalahari: an overview. *Transactions of the Royal Society of South Africa*, 52(2): 113–140.

van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the kgalagadi transfrontier park: modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

Verlinden, A. 1998. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. African Journal of Ecology 36: 117–128.

Wergner, M.J.. 1986. The Karoo and southern Kalahari. In: Evenari, M., Noy-Meir, I. & Goodall, D.W. (eds.). Hot desert and arid shrublands. *Amsterdam: Elsevier*: 283–359.

Wiggs, G.F.S., Livingstone, I., E, Thomas, D.S.G. & Bullard, J. 1994. Effect of vegetation removal on airflow patterns and dune dynamics in the southwest Kalahari Desert. *Land Degradation & Development*, 5(1): 13–24.

Woodroffe, R. & Frank, L.G. 2005. Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation*, 8(1): 91–98.

Chapter 3:
Effective estimation of abundance and demography: Lions (*Panthera leo*) in the Kalahari Gemsbok National Park

3.1. Introduction

Lion (*Panthera leo*) are a threatened species that is vulnerable to extinction due to a range decrease of up to 80% and an approximate 30% decline in numbers in the last 20 years (Chardonnet, 2002; Bauer *et al*., 2005; Bauer *et al*., 2015). Several studies of population size estimates across Africa suggested that as few as 23 000 and up to 39 000 lions still inhabit Africa (Chardonnet, 2002; Bauer *et al*., 2005). A more recent estimate suggests that 32 000 to 35 000 free ranging lions inhabit 65 natural localities across their range (Riggio & Pimm, 2011; Riggio *et al*., 2013). Only ten of these locations were identified as strongholds that protect some 24 000 lions and the Kgalagadi Transfrontier Park (KTP) is one of them (Riggio *et al*., 2013). Despite their rapid decline, there is little consensus on lion numbers, and lion enumeration has yielded discrepancies in some instances due to variation in objectives, methodology and resource constraints (Chardonnet, 2002; Bauer *et al*., 2005; Riggio *et al*., 2013). A key challenge is to identify the optimal technique to define accurate population size, age and sex distributions, demographic variables and trends (Ferreira & van Aarde, 2009; Ferreira & Funston, 2010a). In addition, detecting trends in population size, age and sex structures require measures of precision (Gerrodette, 1978; Ferreira & Funston, 2010a).

Trends in population sizes and structure may inform management decisions in response to human-lion conflict (van Vuuren *et al*., 2005), disease (Ferreira *et al*., 2013), as well as stochastic environmental effects locally and across their range (Foley, 2006). Understanding drivers of demographic variability and associated consequences defines focused conservation actions, as demographic variables compliment trends in population growth (Ferreira & van Aarde, 2009; Trimble *et al*., 2009). On a local scale, a variety of techniques used to define population variables have yielded results on lion abundances in the Kalahari Gemsbok National Park (KGNP) over the past 38 years. These included registration studies, home-range density estimates, track indices, mark-recapture, call-up and modelling techniques (Mills *et al*., 1978; Eloff, 1980; Eloff, 1998; Funston, 2002; Castley *et al*., 2002; van Vuuren *et al*., 2005; Mudongo & Dipotso, 2011; Funston, 2011; Ferreira *et al*., 2013). The first population survey in the KGNP was conducted in 1976 (Mills, 1978). This survey defined age and sex structures from 73 individuals and derived a population size estimate and 95% confidence intervals (CI) from closed-population mark-recapture techniques (N = 130; 95% CI: 108-181) (Mills *et al*., 1978). This was followed in 1996 by another mark recapture survey where age and sex structures were derived from two sampling events of 84 and 79 individuals respectively and the population size estimate yielded N = 131 (95% CI:

106-156) (Castley *et al*., 2002). Both these studies restricted their mark and recapture activities to the KGNP. However, both implied that the mark-recapture study accounted for lions east of the Nossob River into the Gemsbok National Park (GNP), but did not define the extent of the study area (Mills *et al*., 1978; Castley *et al*., 2002).

In 1998, a two and a half year study of the lion population of the entire KTP used registration studies and home-range density estimates to derive population density (Funston, 2002). The sex and age structure of the population during the study between 1998 and 2001 was derived from 216 and 228 known individuals respectively across the KTP (Funston, 2002; Funston, 2011; van Vuuren *et al*., 2005). From the density estimates the relationship between track density and true density as a proxy for population size estimates were used, giving a figure of 120 (95% CI: 113-131) in the KGNP (Funston, 2002; Funston *et al*., 2010; Funston, 2011). This was followed by a track index survey of the KGNP in 2010 that estimated the population size to be N = 130 (95% CI: 91-169) in the KGNP. Observation of 49 different individual lions in 2010 provided age and sex structure information (Ferreira *et al*., 2013).

The surveys spanning nearly 40 years suggest that the population has been stable for some time with approximately 130 lions in the KGNP (Ferreira *et al*., 2013). However, the 2010 study of Ferreira *et al*. (2013) indicated a skew in the sex ratio of lions towards a significantly higher number of males, specifically sub-adults (♂ = 75%), whereas before, the population was biased towards females (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011). The observed change in demography is a reason for concern as changes in demographic signals may have deleterious effects on the local and broader KTP lion population (van Vuuren *et al*., 2005; Ferreira *et al*., 2013).

In this chapter, the aim was thus to determine the abundance of lions within the KGNP in a detailed and accurate manner using multiple techniques. To determine a comprehensive and robust estimate of lion abundance and population characteristics, a registration study was conducted that aimed to identify all the lions within the KGNP lion population. From known individuals, a mark-recapture analysis based on individual identification as a marking method and re-sightings as a capture method was applied. Minimum-known-alive estimates and track indices were also used to estimate population size. The precision of each of these techniques were assessed through Monte Carlo simulation. Furthermore, the effort that is required to derive robust estimates of age and sex structure in the population was addressed to identify sample size requirements

3.2. Materials & methods

3.2.1. Study area

The study took place in the Kalahari Gemsbok National Park (KGNP; 9 710 km²), South Africa (RSA) with a 17 km buffer area into the Republic of Botswana's (RB) Gemsbok National Park (GNP; 26 000 km²) (Figure 3.1).The area lies between 24° - 26° 30' South and 20° - 22° East (Bothma *et al*., 1993). The KGNP and GNP are located in the South West of the Kalahari basin. Collectively, the GNP and KGNP are commonly known as the Kgalagadi Transfrontier Park (KTP). A detailed description of the study area characteristics can be found in Chapter 2 of this thesis.

3.2.2. Field data collection

To define lion population characteristics and determine population size, a registration study, using individual identification, was initiated to identify as many lions as possible in the KGNP (Ogutu & Dublin, 2002; Pennycuik & Rudnai, 1970). To achieve this, systematic transects were driven on a monthly basis representing both the dune and riverbed environments across the extent of the KGNP. Random transects were also driven on management tracks throughout the KGNP (Figure 3.1). Lions were located opportunistically on systematic and random transects through chance encounters, following up on sighting reports, following fresh tracks, and following the direction of roars (Stander, 1991). Seven lionesses were collared with GPS/Radio telemetry collars (African Wildlife Tracking^{cc}, Pretoria, South Africa), for various periods, between three months and one year. Lions were captured and collared using the standard techniques employed by the South African National Parks, Wildlife Veterinary Services (Smuts *et al*., 1977; Anonynous, 2008[2]). These collared lionesses were located approximately once per month during the time which they wore the collars. Data were collected over a 24-month period from May 2013 to June 2015. All lions that were sighted were recorded noting approximate age and sex and GPS locations were recorded with a Garmin GPSMAP 62 (Garmin E-Trex, Garmin International, Olathe, KS, USA).

---

[2] Research was conducted with clearance of the Cape Peninsula University of Technology Ethics Committee (Ref. 09/2013). All necessary permits were obtained from the South African National Parks, Skukuza, South Africa; Ministry of Environment, Wildlife and Tourism, Gaborone, Botswana; and the Department of Environment and Nature Conservation, Northern Cape, South Africa.

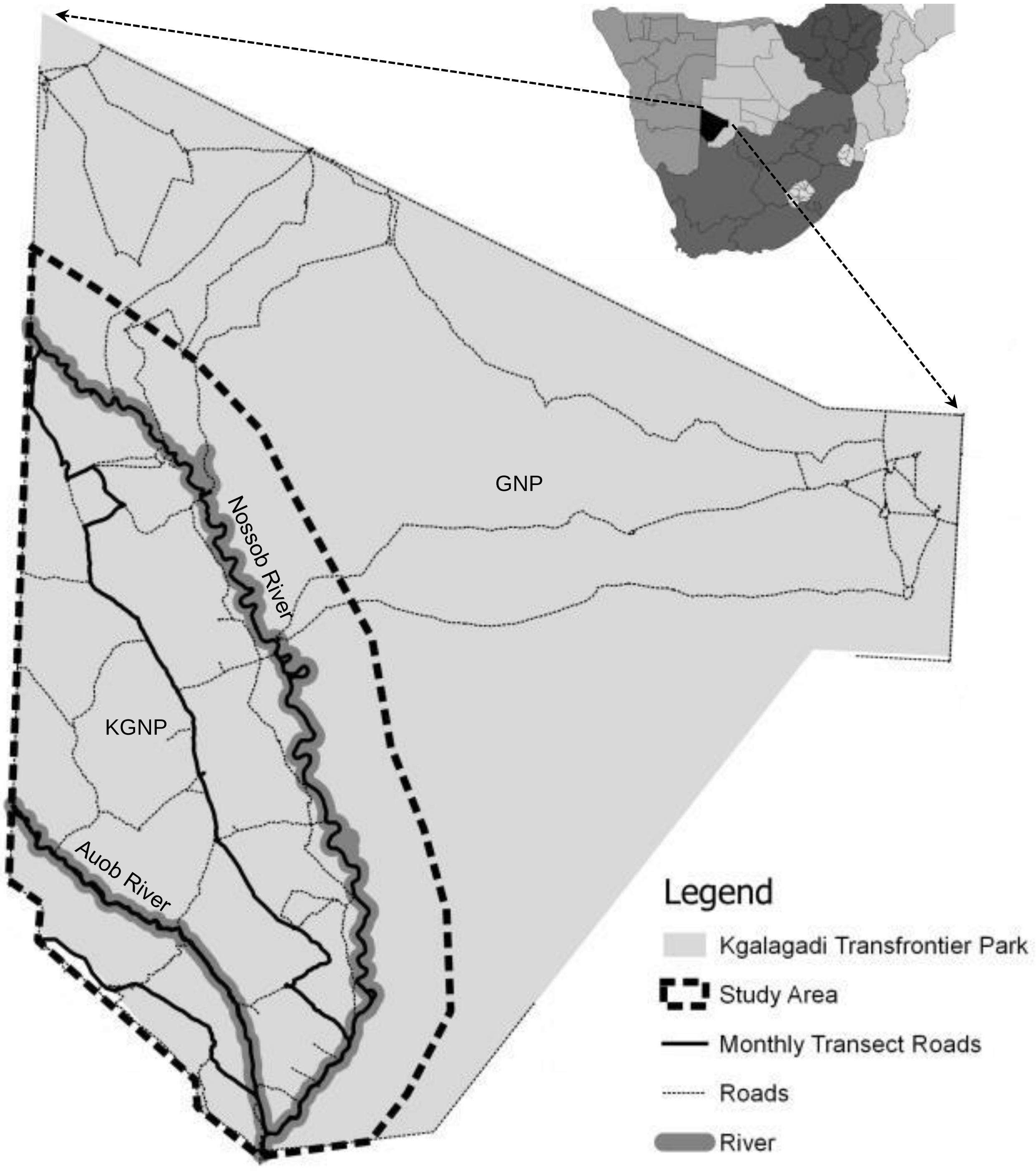

Figure 3.1 Map of the Kgalagadi Transfrontier Park showing the study area (14,250 km²), road networks, riverbeds with a 2.5 km buffer and the transect roads driven during systematic surveys.

3.2.3. Individual identification

Lions were photographed using a Canon 60D camera with either a Sigma 70-500 mm zoom lens or a Canon 25-70 mm macro lens depending on the distance from the subject. Individual identification was achieved primarily by identifying vibrissae spot patterns, which remains constant over time (Figure 3.2) (Pennycuick & Rudnai 1970). Ear nicks (Pennycuick & Rudnai 1970; Elliot *et al*. 2014), nose pigmentation (Whitman *et al*. 2004) and substantial body scars which would remain visible over a long period were used in combination with vibrissae spot patters to further distinguish individuals. A number of lions (n = 39) in the KGNP have been brand marked as part of previous studies or because of being branded when lions transgress from the park. These brand marks aided in the identification of some of these individuals (Funston, 2001; Castley *et al*., 2002; Pers.comm. Ferreira, M. 2015[3]). Sex was determined using visual observation of genitalia and the presence of mane hair in males.

Individual registration of unique individuals was subjected to intense scrutiny of photographic evidence. Individuals were compared to any other individual of the same sex with a similar vibrissae pattern (Pennycuick & Rudnai, 1970). Vibrissae patterns were coded to describe the position of indicator spots (between zero and five spots in the most upper row of vibrissae spots) to the primary spots (between six and nine spots in the row below the indicator spots or the fifth row of vibrissae from the bottom) (Pennycuick & Rudnai, 1970). Comparisons were made of both left and right sides of the face. Coding structure allowed for the creation of a search index of the known individual database that was then used to search for individuals with similar or exactly the same vibrissae patterns. On initial recording an individual identity document (ID) was created for each individual describing its vibrissae patterns, scaring, brand marks, nose pigmentation, ear knicks, group association and location. When individuals with existing IDs were encountered, the ID and database were updated to include any new physical features or refined vibrissae patterns through better images. Individual ID's were compiled into an Identification Catalogue of known individuals in the park (Pennycuick & Rudnai, 1970).

3.2.4. Age assignment

Several subjective factors were used simultaneously to age lions. Ageing methods include the use of nose pigmentation (Whitman *et al*., 2004), tooth wear (Smuts *et al*., 1978; Whitman & Packer, 2006), relative shoulder height of cubs and juveniles in comparison to adults (Smuts *et al*., 1980; Whitman & Packer, 2006; Ferreira & Funston, 2010b) and the

---

[3] Micho Ferreira, Section Ranger, Twee Rivieren, Kalahari Gemsbok National Park, Northern Cape, South Africa. 8800.

extent of mane development in males (Whitman & Packer, 2006). Using a combination of age assignment methods simultaneously provide a comprehensive framework from which to determine approximate age on a subjective basis (Whitman & Packer, 2006). Lions where categorized into four discrete age classes. Cubs were classified as individuals under one year old followed by juveniles, one to two years old; sub-adults, two to four years old and adults over four years old (Whitman *et al*. 2004; van Vuuren *et al*., 2005).

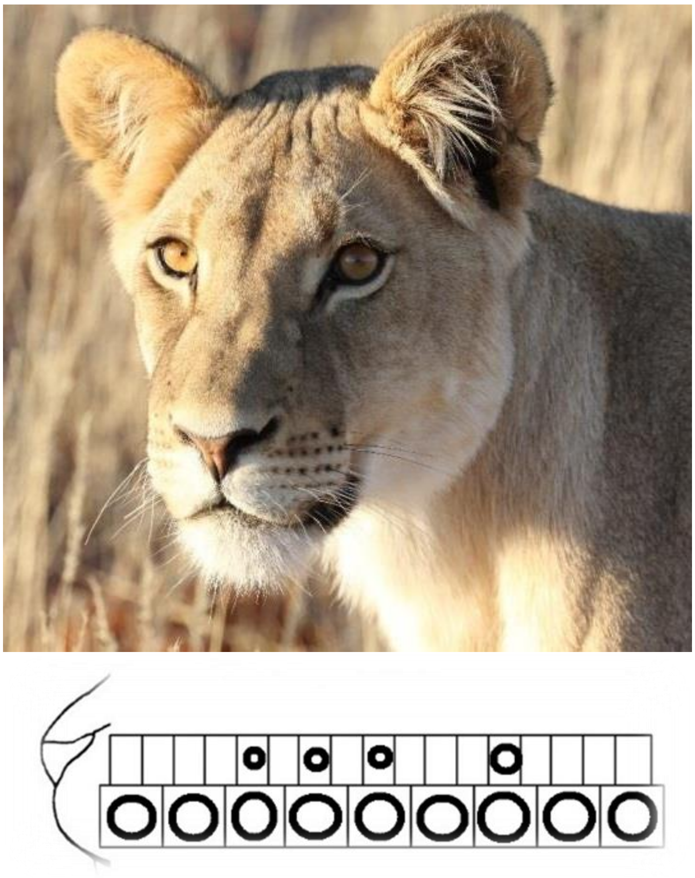

Figure 3.2 Image of a lions face to indicate vibrissae spot patterns. The associated vibrissae spot map indicates the grid system used to define the positioning of the upper two rows of spots.

3.2.5. Mark-recapture

Individual identification was used as a “marking” method (Yoshizaki *et al*. 2008; Sollmann *et al*. 2011; Bonner and Holmberg, 2013). The first time an individual was identified was considered the individuals initial capture and marking event. When an identified individual was re-sighted in a successive recapture event, it was considered as a recapture (Matthews *et al*., 2008). New individuals that were identified during a recapture period were added to the database of known individuals and formed part of the marked population in a subsequent recapture event (Cooch & White, 2015). The initial marking event and subsequent recapture intervals were divided into six discrete periods of four months each. This was done to impose a relatively equal effort distribution across the entire study area. Thus, the initial capture and marking was conducted between May and August 2013 and the five subsequent recapture and marking occasions were conducted in four-month intervals thereafter until May 2015.

3.2.6. Track indices

Lion track density was recorded in the KGNP as a proxy for lion density (Stander, 1991; Funston *et al*., 2010). Six road transects amounting to 774 km (362 km in the dunes and 412 km in the river beds) were surveyed once a month for a twelve month period, totalling 9288 km's (June 2014 to May 2015) (Figure 3.1). Transects were driven slower than 30 km/hour when conducting track counts. Track counts started at least half an hour after sunrise and lasted approximately three hours for the shortest transect (89km) and up to nine hours for the longest transect (273km). Transects that were surveyed in the dunes were single vehicle jeep tracks with a sandy substrate whereas transects in the riverbeds consisted of dual carriage roads with predominantly sandy substrates with some gravel sections.

Track surveys used in the analysis were conducted in the second year of the study (2014/2015) where the same transects were driven consistently on a monthly basis. The same two observers conducted all the track surveys, which increased the consistency in data collection. The position of first encounter of each track set was recorded. Information on the number of tracks (representing individuals i.e. the number of rear left paw prints), the distance that the track was sustained along the transect, the distance between track encounters and the GPS location for the end point of each track set were recorded (Funston *et al*. 2010; Ferreira *et al*. 2013; Balme *et al*. 2009; Stander, 1998). Each of the six road transects were surveyd over six consecutive days when possible, but were not conducted on windy (> 40 km/h) or rainy days as this disturbed the tracks making them difficult to age (Mudongo & Dipotso 2011; Funston, 2001). When track surveys needed to be stopped the process were continued on the next appropriate day. Only tracks considered less than 24 hours old were recorded (Funston, 2002).

3.3. Data analysis

3.3.1. Individual identification

To determine the rate at which new individuals were added to the database of unique individuals, an accumulation curve of new unique individuals were plotted against the number of lions sighted during the study period (Marnewick *et al*., 2014). Using Monte Carlo simulation methods (Robert & Casella, 2013) samples were drawn randomly, at different sample sizes from the complete data set of sightings of the unique individual lions. The number of unique individuals, at each random sample, was counted to determine the variability in the accumulation rate of the number of sightings required to add new individuals to the database. A model was fitted to the simulated accumulation rate data, using the equation Y = a(1-e-bx) (Marnewick *et al*., 2014). The regression describes the acquisition of new individuals on the y-axis as effort (lion sightings) increased on the x-axis. When the accumulation reached a value of less than 0.1 unique individual added per unit of increased effort (lions sighted) it would be considered as evidence that the accumulation curve had reached an asymptote (Marnewick *et al*., 2014).

3.3.2. Track indices

The total number of tracks counted per monthly sample transect (774 km) was converted to tracks per 100 km (Stander, 1998; Funston, 2002; Funston, 2011). A robust ($R^2 = 0.97$) linear relationship was found between track density and true lion density in the KTP (Funston, 2002; Funston *et al.,* 2010). Track densities (n/100km) were translated into lion density per area (lions/100 km²), using the conversion in the linear equation: $t_i = 3.30x_i – 0.32$, where t_i is the spoor density and x_i is the estimated lion density at site i (Funston *et al.,* 2010). The area density was then extrapolated to the study area for a population size estimate. Monte Carlo Simulations were used to determine confidence intervals around the mean track density calculated from different numbers of transects (Rollett & Manohar, 2004; Robert & Casella, 2013). Two hundred iterations for each sample size from one transect through to eleven transects were simulated to determine the variability around the mean, by randomly drawing track densities, with replacement, from the 12 densities estimates obtained from the 12 transects conducted during this study. To identify the minimum number of surveys that can be conducted for reliable populations size estimates of lions, the F-test (Hartley, 1950) was applied in Microsoft Excel (Microsoft Excel, 2010) to discern the point between sample sizes where homogeneity of variance was reached (Hartley, 1950) as track density sample effort increased. Single-factor ANOVA was used to determine significance in the differences in track density between habitats (riverbed and dunes) and between the hot-wet season (November – April) and cold-dry season (May - October) (Bothma & Bothma, 2006).

3.3.3. Mark-recapture

The Program MARK (v.8.1) (White & Burnham, 1999) was used to derive mark-recapture results. Model selection using a Model Likelihood Estimator (MLE) and Likelihood Ratio Test (LRT) (White & Burnham, 1997; Cooch & White, 2015) were used to determine the most

parsimonious model with which to derive population estimates with the available data. A derivative of the Cormack-Jolly-Seber (CJS) model referred to as POPAN was used in an open-population mark-recapture analysis (Goswami *et al*., 2011; Cooch & White, 2015).
The most parsimonious model equation from several candidate equations from POPAN was applied to determine population size (Goswami *et al*., 2011; Reisinger *et al*., 2011; Cooch & White, 2015). Goodness-of-fit (GOF) was calculated in the Program RELEASE (v.3)(Burnham *et al*., 1987; Lebreton *et al.,* 1992; White & Burnham, 2015), an extension of the Program MARK, where six four-month capture occasions were tested to determine whether there was any significant variability in survival or capture probability between each capture occasions and between individuals. Data input into the model included all identified individuals at the initial capture event and five subsequent marking-recapture events. New individuals identified within each recapture interval were catalogued and considered as marked individuals in consequent recapture events. The proportion of marked individuals within the population thus increased with each consecutive mark-recapture interval (Cooch & White, 2015).

The difference between the population size estimates at each mark-recapture event was compared. The F-test (Hartley, 1950; Microsoft Excel, 2010) was used to define the sample size after which point the variance does not decrease significantly by applying more effort (Hartley, 1950; Nylund *et al*., 2007). Point estimates of population size were compared using 95% confidence intervals to determine differences in population size estimates as a function of increased mark-recapture events and the resulting increase in the proportion of marked animals in the sample population. Comparisons where made including and excluding cubs under one year old. This was done because the presence of cubs in the population changes sporadically and may influence final population size estimates (Franklin & Walker, 2010; Castley *et al*., 2002; Pearl, 2000).

3.3.4. Minimum-known-alive

The most conservative population size estimate that can be derived from the registration study is the minimum number of individuals known to be alive within a specific month (Everatt *et al*., 2014). From known individuals identified over multiple sighting events the minimum number of individuals known to be alive can be calculated using a Jolly-Seber mark-recapture matrix design (Efford, 1992; Krebs, 1966). Where a known individual is either recorded or not recorded at a capture interval (i.e. in a specified month), but was recorded in a subsequent capture interval one may infer that the individual was present in the population during the capture interval even when not recorded. When this is applied to each individual, one may substitute a non-record with a record if the individual was observed subsequently;

this is known as a ‘pseudo-record’. Adding all the individuals per month either recorded or pseudo-recorded made it possible to calculate the number of individuals known to be alive within that month (Efford, 1992). Using this rationale the highest number of “minimum-known-alive” lions and the month within which these lions were known to be alive, could be calculated.

3.3.5. Defining age and sex structure

To derive accurate age and sex structure parameters, a sufficient sample size of uniquely identified individuals is required. Monte Carlo Simulation was used to simulate variable results from different sample sizes of age and sex structure from the database of all known individuals in the current study (Rollett & Manohar, 2004). Monte Carlo simulations were applied using randomized number sequences, to select sub-samples of unique individuals at random from the dataset of all the unique individuals identified in this study (Rollett & Manohar, 2004). The simulations were iterated at incremental sample sizes to detect the rate at which precision increased as sample size increased. At each iteration, the proportion of males and females, and the proportions of adults, sub-adults, juveniles and cubs were described for the sub-sample of the “population”. From numerous iterations at different sub-sample sizes, confidence intervals could be calculated at specific sample sizes from the entire dataset (Cortés, 2002). The total number of lions identified in this study was considered representative of the total population and was the sample against which derived estimates and residuals of age and sex structure could be compared. The F-test was used to determine the sample size at which point the variance became homogenous (Hartley, 1950). From this, the optimal number of individuals that are representative of the population could be derived for a robust estimate of age and sex structure.

3.3.6. Method comparison

Point estimates of population size were compared using 95% confidence intervals to determine differences in population size estimates from the different methods that were applied during the current study. As a measure of precision, the percent coefficient of variance (CV) for each method applied during this study was calculated (Thorn *et al*., 2010; Gerrodette, 1978). Mark-recapture and track indices are also compared in their ability to detect a sufficient number of unique individuals to derive robust age and sex structure information from the minimum effort required to determine robust population size estimates.

3.4. Results

3.4.1. Individual identification

Between May 2013 and June 2015 a distance of 49 784 km were driven over 317 sampling days in search of lions. Sixty-two percent (31 162 km) of the distance were covered in the riverbeds and 19 463 km (38%) were driven in the dunes. During the study period, 1162 lions were encountered of which 1022 were identifiable (Figure 3.3). From the 1022 identifiable lions recorded, 261 unique individuals could be identified, which translate to an average of 4.45 lion sightings needed per unique individual. An accumulation of new individuals decreased with increased effort and reached an asymptote (where $y < 0.1$) by 556 sightings, at which point $y = 0.099$ new lions added for every lion sighting ($y = 2.14^{-0.005x}$; $R^2 = 0.83$) (Figure 3.4). At the point where the asymptote was reached, 213 unique individuals had been identified, which accounted for 82% of the known population. Accumulation of unique individuals from sighting events decreased drastically after approximately 800 sightings with only nine new individuals added to the database over the last 222 sightings. The death of 11 of the 261 identified lions could be confirmed during the study period and 74 of the identified lions were cubs born into the population during the survey. Sampling effort was biased towards the riverbed (62% of distance travelled) where most (72%) of the identified lions were encountered. Encounter rates were 1.72 (± SD = 1.72) lions per 100 km driven in the dunes compared to 2.28 (± SD = 1.68) lions per 100 km in the riverbeds. The majority (69%; n = 179) of unique individuals where seen more than once and 45% (n = 117) of the known population were seen three times or more.

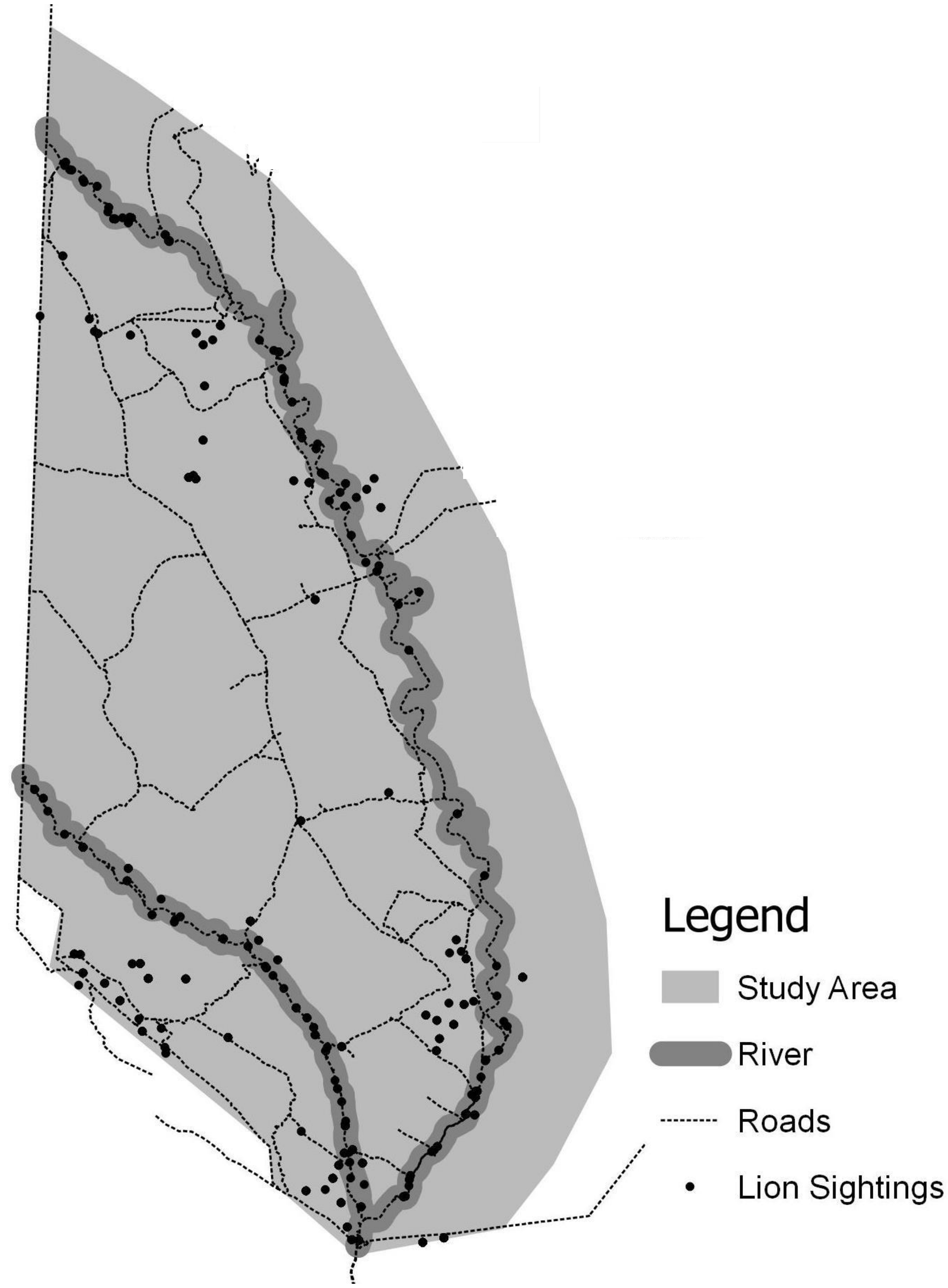

Figure 3.3 The map presents all the identifiable sighting records (n = 1022) over 299 sighting events, from which 261 unique individuals were described. The majority of effort (62%) and the majority of lion sightings (72%) were in the riverbeds and a 2.5 km buffer around the riverbed.

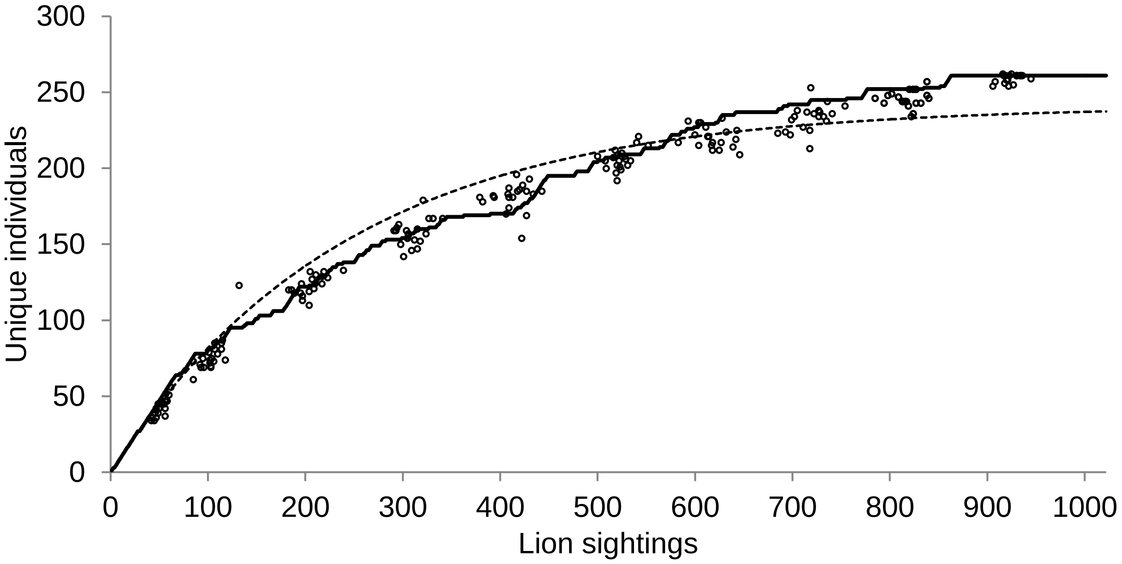

Figure 3.4 The actual accumulation of unique individuals (n=261) over identifiable sighting events (n=1022) (Solid line). Simulated accumulation at intervals of approximately 100 sightings (circles) is presented. From the model (dotted line) fitted to actual accumulation data of unique individuals, an asymptote of unique individuals per unit effort (lion sightings) was reached after 556 sightings ($y = 2.14^{-0.005x}$; $R^2 = 0.83$).

3.4.2. Track indices

Track density (tracks/100 km), were derived from the 12 track surveys that were conducted on a monthly basis between June 2014 and May 2015. The monthly track surveys showed substantial differences in track density per survey with an average track density of 5.29/100 km (95% CI = 3.86-6.72; Range = 2.2-10.3) (Figure 3.5). An insignificant decrease in variance was observed between nine and 10 samples, but homogeneity of variance was not reached as sample size increased. There was no significant difference in variance between two repeated track surveys and 12 track surveys ($F_{0.05} = 0.36$; d.f. = 2; $p = 0.29$). Four out of the twelve track survey point estimates fell outside the 95% confidence limits of the accumulative average track density.

Although the margin of error did not decrease significantly with increased effort from the 12 track surveys conducted, Monte Carlo Simulations indicate a high probability of decreased margins of error when effort is increased (Figure 3.6). Track densities were iterated 200 times at different sample sizes from one track survey to 11 track surveys to determine the probable margins of error at particular sample sizes. The test statistic values for homogeneity of variance between different sample sizes are tabulated for each sample size (Table 3.1). Homogeneity of variance is only reached between nine and 10 track surveys ($F_{1.24} = 1.26$; d.f. = 199; $p = 0.06$). However, variance continues to decrease significantly after 10 track surveys. The variance in confidence intervals decreased by 70% between two and six samples and showed a decrease in variance from two to 11 samples of 90%.

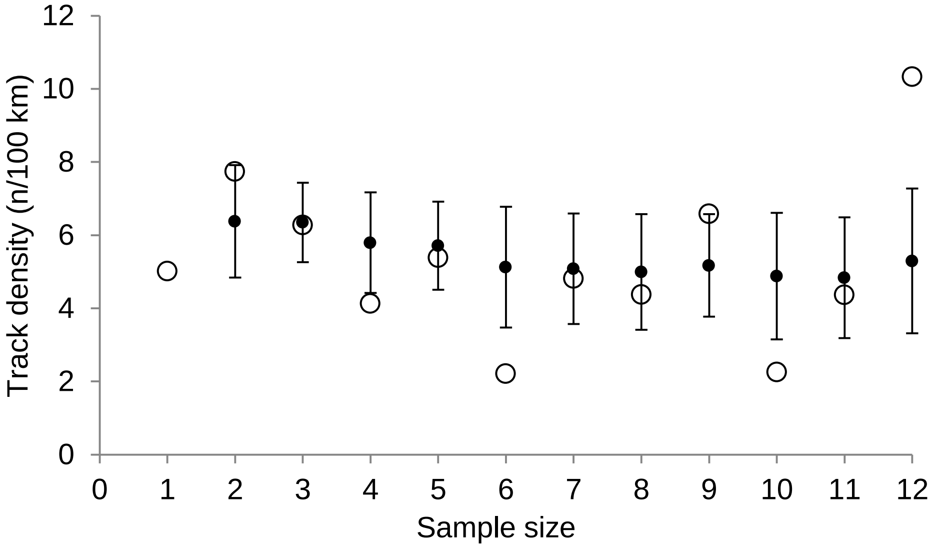

Figure 3.5 Average track density estimates calculated from each of the 12 transect surveys with each transect covering 774km. The average track density encountered per survey event are shown as open symbols while the accumulative mean incorporating the preceding surveys' density values and the present one are represented as closed symbols. Error bars depict 95% confidence intervals derived from the accumulative point estimates of the 12 samples.

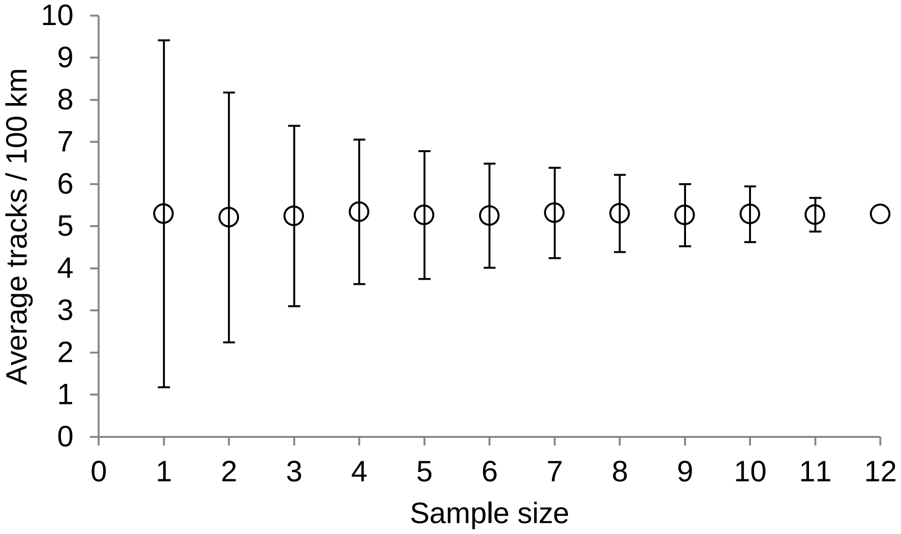

Figure 3.6 Average track densities with 95% confidence intervals for different numbers of transect surveys. Averages and confidence intervals are calculated from 200 Monte Carlo simulations per number of transect surveys randomly drawn from the 12 surveys that were conducted.

Using the conversion factor from track density to true density derived from previous studies in the KGNP (Funston, 2002; Funston *et al.*, 2010) average lion density from all 12 samples was found to be 1.69/100 km² (95% CI: 1.24-2.16). There was no significant difference between track density between the hot-wet and cold-dry seasons ($F_{4.96}$ = 4.33; d.f. = 1; p = 0.06). When lion density is extrapolated to the KGNP (9,780 km²) as with previous track density estimates using similar road networks, the population size translates to 164 (95% CI: 120-209). However, when extrapolated to the study area (14,250 km²) covered by the mark recapture study, the population size was estimated to be 242 (95% CI: 176-307).

Table 3.1 Test statistics using the F-test (two samples for variance) to detect homogeneity of variance between the number of repeated surveys of the sample transects (774 km). Variance was derived from 200 Monte Carlo simulations at incremental sample sizes drawn from the entire dataset (n = 12 transects) in the current study.

Comparable	F-test			
	F	F Crit	P(F ≤ f)	d.f.
1-2 surveys	1.92	1.26	< 0.00	199
2-3 surveys	1.93	1.26	< 0.00	199
3-4 surveys	1.56	1.26	< 0.00	199
4-5 surveys	1	1	< 0.00	199
5-6 surveys	1.5	1.26	< 0.00	199
6-7 surveys	1.33	1.26	< 0.00	199
7-8 surveys	1.36	1.26	< 0.00	199
8-9 surveys	2	1	< 0.00	199
9-10 surveys	1.24	1.26	0.06	199
10-11 surveys	2.78	1.26	< 0.00	199

3.4.3. Mark Recapture

Capture occasions consisted of approximately 52 (± 8) field days (> 8 hours observation), and approximately 8119 km (±1676 km) of survey effort within a four month period. The Goodness-of-fit Test 2 (equal detectability; $\bar{x}$ = 10.98, d.f. = 16, p = 0.81) and Test 3 (equal survival probability; $\bar{x}$ = 26.95, d.f. = 33, p = 0.76) showed that the POPAN model had an adequate combined fit to the data ($\bar{x}$ = 37.93, d.f. = 49, p = 0.87) with no significant differences in survival or capture probabilities between capture occasions. However, Test 3.SR indicated that capture occasion five showed a significant (p = 0.02) probability of transient individuals occupying the dataset. From model selection in the Program MARK (White & Burnham, 1999) the most suitable candidate model equation to use on the available data was determined. The candidate model with the lowest Akaike’s Information Criterion (AIC), Delta AIC below two, highest AIC Weight and with a model likelihood closest to one indicates the most parsimonious fit (Cooch & White, 2015). The most parsimonious equation was where survival probability (phi) was constant and did not change between capture occasions; the capture probability (p) of individuals differed over time. Furthermore, the probability of entry (pent) into the population (either through immigration or birth) differed over time and the “super population” from which the sample is drawn (N) remained constant (Model equation in POPAN = phi(.),p(t),pent(t),N(.)) (Table 3.2). Eight population size estimates were derived using the available data by calculating the population size after each mark-recapture event including and excluding cubs (Table 3.3).

Table 3.2 Candidate model selection for POPAN population size estimation in the Program MARK. The various models operate under the assumptions that a variable is either time dependent (T) or constant (C) over the study period. Factors that are taken into account in the model are survival probability (phi), encounter probability (p), probability of entry into the population (pent) through either immigration or birth, and population size (N). Model selection is achieved through the comparative Akaike's Information Criterion (AIC) which determines the likelihood of suitability of the test against other models. The model at the top of the table was found to be the most parsimonious.

phi	p	pent	N	AIC	Delta AIC	AIC Weight	Model Likelihood
C	T	T	C	1029.276	0	0.595	1
T	C	C	C	1031.905	2.629	0.159	0.269
T	T	T	T	1031.905	2.629	0.159	0.269
C	C	C	C	1034.545	5.269	0.043	0.072
T	T	T	C	1034.545	5.269	0.043	0.072
T	T	C	C	68260.03	67230.8	0	0

Table 3.3 Population size estimates using POPAN mark-recapture in the programme MARK. Estimates are presented as a function of increasing number of re-sighting (recapture) occasions. Estimates are also represented with and without cubs less than one year old. The Coefficient of Variance (CV) is shown to define the measure of precision at a certain sample size. Also presented are the number of individuals captured during the capture occasion (n), the number of marked individuals in the sample and the total number of unique/marked individuals known at the start of the sample occasion.

No. of mark recapture occasions	Cubs included	Best Estimate	Lower 95% CI	Upper 95% CI	CV	No. captured	No. of marked individuals in captured sample	No. of marked/known individuals in population
Three	No	146	130	170	0.14			
Three	Yes	164	146	191	0.14	93	46	101
Four	No	161	152	170	0.05			
Four	Yes	199	183	220	0.09	154	97	148
Five	No	183	175	198	0.06			
Five	Yes	262	251	280	0.06	233	183	205
Six	No	167	160	177	0.05			
Six	Yes	246	238	256	0.04	188	166	255

The results from three mark-recapture events did not show a significant difference between estimates including and excluding cubs as the 95%, confidence intervals overlap (Figure 3.7). However, population size estimates differed markedly between estimates including and excluding cubs at four, five and six mark-recapture events with no overlap in confidence intervals. Particularly, mark-recapture events five and six show distinctly different results including cubs, from all other mark-recapture estimates.

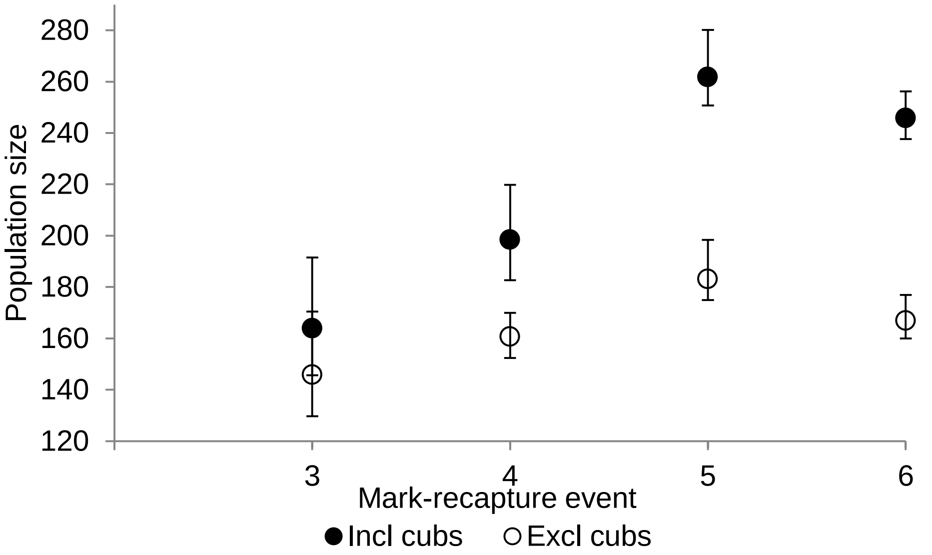

Figure 3.7 Population size estimates using POPAN mark-recapture in the programme MARK. Estimates are presented as a function of increasing number of mark-recapture events (x-axis) including cubs and excluding cubs, to visually compare estimates and illustrate the effect of recruitment on population estimates using mark-recapture.

When cubs were excluded from the estimates, mark-recapture event five showed a difference from capture events three and four but no difference was noted to mark recapture event five. Standard error decreased by 58% from three samples (SE ±12.33) to six samples (SE ±5.11). Homogeneity of variance was reached at three capture occasions exclusive and inclusive of cubs. Precision did not increase significantly with an increase in the proportion of marked individuals after three mark-recapture occasions (Table 3.4). In terms of effort, this would require three repeated mark-recapture occasions, with each occasion comprising of traveling approximately 8119 km looking for lions over approximately 53 sample days with effort equally distributed across the KGNP per capture events.

Table 3.4 Test statistics between capture intervals and cub presence. F-test, two samples for variance was used to determine significant variability between the numbers of sampling occasions.

Comparable	F-test (one tailed)			
	F	F Crit	P(F ≤ f)	d.f.
Incl. cubs 3 vs.4 captures	1.15	3.44	0.42	8
Incl. cubs 4 vs.5 captures	1.2	3.44	0.39	8
Incl. cubs 5 vs.6 captures	0.79	0.29	0.38	8
Excl. cubs 3 vs.4 captures	1.28	5.05	0.39	5
Excl. cubs 4 vs.5 captures	1.22	5.05	0.41	5
Excl. cubs 5 vs.6 captures	0.78	0.19	0.39	5
Incl. vs. Excl cubs 6 occasions	0.76	0.27	0.35	8
Incl. vs. Excl cubs 5 occasions	0.74	0.27	0.34	8
Incl. vs. Excl cubs 4 occasions	0.75	0.27	0.34	8
Incl. vs. Excl cubs 3 occasions	0.83	0.27	0.39	8

3.4.4. Minimum-known-alive

Calculations of minimum known alive individuals reached its highest level in November and December 2014 with 145 unique individuals, representing 65% of the identified population (n = 223) at that point (Figure 3.8). All individuals known to be alive were considered resident as they were recorded associating with prides that are known to reside within the study area.

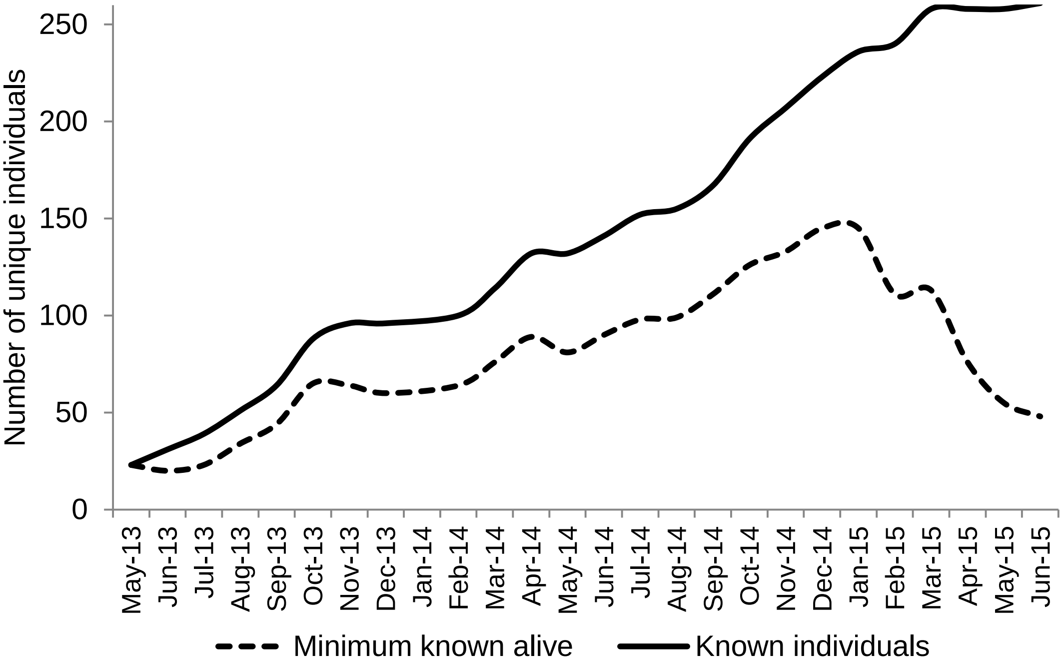

Figure 3.8 Unique individual accumulation (Known ID) and number known to be alive per month (Known alive). Minimum known alive individuals were at their highest during November and December 2014 (n=145).

3.4.5. Age and sex structure

Proportional age class and sex distribution were derived from the total number of known individuals (n = 261). One thousand Monte Carlo Simulations, drawing individuals randomly from the total pool of known individuals, at increments of 10% of the total sample size, indicate that the standard error around the mean decrease rapidly up until 50 samples whereafter the decrease becomes much less pronounced. A standard error of less than 5% of the sex structure is reached at 80 samples (95% CI = ± 9.38). Homogeneity of variance was not reached ($F_{1.11} < 1.57$; d.f. = 999; $p < 0.001$) and precision continued to increase significantly with increased effort (known ID's) (Figure 3.9). Even at 240 samples of unique individuals of the sample set of 261, 95% confidence intervals could have up to two percent margin of error in the upper and lower limits of the sex ratios. From the registration of individuals, the overall proportional sex structure was calculated at 49% males to 51% females. Age structure showed a relationship of 55% adults to 12 % sub-adults, 13% juveniles and 20% cubs at the end of the study period.

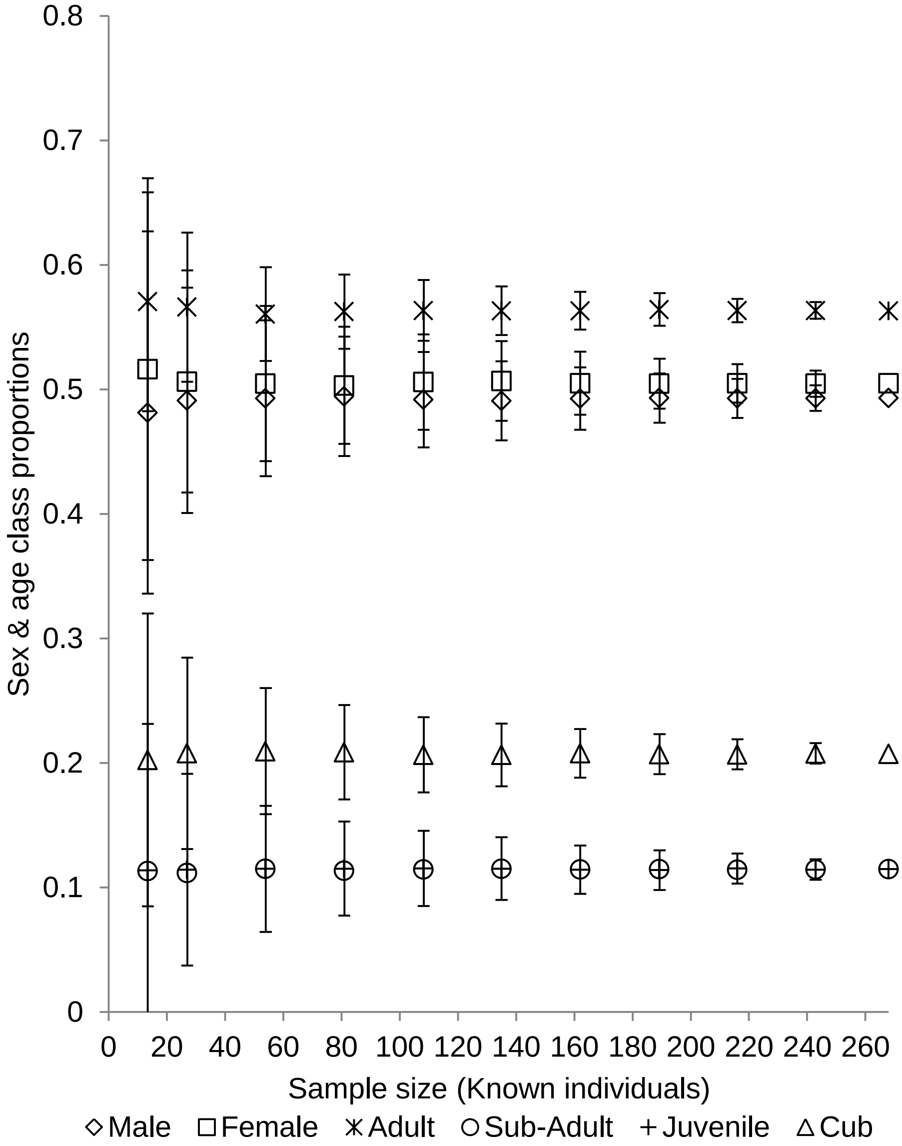

Figure 3.9 The average proportion of age classes and sex ratios were derived from subsampling the total dataset comprising of 261 unique individuals using Monte Carlo simulation. Standard errors were derived from 1000 Monte Carlo simulations drawn randomly from the database of unique individuals. Homogeneity of variance was not reached between sample sizes and precision increases significantly with an increased number of samples.

3.4.6. Method comparison

The accumulation curve identifying unique individuals reached an asymptote after 556 lion sightings which was reached 18 months into the study (October 2014) and represented 213 unique individuals from the database of all registered individuals (n = 261). Mark recapture from known individuals over six repeat mark-capture events of four month periods each, gave a population size estimate of 246 (95% CI: 237-256). From 12 repeated samples of track indices the population size was estimated at 242 (95% CI: 176-307) for the study area. The population size estimates of mark-recapture estimates and track indices showed corresponding 95% confidence limits with the known population of unique individuals (n =

261) with the exclusion of known deaths (n = 11) and potential transient individuals (n = 36) which were present in the study area during the study period (Figure 3.10). This indicates that both mark-recapture estimates and track indices are representative of the population being measured. The minimum-known-alive calculation falls outside of the confidence limits of mark-recapture estimates and track index estimates which indicates an under representation of the measured population size. Using coefficient of variance (CV) as a measure of precision on mark recapture (CV = 0.037; SE = 0.014) and track indices (CV = 0.42; SE = 0.042), mark-recapture was the most precise throughout the study.

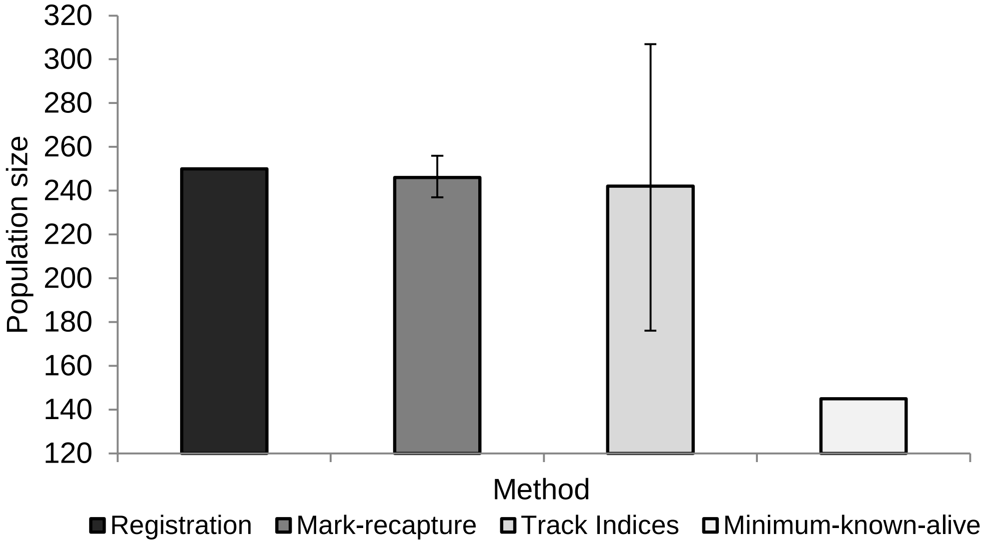

Figure 3.10 Population size estimates from the registration study indicate the identified individuals excluding known mortalities during the study period. Mark-recapture estimates including cubs (> 1 yr) and track index estimates are presented with 95% confidence limits at the end of the study period (May 2015) and the minimum-known-alive figure is presented for November/December 2014.

Considering that homogeneity of variance was not reached for age and sex structure estimates derived from different sample sizes it was not possible to define a minimum sample size from which to derive robust estimates. However, the potential margins of error that would exist at different sample sizes could be defined and related to the minimum effort required to derive population size estimates from the various methods that were applied during the study. For mark-recapture estimates, the minimum required effort to derive robust estimates of the population older than one year would be three mark-recapture events. The number of unique individuals acquired within the effort for three mark-capture events amounted to 131 unique individuals in the current study. At a sample size of 131 unique individuals, the margin of error that may be expected in age and sex structure would be approximately ± 4.1% and ± 6.2% (95% CI) respectively.

3.5. Discussion

Population size estimates from mark-recapture of (N = 246; 95% CI: 237-256), track indices (N = 242; 95% CI: 176-307) as well as a registration study (N = 250, after removing known deaths), gave similar estimates of lion population size in the KGNP. Mark-recapture estimates showed the greatest precision in population size estimates in comparison to track indices and minimum-known-alive estimates derived from the registration study. Minimum-known-alive calculations grossly underestimated the size of the population under observation, which may be expected (Efford, 1992). Total enumeration of all the individuals in a lion population is the most robust method in defining lion population characteristics (Pennycuick & Rudnai, 1970; Franklin & Walker, 2010). However, registering individuals, particularly at low population densities, over large study areas, takes large amounts of resources and time (Carbone *et al*., 2008; Balme *et al*., 2009; Blanc *et al*., 2014).

Constraints on identifying individuals in the KGNP pertain to the open (unfenced) nature of the ecosystem. Survey efforts were mostly constrained to the KGNP and extended marginally into the GNP. It is possible that lions that were identified throughout the study period will utilize areas outside the core study area in the KGNP, within the larger KTP. Defining the exact extent of the area occupied by lions counted in this study, which were considered to be the lions observed predominantly in the KGNP, remains a challenge. In the current study, the study area was defined through observing the movements of five lionesses, fitted with GPS collars in the KGNP that had measurable home ranges that extended into the GNP. From the home-range data obtained from the collared lions, it was assumed that the lion population that was observed during this study, had home-ranges that were predominantly in the KGNP, but could have extended approximately 17 km east of the Nossob River, into the GNP (Chapter 2).

Open-population mark-recapture analysis faces constraints in that the sample population is not defined by spatial boundaries. The POPAN model, which was applied in the program MARK, derives population estimates from what is known as the “super-population” (Fearnbach *et al*., 2012). The super-population identifies the number of individuals that could potentially enter the core study area, from an area that extends beyond the boundaries of the study area. The calculations made in the Cormack-Jolly-Seber models (CJS) models, account for the probability of entry into the observed population from the “super-population”, but do not define the area from which the sample is drawn (White & Burnham, 1997). This provides challenges when comparisons are made between various abundance estimates in an open system such as the KTP (Matthews *et al*., 2008).

In this study, the open population mark-recapture method was applied, due to the extended sampling period, the size of the marked dataset and the nature of the open ecosystem. The open population mark-recapture method was identified as the most appropriate method, considering the assumptions under which the CJS models function (Cooch & White, 2015). Results obtained through the open population mark-recapture method are limited in that they may not be directly comparable to previous mark-recapture results or track indices. The open population mark-recapture method is however, a more precise method as observed in this study and is more likely to detect trends in the population. The open population mark-recapture method has been identified as being more apt in detecting changes in population size (Gerrodette, 1978), whilst simultaneously defining demographic characteristics when using identification as a marking method.

Several assumptions are made when using CJS models (Cooch & White, 2015), one of which, namely the equal detection probability, was compromised in the data collection in this study. During the study period, seven individual lionesses were fitted with GPS collars for a period of between three months and one year, which may have compromised the probability of equal detection of individuals who were associated to collared individuals. Furthermore, the capture probability of collared individuals themselves, changed when the collars were either fitted or removed from the individuals. Due to the social nature of lions, the assumption of individuals being equally catchable is also violated. Detection probabilities are higher for individuals with strong social relationships and occur in groups, compared to individuals who commonly separate from social groups, due to the fission-fusion nature of lion social dynamics in the KTP (Funston, 2011; Marnewick *et al*., 2014). Furthermore, cubs are dependent on their mothers and the probability of their ‘capture’ (detectability) increases when their mothers are captured. However, this can be mitigated by removing cubs from the analysis (Marnewick *et al*., 2014).

The effects of variability in population size estimates, is seen in the current analysis where population size estimates do not drastically change between mark-recapture events, when cubs are excluded from the analysis. However, the POPAN programme has the ability to differentiate individual capture probabilities, through individual capture histories. The POPAN programme then compensates for the variable capture probabilities between capture occasions for each unique individual, based on the individuals capture history (Cooch & White, 2015). Nonetheless, bias in capture probabilities should be considered in the interpretation of the current results. Measures should be taken in future studies to further mitigate bias in capture probabilities by compensating for group formation or through categorical exclusion from datasets (Marnewick *et al*., 2014).

Other assumptions made when conducting the mark-recapture survey such as tag loss or equal survival probability of all individuals between capture occasions, were not considered to impose notable bias on the results. Animals retained their tags or marks throughout the experiment as they were permanent physical features (Pennycuick & Rudnai, 1970), accompanied in some cases by brand marks. Individuals were accurately identified using an 'individual identification catalogue, which was continuously reviewed throughout the study period. A relatively long sampling period, of four months per capture events, was required in order to equally distribute survey effort across the study area and between each mark-recapture occasion. The four-month duration of a mark-recapture period was not considered as enough time to alter an individual's survival probability between sampling events (Mills *et al.*, 1978). Marked and un-marked animals had the same survival probability, as the marking of animals through registration was non-invasive and had no direct effect on an individual's health (Goswami *et al.*, 2011). The study area remained the same throughout the survey, with equally distributed and repeated effort across the study area.

The majority of the cubs (92%, n = 68), that were identified throughout the study period, where born during the period of the fourth and fifth mark-recapture events. An additional six cubs were included through births during the sixth and final mark-recapture event. The peak in births noted between the fourth and sixth mark-recapture events, account for the inflation of mark-recapture estimates (±63 individuals) between estimates, including cubs and excluding cubs at mark-recapture event six. Mark-recapture events three, four and six showed overlapping confidence limits in their estimates. The difference in the estimates of mark-recapture event five may have been on account of temporary immigration of transient individuals. Transient individuals, which could not be associated to a pride, accounted for 14% (n = 36) of the population, and may have accounted for some temporary inflation in population estimates during mark-recapture event five. Considering that when cubs were excluded, mark-recapture occasions three, four and six showed no definitive difference in their estimates, three capture occasions may be sufficient to derive population size estimates when excluding cubs. However, to detect discernible differences between population estimates, including cubs and excluding cubs, four or more mark-recapture events would be required.

Open population mark-recapture estimates appear to be sensitive to the recruitment of new individuals into the population. Where cubs are included in population estimates, results show larger variability over the study period. Including cubs into the mark-recapture simulation may impose larger variability to population estimates, as the presence of cubs in the population fluctuates over time (Castley *et al.*, 2002). Synchronous and seasonal births in lion may periodically increase population size (van Vuuren *et al.*, 2005; Packer & Pusey, 1983). Therefore, excluding cubs (< 1yrs) from mark-recapture analysis may give a more consistent estimate of the population size that is not influenced by influxes of cub births (Franklin & Walker, 2010). However, since there were no apparent differences in estimates when cubs were excluded, and that the variance did not decrease significantly as effort increased, indicates that three mark-recapture occasions (excluding cubs) should be sufficient to derive an accurate and precise estimate of the adult population size.

Track indices on the other hand have been specifically designed to assess the local lion population of the dune savannah habitat within the KGNP and western GNP (Funston, 2002). The equations used in track indices were based on a combination of relationships between track density, population estimates from known individuals (n = 122), and density estimates from collared individuals and associated prides (n = 21) (Funston, 2002). Track indices however, have large spatial and temporal discrepancies, which demand large amounts of effort to be able to derive reliable results from which trends can be detected (Funston *et al*., 2010; Midlane *et al*., 2015), particularly in the dune savannah habitat of the KTP. Track indices are also variable across substrates and may influence the disparity in track density across the park. For instance, there are a number of roads in the KGNP that have been transformed from sand into gravel substrates, making spoor more difficult to detect (Funston *et al*., 2010). This would bias the equations for track indices in the KGNP, towards sandy substrates, on which lion tracks are more easily detected. Furthermore, several of the management tracks on which track counts were conducted, receive little maintenance, leading to seasonal vegetation cover that may obscure tracks, particularly during the rainy season (Pers. Obs. 2013-2015). Several road transects that were used to conduct track counts were only travelled sporadically by park staff, whilst other roads were used more frequently by tourists. A high frequency use of the road transects by other users could have destroyed evidence of lion tracks that may have been present. This however, is unavoidable, and all track surveys prior to this study, and those that will be replicated in the future will encounter the same disturbance imposed on tracks by other users, negating the significance of this bias. Considering the large margins of error on occasional track surveys, and the large presence of outliers from the mean track density, the use of track indices to determine trends in the population may not be feasible in the KGNP.

Even though a substantial amount of effort and a broad spectrum of techniques have been applied to determine the population characteristics of lion in the KGNP, several methods have been neglected. Alternative methods of determining lion population characteristics may be well suited to estimating abundance and demographic parameters in the KGNP. For instance, individual identification, through the use of genetic markers has been used to identify individuals from DNA extracted from faecal samples (Tende *et al*., 2014). Individual identification using DNA analysis does however, bare considerable costs in analysing the data and is more often used in managing human-lion conflict and in wildlife forensics (Miller & Bloomer, 2014; Caniglia *et al*., 2013). Scat collection in itself is a costly endeavour in the KGNP, at approximately 263 km travelled per scat collected (Beukes, 2016).

Call-up stations were used opportunistically throughout the study, in conjunction with evidence of fresh lion spoor. However, there was no systematic use of call-ups and the primary purpose was to aid in locating lions for individual identification. Call-ups have been used in previous lion studies in the KGNP, for mark-recapture purposes and to derive age and sex structures, but not with the objective of determining population size as a direct method (Ferreira *et al*., 2013; Funston, 2002). Call-ups were used in the Wildlife Management Areas bordering the KTP to the east and north of the park, but gave comparatively low-density figure compared to other methods (Mudongo & Dipotso, 2011). Call-ups have however, been used successfully in other areas to attain abundance estimates of lion (Groom *et al*., 2014; Omoya *et al*., 2013; Ferreira & Funston, 2010a; Midlane *et al*., 2015). Call-ups in arid areas are hindered by low lion densities, which result in poor lion response rates, unless accompanied by fresh lion tracks (Ferreira *et al*., 2013; Mudongo & Dipotso, 2011). Call-ups are subject to high seasonal and spatial variability (Cozzi *et al*., 2013). Furthermore, where track indices have been used in conjunction with call-ups, track indices had a significantly higher return rate and precision, and were more efficient in terms of effort and cost in some instances (Mudongo & Dipotso, 2011; Thorn *et al*., 2010). However, in Kafue National Park, Zambia, track indices required more effort and resources and tended to underestimate the lion population (Midlane *et al*., 2015). Call-ups can bias results due to lion behavioural responses, such as in cubs, which often do not accompany adults to the lure (Young-Overton *et al*., 2014).

Camera trapping has become a common method in identifying population size and demographics, particularly for cryptic species such as felids (Maputla *et al*., 2013; Gutierrez-Gonzalez *et al*., 2012; Rowcliffe & Carbone, 2008). Mark-recapture analysis and occupancy modelling can be used to estimate population size through individual identification using photographs obtained from camera traps (Maputla *et al*., 2013). The use of camera trap photographs for individual identification proves inadequate for use on lions. This is because lions have few obvious features from which to identify individuals, and very specific photographs of identifiable features are required for identification (Cozzi *et al*., 2013). We collected the vast majority of images which were used to identify individuals in the current study by observing subjects for several hours taking multiple images (often more than a hundred) to attain the required image quality with which to confirm individual identity. Therefore, camera traps were not considered as an appropriate method for use in the current study. Occupancy modelling, based on presence (detection) or absence (non-detection) data in a defined area, is also frequently used in conjunction with camera trapping and sign surveys (indices of abundance) to detect presence or absence as a surrogate for density estimates (Mackenzie & Nichols, 2004; Midlane *et al*., 2014). The analysis of occupancy modelling, however, operates under similar assumptions to closed population mark-recapture analysis, which could not be accounted for in this study (Everatt *et al*., 2014; Midlane *et al*., 2014).

All population size estimates obtained in this study, except open population mark-recapture, show very poor precision. Methods with large confidence intervals, such as track indices (CV = 39%), require much greater sampling effort in order to compensate for the lack of precision. The large sampling effort required could render a method such as track indices impracticable, as resource constraints often restrain research design and could bias results (Garton *et al*., 2011). Alternately, mark-recapture is a relatively intensive technique, with large resource requirements. However, due to the precision that was found for the mark-recapture method, it may require less repetition than the other methods to detect trends. Mark-recapture may thus be the most practicable solution to identifying trends in the KGNP lion population. The extent to which the mark-recapture, track indices and registration study techniques are capable of identifying trends in lion population demographics remain undefined and require further investigation.

The mark-recapture method has been identified as the most appropriate method to define population size while simultaneously identifying demographic characteristics through registration. Identifying characteristics of the age and sex structure of lion within a population appears to be significantly influenced by the sample size of unique individuals obtained through registration. The variability in age and sex structures, at different sample sizes, may hold challenges for detecting trends in demographic parameters. The probability of misrepresenting the population characteristics at small samples, which carry large margins of error, can have consequences for conservationists, who need to detect trends to be able to take appropriate action when required. The male biased sex ratio that was observed in 2010 (56% ♂; Ferreira *et al*., 2013), could have been influenced by the small sample size (n = 49) that was used to derive lion age and sex structures. The relatively equal sex ratio observed in the current study, was derived from the largest dataset of individual lions in the KGNP acquired to date.

The sufficient size of the database is further supported by the asymptote that was reached on the accumulation curve of known individuals. The asymptote indicated that new individuals would most likely be added to the dataset through births and immigrations into the population. Therefore the populations characteristics derived from the current study (n = 261) are likely to be truly representative of the KGNP lion population. A high proportion (88%) of the individuals encountered in the current study could be identified. In the KGNP, this is made possible by the accessibility of the off-road terrain with low vegetation density, allowing observers to get within close proximity of the subject and attain high resolution imagery from which individuals can be identified. The opportunity to attain accurate identification from which to conduct mark-recapture analysis in the KGNP are not challenged by image quality to the same extent as are surveys in densely vegetated terrain (Marnewick *et al*., 2014) or aquatic systems (Reisinger *et al*., 2011) where image quality limits identification.

Equal sex ratios are uncharacteristic of lion populations (Ferreira *et al*., 2013) and the change in demographic characteristics from a female dominated population (Mills *et al*., 1978; Castley *et al*., 2002, Funston, 2011), to a greater or equal proportion of males in the KGNP lion population (Ferreira *et al*., 2013; Current study) remains a concern. The demographic characteristics of lion in the KGNP are defined in more detail in chapter 4. In chapter 5 the findings on population size estimates and demographic characteristics from the current study are compared to findings from historic studies in order to critically assess change over time.

3.6. References

Anonynous. 2008. Kalahari Gemsbok National Park management plan. South African National Parks, Pretoria, South Africa.

Balme, G.A., Hunter, L.T.B. & Slotow, R. 2009. Evaluating Methods for Counting Cryptic Carnivores. *Journal of Wildlife Management*, 73(3): 433–441.

Bauer, H., Chardonnet, P. & Nowell, K. 2005. Status and distribution of lion (*Panthera leo*) in East and Southern Africa. *East and Southern African Lion Conservation Workshop, January 2006, Johannesburg, South Africa*: pp28.

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2015. *Panthera leo. The IUCN Red List of Threatened Species 2015: e.T15951A50658092.*

Blanc, L., Marboutin, E., Gatti, S., Zimmermann, F. & Gimenez, O. 2014. Improving Abundance Estimation by Combining capture-recapture and occupancy data. *Journal of Applied Ecology*, 51(6): 1733–1739.

Beukes, M. 2016. *Spatial and temporal variation of lion (Panthera leo) diet in the Kalahari Gemsbok National Park*. Unpublished masters thesis. Cape Peninsula University of Technology. Cape Town. South Africa.

Bothma, J. du P. & le Riche, E.A.N. 1994. The relationship between minimum air temperature and daily distances moves by Kalahari leopards. *South African Journal of Wildlife Research*, 24(1 & 2): 18–20.

Bothma, J. du P., van Hoven, S. & Le Riche, E.A.N. 1993. GPS-corrected and GIS-based remapping of the Kalahari Gemsbok National Park and the adjacent area in Botswana. *Koedoe*, 36(2): 105–108.

Bothma, J.P. & Bothma, M.D. 2006. Activity patterns in southern Kalahari leopards. *African Zoology*, 41(1): 150–152.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release–recapture. *American Fisheries Society Monograph* 5:1–437.

Caniglia, R., Fabbri, E., Mastrogiuseppe, L. & Randi, E. 2013. Who is who? Identification of livestock predators using forensic genetic approaches. *Forensic Science International: Genetics*, 7: 397–404.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J. & Al, E.T. 2008. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4: 75–79.

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 using a capture–recapture survey. *African Zoology*, 37(1): 27–34.

Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a Status Survey. *International Foundation for the Conservation of Wildlife, France & Conservation Force, USA.*: pp21.

Cooch, E.G. & White, G.C. 2015. Program MARK - A Gentle Introduction (14th edition). *University of Collorado and Cornell University, USA*: pp1067.

Cozzi, G., Broekhuis, F., Mcnutt, J.W. & Schmid, B. 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity Conservation*, 22(12): 2937–2956.

Efford, M. 1992. Revised estimates of the bias in the ‘minimum number alive’ estimator. *Canadian Journal of Zoology*, 70(3): 628–631.

Eloff, F.C., 1980. Cub mortality in the Kalahari lion *Panthera leo vernayi* (Roberts, 1948). *Koedoe*, 23(1): 163-170.

Eloff, F.C. 1998. The life of the Kalahari lion (*Panthera leo vernayi*). *Transactions of the Royal Society of South Africa*, 53: 267–269.

Everatt, K.T., Andresen, L. & Somers, M.J. 2014. Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PLoS ONE*, 9(6): p.e99389.

Fearnbach, H., Durban, J. & Parsons, K. 2012. Photographic mark – recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications*, 22(5): 1689–1700.

Ferreira, S.M. & Funston, P.J. 2010a. Estimating lion population variables : prey and disease effects in Kruger National Park , South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M. & Funston, P.J. 2010b. Age assignment to individual African lions. *South African Journal of Wildlife Research*, 40(1): 1–9.

Ferreira, S.M. & van Aarde, R.J. 2009. Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. *South African Journal of Wildlife Research*, 39(2): 181–191.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Foley, P. 2006. Predicting Extinction Times from Environmental Stochasticity and Carrying Capacity Patrick Foley. *Conservation Biology*, 8(1): 124–137.

Franklin, S. & Walker, C. 2010. *Survey Methods and Practices* F.S. & W.C., eds. Statistics Canada, Ottawa, Ontario, Canada K1A 0T6, (12): pp408.

Funston, P.J. 2002. *Kalahari Transfrontier Lion Project: Executive Report*. Endangered Wildlife Trust, Upington. South Africa: pp236.

Funston, P.J. 2011. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41(1): 1–10.

Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A. & Ferreira, S.M. 2010. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281: 56–65.

Garshelis, D.L. 1992. Mark-recapture density estimation for animals with large home ranges. *. In Wildlife 2001: populations (pp. 1098-1111). Springer Netherlands.*

Garton, E.O., Ratti, J.T. & Giudice, J.H., 2005. Research and experimental design. *Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland*, pp.43-71.

Gerrodette, T.I.M. 1978. A Power Analysis for Detecting Trends Author. *Ecology*, 68(5): 1364–1372.

Goswami, V.R., Lauretta, M.V., Madhusudan, M.D. & Karanth, K.U. 2011. Optimizing individual identification and survey effort for photographic capture – recapture sampling of species with temporally variable morpho;ogical traits. *Animal Conservation*, doi:10.111: 1–10.

Groom, R.J., Funston, P.J. & Mandisodza, R. 2014. Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: what is driving the population collapse? *Oryx*, 48(3): 385–393.

Gutierrez-Gonzalez, C.E., Gomez-Ramirez, M.A. & Lopez-Gonzalez, C.. 2012. Estimation of the density of the Near Threatened jaguar Panthera onca in Sonora, Mexico, using camera trapping and an open population model. *Oryx*, 46(3): 431–437.

Hartley, H.O. 1950. The maximum F-ratio as a short-cut test for heterogeneity of variance. *Biometrica*, 37(3/4): 308–312.

Lebreton, J., Burnham, K.P., Clobert, J., & Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62, 67– 118.

Mackenzie, D.I. & Nichols, J.D. 2004. Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation*, 27(1): 461–467.

Maputla, N.W., Chimimba, C.T. & Ferreira, S.M. 2013. Calibrating a camera trap–based biased mark–recapture sampling design to survey the leopard population in the N'wanetsi concession , Kruger National Park , South Africa. *African Journal of Ecology*, 51: 422–430.

Marnewick, K., Ferreira, S.M., Grange, S., Watermeyer, J., Maputla, N. & Davies-mostert, H.T. 2014. Evaluating the Status of and African Wild Dogs Lycaon pictus and Cheetahs Acinonyx jubatus through Tourist- based Photographic Surveys in the Kruger National Park. *PLoS ONE*, 9(1): e86265. doi:10.1371.

Matthews, S.M., Golightly, R.T. & Higley, J.M. 2008. Mark – resight density estimation for American black bears in Hoopa , California. *Ursus*, 19(1): 13–21.

Melville, H.I.A.S. & Bothma, J.R. 2006. Possible optimal foraging for Brants ' s whistling rats by caracals in the Kgalagadi Transfrontier Park. *African Zoology*, 41(1): 134–136.

Midlane, N., O'Riain, M.J., Balme, G.A., Robinson, H.S. & Hunter, L.T.B. 2014. On tracks : A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park , Zambia. *Biological Conservation*, 172: 101–108.

Midlane, N., O'Riain, M.J., Balme, G.A. and Hunter, L.T., 2015. To track or to call: comparing methods for estimating population abundance of African lions Panthera leo in Kafue National Park. *Biodiversity and Conservation*, 24(6):1311-1327.

Miller, S.M. & Bloomer, P. 2014. Evaluation of Microsatellite Markers for Populations Studies and Forensic Identification of African Lions (*Panthera leo*). *Journal of Heredity*: doi:10.1093/jhered/esu054.

Mills, M.G.L., Wolff, P., le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion *Panthera leo* in the Kalahari Gemsbok National Park. *Koedoe*, 21: 163–171.

Mudongo, E.I. & Dipotso, M.F. 2011. Predator population estimates in Kgalagadi wildlife management areas , through spoor counts and call-ups.Chapter 2 in 2011 Kgalagadi District, District Biologists Reports. Wildlife populations and problem animal trends in Kgalagadi, southwestern Botswana. *Internal report, Department of Wildlife and National Parks,Tsabong, Botswana.*: pp28.

Nylund, K.L., Asparouhov, T. & Muthén, B.O. 2007. Deciding on the Number of Classes in Latent Class Analysis and Growth Mixture Modeling : A Monte Carlo Simulation Study. *Structural Equation Modeling*, 14(4): 535–569.

Omoya, E.O., Mudumba, T., Buckland, S.T., Mulondo, P. & Plumptre, A.J. 2013. Estimating population sizes of lions *Panthera leo* and spotted hyaenas Crocuta crocuta in Uganda ' s savannah parks , using lure count. *Oryx*, 84(3): 394–401.

Packer, C. & Pusey, A.E. 1983. Male takeovers and female reproductive parameters: A simulation of oestrous synchrony in lions (*Panthera leo*). *Animal Behaviour*, 31(2): 334–340.

Pearl, M.C. 2000. *Research Techniques in Animal Ecology: Methods and Cases in Conservation Science*. L. B. and T. K. Fuller, ed. Columbia University Press, New York. pp. 442.

Reisinger, R.R., de Bruyn, P.N., & Bester, M.N. 2011. Abundance estimates of killer whales at subantarctic Marion Island. *Aquatic Biology*,*12*(2), 177-185.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, 22(1): 17–35.

Riggio, J.S. & Pimm, S.L. 2011. *The African lion (Panthera leo leo): A Continent-wide species distribution study and population analysis*. Masters project submitted in partial fulfillment of the requirements for the Master of Environmental Management degree, Nicholas School of the Environment, Duke University.

Robert, C. and Casella, G., 2013. *Monte Carlo statistical methods*. Springer Science & Business Media.

Rollett, A.D. & Manohar, P. 2004a. The Monte Carlo Method. In L.-Q. C. C. Dierk Raabe, Franz Roters, Frederic Barlat, ed. *Continuum Scale Simulation of EngineeringMaterials: Fundamentals–Microstructures–Process Applications.* Wiley-VCH Verlag: 56–78.

Rowcliffe, J.M. & Carbone, C. 2008. Surveys using camera traps : are we looking to a brighter future ? *Animal Conservation*, 11: 185–186.

Pennycuick, C.J. & Rudnai, J. 1970. A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, 160(4): 497–508.

Smuts, G.L., Whyte, I.J. & Dearlove, T.W. 1977. A mass capture technique for lions. East African Wildlife Journal, 15: 81–87.

Smuts, G.L., Anderson, J.L. & Austin, J.C. 1978. Age determination of the African lion (*Panthera leo*). *Journal of Zoology London*, 185: 115–146.

Smuts, G.L., Robinson, G.A. & Whyte, I.J. 1980. Comparative growth of wild male and female lions (*Panthera leo*). *Journal of Zoology*, 190: 365–373.

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.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M. & Silveira, L. 2011. Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatially explicit capture-recapture models for jaguars in central Brazil. Biol. Conserv. 144: 1017–1024.

Tende, T., Hansson, B., Ottosson, U., Åkesson, M. & Bensch, S. 2014. Individual identification and genetic variation of lions (*Panthera leo*) from two protected areas in Nigeria. *PLoS ONE*, 9(1): p.e84288.

Thorn, M., Green, M., Bateman, P.W., Cameron, E.Z., Yarnell, R.W. & Scott, D.M. 2010. Comparative Efficacy of Sign Surveys, Spotlighting and Audio Playbacks in a Landscape-Scale Carnivore Survey. *South African Journal of Wildlife Research*, 40(1): 77–86.

Trimble, M.J., Ferreira, S.M. & Aarde, R.J. Van. 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. *Journal of Zoology*, 279(1980): 18–26.

van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organization (*Panthers, leo*). *Journal of Zoology*, 206(1): 97–112.

van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the kgalagadi transfrontier park: modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

White, G.C. & Burnham, K.P. 1997. Program MARK : Survival estimation from populations of marked animals. *Bird Study*, 46(S1): S120–S139.

Whitman, K.L., Starfield, A.M., Quadling, H. & Packer, C. 2007. Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology*, 21(3): 591–601.

Whitman, K.L. & Packer, C. 2006. A practical guide to aging African lions. *Conservation Force, USA*.

Young-Overton, K.D., Funston, P.J. & Ferreira, S.M. 2014. Rainfall driven changes in behavioural responses confound measuring trends in lion population size. *Wildlife Biology*, 20: 344–355.

Yoshizaki, J., K. H. Pollock, C. Brownie, and R. A. Webster. 2009. Modeling misidentification errors in capture–recapture studies using photographic identification of evolving marks. Ecology 90: 3–9.

Chapter 4:
Lion (*Panthera leo*) demographics in the Kalahari Gemsbok National Park

4.1. Introduction

Vital rates such as survival and recruitment are a consequence of environmental and social factors (Trimble *et al*., 2009; Gardner *et al*., 2010). Demographic parameters translate into population growth rates, which summarise a species' response to the environment (White & Burnham, 1997; Trimble *et al*., 2009). Vital rates and demographic characteristics can thus serve as indicators of change which aid in defining a population's susceptibility to extinction or ability to recover from negative responses to their environment (Carroll *et al*., 2013; Andresen *et al*., 2014).

A 2010 study in the Kalahari Gemsbok National Park (KGNP) postulated a pending population collapse of lion (*Panthera leo*) population due to a sex skew towards a higher proportion of males in the population (56%) (Ferreira *et al*., 2013). This showed a disparity from preceding studies which found population characteristics within the expected proportional age and sex structure range for the population (24% - 43% males) (Mills *et al*., 1978; Castley *et al*., 2002; van Vuuren *et al*., 2005; Funston, 2011) although some age class specific abnormalities were detected (Funston, 2011).

A 2001 study on lions in the Kgalagadi Transfrontier Park (KTP) including the KGNP, found a sex skew in cubs, where males accounted for two thirds of the age class (Funston, 2011). It was postulated that the high proportion of male cubs born was a response to compensate for higher natural mortality rates in males (Funston, 2011). In addition, the sub-adult age class was also skewed towards males suggesting lower mortality amongst young male individuals. Female lions accounted for 80% of the adult population in 2001 (Funston, 2011). By 2010, observed adult sex ratios were found to be equal and sub-adults remained male biased (Ferreira *et al*., 2013). The persistence of a male biased recruitment or proportional dominance of males may have deleterious effects on the conservation of lions in the KTP (van Vuuren *et al*., 2005; Ferreira *et al*., 2013).

Variability in the proportion of males and females is a major factor in the life history traits of a population (Cameron, 2004). A key hypothesis to the observed sex skew in 2010 suggested that vital rates are influenced by body condition as a result of shifting prey dynamics and consequent physical condition (Trivers & Willard, 1973; Cameron, 2004; Ferreira *et al*., 2013). The Trivers & Willard theory predicted that particularly, a greater proportion of male offspring should be produced by breeding females in response to improved health (Trivers &

Willard, 1973; Huck *et al*., 1986; Sheldon & West, 2004; Holand *et al*., 2006). A skew towards males in a polygamous species such as lions, increases conflict and can perpetuate male recruitment (Packer & Pusey, 1983b; Yamazaki, 1996; Woodroffe & Frank, 2005). The Trivers and Willard (1973) theory has been well observed in primates, rodents, marsupials and ungulates, but has not been extensively observed in large carnivores (Cameron, 2004; Sheldon & West, 2004).

Survival probability of lions is strongly correlated to prey biomass and availability (van Orsdol *et al*., 1985; Mosser *et al*., 2009; Ferreira & Funston, 2010), and climatic conditions such as rainfall and temperature (Celesia *et al*., 2010). Furthermore, survival rates in cubs have been strongly associated with group territoriality, pride size and synchronous breeding of females (Packer *et al*., 2001; Mosser & Packer, 2009). These social factors are in turn influenced by environmental stochasticity (Celesia *et al*., 2010). In the KGNP, cub survival in certain areas has been as low as 5%, primarily attributed to starvation (Eloff, 1998). Density dependent social factors that determine group success and conflict further define survival rates (Mosser & Packer, 2009). In the KGNP, lion density is relatively low in comparison with other populations, and mortality due to intra-species conflict is negligible (Funston, 2011). However, mortality due to human-lion conflict may be as high as 17 individuals per annum in the boundary prides of the KTP (van Vuuren *et al*., 2005) and appears to predominantly affect sub-adult males (Funston, 2011).

A higher proportion of males in the population might perpetuate male recruitment if conflict between males ensues and infanticide occurs as a result (Packer & Pusey, 1983a; Yamazaki, 1996). In cases where infanticide occurs after coalition changeovers, females are more likely to produce male offspring in their first litter after the takeover (Packer & Pusey, 1983b; Yamazaki, 1996; Woodroffe & Frank, 2005). The unpredictability of environmental conditions and extremes of the Kalahari may be a driver of large variability in demographic responses to social, environmental and resource based drivers (Krebs, 1995; Celesia *et al*., 2010; Mills, 2015). Along with anthropogenic stressors (van Vuuren *et al*., 2005) and stochastic disease epidemics (Ferreira *et al*., 2013), these can exacerbate changes in social parameters, vital rates and demographic signals (Loveridge *et al*., 2007; Davidson *et al*., 2011). Considering the state of lion conservation across their range and the significance of the KGNP and broader KTP to the conservation of the species (Bauer *et al*., 2015a; Bauer *et al*., 2015b), the importance of accurately monitoring lion demographics cannot be over-stressed.

Past studies into lion population demographics made use of various methods and sample sizes that makes it difficult to detect and verify trends. Here the results of a registration study of unprecedented effort are presented to provide the most accurate demographic information and estimations of this population’s vital rate to date. This information will contribute substantially to understanding lion ecology in this arid environment within a key lion management unit, critical to the conservation of the species.

4.2. Materials & methods

4.2.1. Study area

The study took place in the arid South Western Kalahari’s Kalahari Gemsbok National Park (KGNP; 9710km²), South Africa (RSA). The KGNP is adjoined to the Gemsbok National Park (GNP; 26000km²) part of the Republic of Botswana and collectively known as the Kgalagadi Transfrontier Park (KTP) an open protected area of some 36 000 km². The study area lies between 24° - 26° 30’ South and 20° - 22° East (Bothma *et al*., 1993) and falls entirely within the Dune Savanna vegetation type of the Savanna Biome (van Rooyen *et al*., 2008). Two ephemeral river valleys, the Auob and Nossob, bisect the study area with the Nossob delineating the border between South Africa and Botswana (Bothma *et al*., 1993). The area is covered by Kalahari sand with a mixture of parallel and irregularly shaped, vegetated dunes (van Rooyen *et al*., 2008). The region is classified as semi-desert with approximately 220mm of precipitation across the KGNP and a large variance in regional and localized rainfall ranging from 180mm in the South West to 230 mm in the North of the KGNP per annum (Grist *et al*. 1997). Temperature extremes range from 45°C in summer to -5°C in winter (Mills, 2015). An extensive study area description can be found in Chapter 2 of this thesis.

4.2.2. Field data collection

Data was collected over a 24-month period from May 2013 to June 2015. To define lion population demographic characteristics and vital rates, a registration study (Ogutu & Dublin, 2002; Pennycuik & Rudnai, 1970) was initiated to identify as many lions as possible in the KGNP. To achieve this, systematic transects were driven by vehicle on a monthly basis representing both the dune and riverbed environments across the extent of the KGNP. Random transects were also driven on management tracks throughout the KGNP. Lions were located opportunistically through chance encounters, following up on sighting reports, following fresh tracks, and following the direction of roars (Stander, 1991). Seven females from seven different prides were collared (African Wildlife Tracking^{cc}, Pretoria, South Africa) in association with a dietary study of lion in the KGNP for periods of three to 12 months

(Beukes, 2016). During the study period the lionesses were located approximately once per month for the duration that the collars were active. Collars were applied under all required ethical clearance (Chapter 3) and were removed at the end of the study period. An attempt was made to identify all lions that were sighted and their locations were determined using a Garmin GPSMAP 62 (Garmin E-Trex, Garmin International, Olathe, KS, USA).

4.2.3. Individual identification

A register of individual lions were created to construct the age and sex structure of the population. Individuals were identified using vibrissae spot patterns, ear nicks (Pennycuick & Rudnai 1970; Elliot *et al*. 2014), nose pigmentation (Whitman *et al*. 2004) and existing brand marks (Funston, 2001; Castley *et al*., 2002; Pers.comm. [4]Ferreira, M. 2015). Individual identification was supported by a photographic database of all unique individuals.

4.2.4. Age and sex structure

Age was assigned on a subjective basis using the lions relative size, nose pigmentation, tooth wear, leg markings and mane development in the case of males (Whitman *et al*. 2004; Whitman & Packer, 2006; Ferreira & Funston, 2010). Lions were categorized into five discrete age classes. Cubs were classified as individuals under one year old, juveniles as animals between one and two years; sub-adults were considered two to four years old and lions estimated to be over four years old were considered adult (Whitman *et al*. 2004; van Vuuren *et al*., 2005). Adults were further divided based on survival probability, in that old individuals (>10 years) are expected to have higher rates of mortality (Starfield *et al*., 1981). This resulted in an adult age class from four to 10 years old and old adults over 10 years of age. For more detail on the ageing criteria see Chapter 3.

4.2.5. Pride structure

Prides were considered to be groups of females and their offspring along with males who attend the group for definite periods of time and associate in a non-aggressive manner (Packer & Pusey, 1987; Arsznov & Sakai, 2012). Prides were defined through direct observation of collared individuals and their associated pride members as well as opportunistic observations of individuals associating with one another (Funston, 2001;

---

[4] Micho Ferreira, Section Ranger, Twee Rivieren, Kalahari Gemsbok National Park, Northern Cape, South Africa. 8800.

Funston, 2011). Spurious relationships were derived from indirect association between individuals in a pride, over multiple sighting events (Frank, 1995). Where individuals were associated by a mutual pride member or members, but never seen associating directly, they were still considered to be from the same pride. Individuals who were never seen associating with a pride or individuals from a pride were considered to be transient individuals. These included small groups of dispersing sub-adult and adult males.

4.2.6. Reproductive characteristics

Reproductive schedules were derived from observations of cubs being born into prides. An attempt was made to identify the average age of adult females at conception and at birth through backdating from the estimated age of individuals when they were identified to the time they may have conceived or given birth. Litter size, sex structure, birth timing and birth intervals were also recorded.

4.2.7. Survival

Cormack-Jolly-Seber mark-recapture simulation was used to define apparent survival probability of various age classes and sex (Cam, 2009; Fearnbach *et al*., 2012). Individual identification was used as a “marking” method (Bonner and Holmberg, 2013; Sollmann *et al*. 2011; Yoshizaki *et al*. 2008). The first time an individual was identified was considered the initial capture and marking event. When individuals were re-sighted, it was considered as a recapture (Matthews *et al*., 2008). The initial marking occasions and subsequent recapture intervals were divided into six four-month periods between May 2013 and June 2015. Immigration and emigration were not accounted for; however, mark-recapture survival estimation accounts for the probability of detection without accounting for the specific cause (Horton & Letcher, 2008).

4.3. Data analysis

4.3.1. Age and sex structure

The number and proportion of males and females in each age class were derived for the entire known population. The age structure of the population at the 30th of June 2015 (end of study) was established by calculating the age of each identified lion at the end of June 2015. That was done by adding the time that expired since a lion has been identified and 30 June 2015 to the estimated age at time of first identification. Sex ratios were derived for each age class separately to determine changes in sex ratios between specific age classes. Age classes were also grouped in some instances to render them more comparable to demographic studies in other lion populations (i.e. Smuts, 1976; Mills, 1995 only identified three age classes) as well as historic studies conducted in the KGNP lion population (Ferreira *et al*., 2013).

4.3.2. Pride structure

Pride structures were derived from 1022 lion sightings at 299 events comprising of 261 unique individuals. Pride structures derived from the regular observation of collared individuals were compared to the opportunistically observed and less often seen prides to determine if sighting frequency might influence pride composition estimates with regard to sex ratios, age structure and pride size. These were compared using the Hartley's Chi-squared test (Franklin & Walker, 2010). Pride size and structure in the current study were compared to that of the study conducted in the KTP between 1998 and 2001 (Funston, 2011) using ANOVA.

4.3.3. Reproductive characteristics

Birth rates were calculated as the average number of cubs born per reproductively mature female (> 4 Years old) per year (Lehmann *et al*., 2008; Funston, 2011). The age of females at first conception, age of females at first known birth and average age of females producing cubs in the population were determined through observing unique individuals of approximate known age (Jansen & Jenks, 2012). Litter sizes and sex ratios were compared at three-month intervals throughout the cubs first year of life to detect changes in sex ratios from assumed sex ratios at birth (i.e. the sex ratio of cubs at first sighting). Cubs were rarely sexed before three months old. Seasonal birth timing was tested using conventional Single Factor ANOVA in the programme Excel (Microsoft Office, 2010). Cub's ages and adult female age estimates at conception and birth were backdated to determine approximate month of birth and the season in which they were born (Smuts, 1978).

4.3.4. Survival

The Program MARK (v.8.1) (White & Burnham, 1999) was used to derive apparent survival rates using the Cormack-Jolly-Seber (CJS) simulation for survival rate estimation. Model selection using a Model Likelihood Estimator (MLE) and Likelihood Ratio Test (LRT) (Cooch

& White, 2015; White & Burnham, 1997) were used to determine the best suited equation out of four possible CJS equations with which to derive survival rates with the available data (Lebreton *et al*., 2010). The most preferable model has the lowest AIC, Delta AIC below two and model likelihood closest to one. Goodness-of-fit (GOF) was calculated in the Program RELEASE (v.3)(Burnham *et al*., 1987; Lebreton *et al.,* 1992; White & Burnham, 2015), an extension of the Program MARK to determine whether there was any significant variability in survival or capture probability between each capture occasions and between individuals (Reisinger *et al*., 2011; Cooch & White, 2015).

Survival rates as measured by the Cormack-Jolly-Seber model does not account for the manner in which an individual leaves the population i.e. through death or immigration and is therefore termed “Apparent” survival rates (Pledger *et al*., 2003; Horton & Letcher, 2008). Data input into the model included all identified individuals at the initial capture event and subsequent 23 re-capture events. At each monthly interval capture event, an individual was either recorded and denoted as a “1” in the mark-recapture matrix or a “0” in the event where an individual was not captured during a mark-recapture event (Cooch & White, 2015). Through the capture history of each individual over a twenty-four month period, apparent survival rates were calculated taking into consideration the capture probability of each unique individual (Pledger *et al*., 2003; Horton & Letcher, 2008). Apparent survival rates were calculated for males and females separately, for age classes separately and for different sexes within each age class where sufficient data was available. These provided apparent survival rates for male and female cubs, juveniles, sub-adults, adults and old adults separately.

4.4. Results

4.4.1. Age and sex structure

Between May 2013 and June 2015, 261 unique lions were identified and their sex and age structure was calculated for the end of the study period (June 2015) (Figure 4.1). In the adult age class (>4 Yrs; n = 147), 49% (n = 72) were males and 51% (n = 75) were females. In the sub adult age class (2-4 Yrs; n = 29), 54% (n = 16) were males and 46% (n = 13) were females ($\bar{x}$ = 2.01; d.f. = 2; p = 0.63). Juveniles (1-2 Yrs; n = 34) showed an equal sex ratio (n = 30). Seventy-four individuals under one year old were observed which accounts for the minimum known to have been born over the study period. The sex ratio of these cubs was 49% males to 51% females (n = 61) with 17% (n = 13) of cubs sex being indeterminable. There were no significant differences ($\bar{x}$ = 0.18; d.f. = 3; p = 1) in sex ratios of cubs who were known to have survived to three months, six months, nine months or 12 months old (♂1:1♀) (Table 4.1). Sex ratios of cubs at the end of the study were 49% male (n = 34) and 51% female (n = 35). The relationship between males and females in the total population was 49% male and 51% female. When sub-adults and adults were combined (>2 Yrs) the ratio between males and females were 51% (n = 88) and 49% (n = 87) respectively. The age structure of the population (n = 261) at the end of the study period showed a relationship of 55% adults, 12% sub-adults, 13% juveniles and 20% cubs.

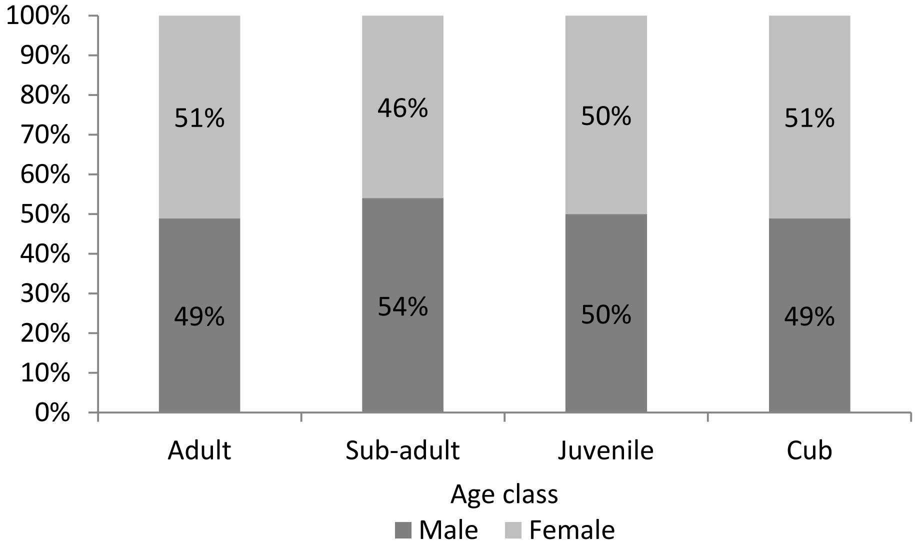

Figure 4.1 Sex and age class structure of the KGNP lion population on 30 June 2015 derived from 261 unique individuals observed between May 2013 and June 2015.

Table 4.1 The observed sex ratios of cubs in the KGNP that are known to have survived at three month intervals up to one year. Cubs that could not be sexed are excluded (n = 13).

	3 Months	**6 Months**	**9 Months**	**12 Months**
Male	51% (n = 34)	51% (n = 34)	51% (n = 30)	51% (n = 23)
Female	49% (n = 33)	49% (n = 33)	49% (n = 29)	49% (n = 22)

The estimated age of unique individuals, derived from subjective criteria, showed greater disparity in the sex ratios at specific ages than in broad age classes (Figure 4.2). Sex ratios were near or at parity across 36% of the age structure, whereas male bias was primarily observed in adults six, seven and nine years old. Negative exponential regression lines which were fitted to the data of sex ratios at specific ages, indicate a more rapid rate of decline in the number of males ($y = 25.855e^{-0.173x}$; $R^2 = 0.71$) from one year to the next than for females ($y = 14.789e^{-0.098x}$; $R^2 = 0.23$) (Figure 4.2).

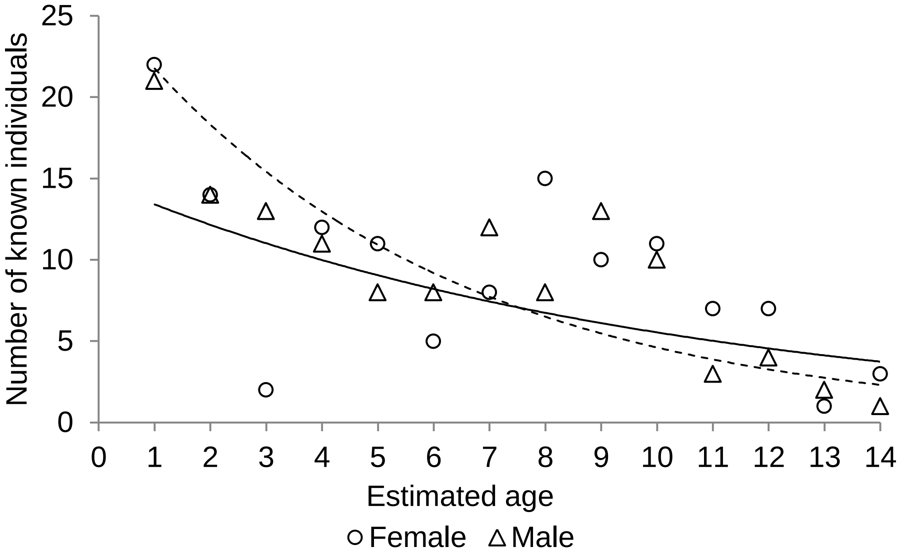

Figure 4.2 The observed age structure for males and females of the KGNP lion population at the end of June 2015 derived from 261 known individuals. Exponential trend lines show the rate of decline in the number of individuals for males (dash line; $y = 25.855e^{-0.173x}$; $R^2 = 0.71$) and females (solid line; $y = 14.789e^{-0.098x}$; $R^2 = 0.23$) from one year to the next.

4.4.2. Pride structure

Fourteen prides were identified through direct observations (Table 4.2) of individuals associating with each other in 285 out of 299 sighting events. The composition of six prides could be identified with confidence as a pride female of each was collared and could be located on a regular basis (Ave = 30; SD = 11 observations per pride) depending on the duration of the collars being active. Prides which did not have an individual collared (n = 8) were seen less regularly (Ave = 13; SD = 6 observations per pride).

Pride composition for the 6 collared prides (117 individuals) did not differ significantly ($F_{4.35}$ = 0.003; d.f. = 1; p = 0.96) from the average age and sex structure observed in the population (261 individuals). Pride composition for the 6 collared prides also did not differ significantly from the average age and sex structure of the other eight non-collared prides (108 individuals) ($F_{4.35}$ = 0.01; d.f. = 1; p = 0.92) for which there was less observations of individuals. Of the identified individual lions, 225 (86%) could be associated with prides. Only 36 known individuals could not be associated with any particular pride and were considered to be transient. Transient individuals were identified at 14 of the 299 sighting events and comprised 16 adult and 14 sub-adult males as well as three adult and three sub-adult females. The average pride size was 11.57 (SD = 4.97) excluding cubs and 16.07 (SD = 8.71) including cubs. Pride structure showed an average adult composition of 2.42 (SD = 0.49) males and 5.29 (SD = 3.34) females. Prides showed a fission-fusion relationship (Funston, 2011) and sub-groups, which comprised the 299 sighting events, consisted on average of 3.53 (SD = 2.88; Range = 1-21) individuals per sighting event.

Table 4.2 The composition of observed prides from May 2013 until June 2015 which were identified over 285 sightings of pride members associating in groups. Five prides, which had a lioness that was collared for a one year period are indicated with an asterisk (*) after the pride name.

Pride name	**Adult**		**Sub-adult**		**Juvenile**		**Cub**			**Total**
	Male	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Unknown**	
Bitterpan		1	4		2	1				8
Dankbaar	2	3		1		2			3	11
Dikbaardskolk	2	4	3						1	10
Gnurrie*		1		2			2			5
Grootkolk	2	4		2			2	1		11
Houmoed*	2	9			5	3	0	4		23
Kieliekrankie	2	3		2	4					11
Kij Kij	2	3		1	1	6	1	3		17
Kransbrak*	3	10	3				3	6	5	30
Kwang*	2	5		1		1	2	2		13
Marie se gat	3	12					11	5	5	31
Polentswa	3	3								6
Sitsas	3	6	6	2	1	2				20
Xaus*	3	10	1	2		1	6	5	1	29
Average	2.42	5.29	3.40	1.57	2.60	2.29	3.57	3.71	2.50	16.07

4.4.3. Reproductive characteristics

Thirty-seven per cent of the adult females (n = 31) are known to have produced cubs immediately prior to or during the study period. The minimum average litter size as derived from first observations of cubs, thus not necessarily the actual number born, were 2.39 (SD = 0.72; Range = 1-4) cubs per female. This translated to an average adult female birth rate of 0.44 cubs per female per annum. No females were observed giving birth more than once during the two year study period. Nineteen cubs are known to have been born to eight females in 2013. During 2014, 52 cubs were born to 22 females and in the first half of 2015 three cubs were born to one female. The range between the first and second year of the study was 0.3 - 0.57 cubs per female per year.

Although the sex ratio of cubs that could be sexed was at parity (n=61), a large range of sex ratios at birth were observed between females. If we assume all the cubs born survived till they were first observed, five of the 31 females (16%) produced cubs at parity, while 10 females (32%) produced more males and 8 (26%) produced more females. However, for eight females that produced 24 cubs between them only 13 could not be sexed and can thus not be included in the analysis of sex ratios at birth.

The month with the highest birth frequency was May (29% of births), but in the months of July and August an additional 45% of the cubs were born (Figure 4.3). The majority of births (77.4%) occurred between May and September. Only one female was known to give birth between October and December. Birth timing was significantly ($F_{4.96}$ = 5.29; d.f. = 1; p = 0.04) higher in the winter period (April to September).

The average age of females that gave birth during the study was 6.9 years old (SD = 1.83; Range = 4-9) and the youngest, approximately four years old. Birth synchrony, cubs born into cohorts within a month of each other, was observed in three prides out of ten which produced cubs during the study period. Cubs born into these three cohorts accounted for 57% (n = 42) of known cubs during the study period. In the Kransbrak pride, seven cubs were known to have been born to three females within two weeks of each other. Similarly, the Xaus pride produced seven cubs from three females within two weeks. The Marie se draai pride produced 24 cubs from seven females within one month.

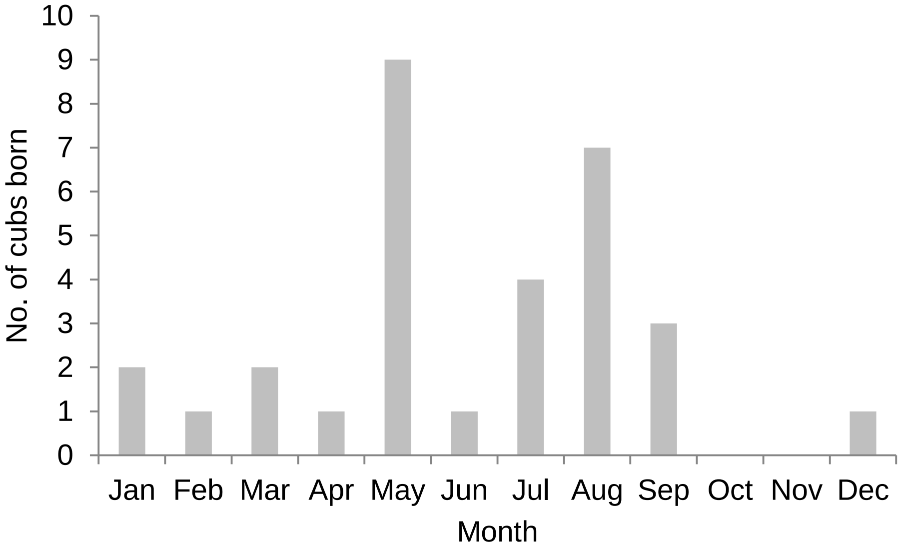

Figure 4.3 Number of cubs born in each month calculated from approximate age at first sightings from May 2013 until June 2015 (n=74).

4.4.4. Survival

Sixty seven cubs were seen and identified within the first 3 months of their lives. Of these 96% are known to have survived to three months, 89% to six months, 84% to nine months and 57% are known to have survived their first year. Although 29 cubs were not observed reaching an age of one year, only seven cub mortalities were observed. The minimum cub survival rate to one year is thus 57%. Four confirmed adult mortalities were recorded during the study period.

From mark-recapture Cormack-Jolly-Seber (CJS) candidate models in the Program MARK (White & Burnham, 1997), the best fitting parameters to determine apparent survival were where survival probability remained constant and capture probability was time dependent (Model equation in the CJS survival estimates = phi(.)p(t)) (Table 4.3). Survival estimates could only include 227 of the 261 identified individuals as insufficient data on encounter histories to estimate survival parameters with confidence were available for the remaining 34 lions (Cooch & White, 2015). The Goodness-of-fit test on a fully time dependent CJS model showed non-significant variability for detection and survival between capture occasions. TEST 2 for overall equal detectability ($\bar{x}$ = 2.27, d.f. = 3, p = 0.43), TEST 3.SR for equal survival probability independent of capture history ($\bar{x}$ = 4.8, d.f. = 4, p = 0.31), TEST 3.Sm for capture probability independent of capture history ($\bar{x}$ = 0, d.f. = 3, p = 1) and the overall test statistic, TEST 2 + 3 showed no significant variability in survival or capture probability ($\bar{x}$ = 0, d.f. = 3, p = 1).

Table 4.3 Candidate model selection for Cormack-Jolly-Seber apparent survival rate estimation in the Program MARK. The various models operate under the assumptions that a variable is either time dependent (T) or constant (.) over the study period. Factors which are taken into account in the model are survival probability (phi) and encounter probability (p). Model selection is achieved through the comparative Akaike's Information Criterion (AIC) which determines the likelihood of suitability of the test against other models. The most preferable model has the lowest AIC, Delta AIC below two and model likelihood closest to one.

Model Formula	AIC	Delta AIC	AICc Weight	Model Likelihood	Deviance
phi(.)p(t)	801.6286	0	0.90674	1	623.08
phi(.)p(.)	806.1799	4.5513	0.09315	0.1027	677.38
phi(t)p(t)	819.5624	17.9338	0.00012	0.0001	585.64
phi(t)p(t)	835.2111	33.5825	0	0	656.66

One hundred and seventy-nine out of the 261 known individuals (68%) where seen more than once. Although apparent survival probabilities indicated a higher average annual survival rate for female lions than for male lions, confidence limits only define a noticeable difference between male and female cubs (Table 4.4). For juveniles and old adults, sex specific survival rates could not be estimated with any measure of precision, as sample sizes were too small. Apparent survival rates from mark-recapture analysis for the entire known population was 82% (95%CI = 78-86), which were expected to survive to the following year.

Table 4.4 Apparent annual survival rates derived from mark-recapture data using the Cormack-Jolly-Seber model. Male and female apparent survival probabilities are presented separately where possible. Where sex dependent survival could not be calculated, a survival probability is presented for both sexes (*). 95% Confidence intervals from mark-recapture analysis and sample size are also presented.

Age class	Sex	Survival estimate	Lower 95%	Upper 95%	Sample Size
Cub	Female	94%	87%	98%	29
Cub	Male	76%	67%	83%	33
Juvenile*	Fe/Male	85%	65%	94%	9
Sub-adult	Female	91%	83%	96%	23
Sub-adult	Male	92%	81%	97%	24
Adult	Female	93%	88%	95%	58
Adult	Male	87%	81%	92%	47
Old Adult*	Fe/Male	72%	37%	90%	14
Total	-	82%	78%	86%	227

4.5. Discussion

This study indicates that there was no apparent sex skew in the population between June 2013 and May 2015. Rather, it appears that the sex ratio in the population is near equal in all age classes. The largest discrepancy in sex ratios was within the sub-adult age class that favoured males by four per cent. In adults and cubs, females were favoured marginally by one and two per cent respectively and the sex ratio of juveniles was equal. The sex skew favouring males observed in 2010 with a sample size of 49 lions might have been a result of the small sample size rather than a representative observation (Ferreira *et al*., 2013; Chapter 3). However, an equal proportion of males and females in lion populations are uncharacteristic, the norm fluctuating around a ratio of between two to three females for each male (Bertram, 1973; Smuts, 1976; Mills *et al*., 1978; Standers, 1991; Castley *et al*., 2002; Funston *et al*., 2003; Funston, 2011).

The adult age class (>4 Yrs) accounted for the majority of the population at 66%. Compared to studies in other areas this is relatively high. In Kruger National Park (KNP) adults comprise 40-53.3% of the population (Smuts, 1976; Ferreira & Funston, 2010) while they made up 41% of the Etosha National Park (ENP) lion population in 1989 (Stander, 1991). Only a third (34%) of the lions in this population are under four years old compared to 46-58% and 59% in KNP and ENP studies respectively (Smuts, 1976; Standers, 1991; Ferreira & Funston, 2010). Similarly, cubs and juveniles occupied a small proportion of the population (27%) compared to the KNP (39.6%; Ferreira & Funston, 2010) but is higher in proportion than found in the ENP which ranged between 16.8% and 21.3% between 1987 and 1989 (Stander, 1991).

Long-term trends or continuously low proportions in the young age classes would indicate low recruitment rates into the population, which would contribute to a decline in the population size and probability of persistence (Eberhardt, 2012). However, transition from young age classes are rapid and large variability in age class structure can be observed over a relatively short period (Funston, 2011; Eberhardt, 2012; Trinkel, 2013). The study of lion demographics in the KTP between 1998 and 2001 showed large variability in the proportion and number of cubs (average, 42%; Range, 61-118 individuals) and sub-adults (average, 19%; Range: 18-52 individuals) present in the population over a two and a half year period. Age structure data in the current study were presented for the end of the study period. However, similar variation in age structure were observed in the current study, where cubs (<2 Yrs) ranged between 12 and 61 individuals over the study period. The regression analysis conducted on the standing age structure of the population at the end of the current study (see Figure 4.2) showed a greater rate of decline from one age to the next for males than for females. However, the regression did not accurately explain the trend in females ($R^2 = 0.23$). This could be explained by greater heterogeneity in mortality rates between different age classes in females (Eberhardt, 2012; Barthold *et al*., 2016), but could also be a function of incorrect age assignment of individual females.

Individual ages of lion were determined using a combination of subjective criteria including relative shoulder height (Whitman & Packer, 2006; Ferreira & Funston, 2010), male mane development (Whitman & Packer, 2006), proportional nose pigmentation, leg markings and tooth wear (Whitman *et al*., 2004). These methods alone carry inherent limits and along with the subjective nature of age assignment may well lead to bias in age specific categorization and may vary between geographic regions (Hanby *et al*., 1995). However, defining age classes as have been done here may be more accurate as ages were grouped into broad categories, negating some potential inaccuracy. Multiple sighting events of individuals and the use of an individual identification catalogue served as comparative age references. Several individual lions aged by SANParks veterinarians while under sedation using nose pigmentation and tooth wear as indicators of age (Pers. Comm. [5]M. Hoffmeyr, 2013-2015; [6]D. Zimmerman, 2013-2015) served as points of reference and assisted in refining ageing criteria. Determining the sex of individuals was not as challenging as lions are sexually dimorphic (Whitman & Packer, 2006) and of the 261 lions that could be uniquely identified only 13 cubs could not be sexed.

In the Kgalagadi, prides are known to form sub-groups (Funston, 2011) which is attributed to resource restraints (Stander, 1991; Celesia *et al*., 2010; Funston, 2011). The fission-fusion group association persisted throughout this study with small groups of less than six individuals making up the majority of observations (89%). This greatly challenged the identification of pride composition, as it required several observations to identify group associations. Many relationships between individuals and a known pride were based on indirect relationships (Abell *et al*., 2013) and many members of the same pride were never seen associating.

The fission-fusion nature of the prides also made it difficult to identify immigrating and emigrating individuals. Similarly, coalition changeovers were difficult to observe. From two known coalition changeovers, the five ousted males were classified as transient animals along with those who could not be associated to prides (n = 36). Furthermore, several individuals were described by park staff associated with known prides that could not be accounted for and were therefore not reported on. For instance, two adult males and another

---

[5] Dr. M. Hoffmeyr, Veterinary Wildlife Services, SANParks, Skakuza, 8800

[6] Dr. D. Zimmerman, Veterinary Wildlife Services, SANParks, Port Elizabeth,

three adult females were reported to be associated with the Bitterpan pride, but could not be verified and an adult female with three cubs was never seen, but was reported to associate with the Dankbaar pride.

The observed pride size and the number of males within prides differed between the observations in 2001 (Funston, 2011) and the current study. Prides were larger in the current study, with a significantly higher number in overall pride size (16.07 vs. 7.55; ANOVA; $F_{1.14}$ = 8.17; d.f. = 1; p = 0.01) and the number of adult males per pride (2.42 vs. 1.6; ANOVA; $F_{4.14}$ = 6.29; d.f. = 1; p = 0.02). Prides remain within the expected size range and structural composition to prides in other populations (2-9♀ and 2-6♂) (Packer *et al*., 1988; Standers, 1991; Hanby *et al*., 1995; Funston, 2011). Pride size is correlated to environmental conditions and prey availability in other lion populations (van Orsdol *et al*., 1985). A change in pride size and an increased proportion of males within prides in the KGNP are indicative of changing demographics and population size in response to environmental conditions (van Orsdol *et al*., 1985; Celesia *et al*., 2010). Increased pride size could have density dependant consequences for sex ratios (Smuts, 1976) and could lead to increased competition, higher dispersal rates of both males and females and greater risks of human-lion conflict on the boundaries of the KGNP (van Vuuren *et al*., 2005).

Annual adult female birth rates were much lower (0.43 cubs per female per year) than what was observed in 2001 in the KTP at 0.67 cubs per adult female per year and 1.33 cubs per female per year in five prides bordering the Southern and Western boundaries of the KTP (van Vuuren *et al*., 2005). Fecundity rates in the KGNP may be as much as two thirds less than in some other known populations which range between 0.8 – 1.4 cubs per female per year in Kenya (Woodroffe & Frank, 2005), Namibia (Orford *et al*., 1988), South Africa (Lehmann *et al*., 2008), Tanzania (Caro *et al*., 2009) and Zambia (Yamazaki, 1996). The current record for the KGNP may well have the lowest recorded fecundity rates in Southern Africa, surpassed only by the *Panthera leo persica* sub species of the Gir Forest, India (0.37 cubs per female per year) (Banjerjee & Jhala, 2012).

Modelled survival (mark-recapture) of cubs in the KGNP were between 67–97% (95% confidence limits), relatively high in comparison to populations in Kruger National Park, South Africa (40 – 80%; Funston *et al*., 2003) and Etosha National Park in Namibia (40%; Pienaar, 1960). However, cub survival rates are known to be extremely variable and correlate strongly with lean season prey abundance (Celesia *et al*., 2010). The synchronous breeding of females in prides as was observed during this study may also contribute to increased cub survival due to allo-caring of cubs (Packer & Pusey, 1997; Packer *et al*., 2001), with over half of known cubs having been born into three large pride cohorts. Survival rates of cubs in the current study could be as high as 90% if no more than the observed deaths (n = 7) had occurred. Cub survival during the study period was higher than observed in the Northern KGNP in 1978 (5%) (Eloff, 1980), but comparable to the results of 2001 (61%) (Funston, 2011). The survival rate estimate for juveniles was lower than for cubs on average but had broader confidence limits, a probable relic of small sample size for juveniles (n = 9). Survival rates for females were also higher on average and showed narrower confidence limits than for males (Starfield *et al*., 1981; van Vuuren *et al*., 2005; Ferreira & Funston, 2010).

Although not all known cubs were tracked throughout their first year, cubs whose fate was known remained equal in sex ratio throughout their first year of life with no signs of selective mortality between males and females. Juveniles (1-2 Yrs) showed an equal sex ratio, supporting the postulation of non-selective mortality in cubs. Sex ratios at birth are expected to be at parity in lions (Smuts, 1976; Funston, 2011) and sex specific mortality is generally expected to influence sub-adult (2-4 Yrs) males during dispersal (Smuts, 1976; Packer & Pusey, 1987). Sex skews at birth were expected to be associated with environmental stressors such as human-lion conflict or coalition changeovers (Ferreira *et al*., 2013). However, in this study the sub-adult age category had more males (56%) than females (44%) at the end of the study period.

To define apparent survival estimates from mark-recapture analyses, the most appropriate Cormack-Jolly-Seber model made the assumption that capture probability changed during the study period but that the survival probability of individuals did not change between capture occasions (White & Burnham, 1997). The seven females that were collared during some portion of the study period may bias apparent survival rates as they were added to the capture matrix used to analyse mark-recapture survival parameters. Although the capture probability of collared individuals is higher and potentially that of their associated pride members the assumption that capture probability is not equal over time or between individuals should reduce bias in survival estimates (Pledger *et al*., 2003).

In some of the previous studies of the population, cubs are described as individuals between zero and two years old (Funston, 2011). However, the current study cubs (0-1 years old) and juveniles (1-2 years old) were considered separately as the survival probability, between these age classes can differ (van Vuuren *et al*., 2005). No sex selective mortality was observed in the current study for the number of known cubs (n = 74). However, mark-recapture survival estimates had non-overlapping confidence limits, indicating a markedly higher survival probability for female cubs than male cubs. The observed survival rates for cubs fell below the apparent survival rate confidence limits identified from mark-recapture results. This may have been due to failure in locating cubs rather than the fact that they died.

Observations of survival and mortality may be biased by encounter probabilities but for which models such as the Cormack-Jolly-Seber account for in its estimates.

There appeared to be no selective mortality among cubs as equal ratios of males and females appear to have survived their first two years. Considering that sex ratios of cubs were relatively equal in the first year, and assuming that these ratios are representative of actual births, it does not appear that pre-natal sex selection occurs, as would have been predicted by the Trivers and Willard theory (Trivers & Willard, 1973). Rather, the high proportion of males observed in the population may be due to post-natal selection caused by either a higher rate of male survival or female mortality (Eberhardt, 2012), which contradicts the mark-recapture survival parameters suggesting the opposite. Assuming that the Trivers and Willard hypothesis holds true, it would be expected that sex selection would occur during gestation and would be expressed at birth. It could also be expected that such sex ratio skews at birth would be detected in overall cub sex ratios. Variables in reproductive schedules would change over time in response to environmental and social restraints and concurrent body condition responses (Trivers & Willard, 1973). However, no sex selection was observed in cubs at three month, six month, nine month or 12 months. Therefore, shifts in sex ratio must be occurring because of survival probability at a later stage (Durant *et al*., 2004). This may be associated with resource and social restraints (Bertram, 1975; Celesia *et al*., 2010) or in response to human-lion conflict (van Vuuren *et al*., 2005; Woodroffe & Frank, 2005).

Three quarters of all known births occurred in the cold dry season between April to September suggesting some seasonal preference. This trait is uncommon in lions (Bertram, 1975; Funston, 2011; van Vuuren *et al*., 2005), but may be explained by the environmental extremes present in the KTP (Mills, 2015) which may increase mortality rates of cubs born in summer (Eloff, 1980). Producing cubs in favourable climatic conditions may increase survival rates (Celesia *et al*., 2010; Banjerjee & Jhala, 2012). Similarly, oestrous and birth synchrony within prides may increase offspring survival (Packer *et al*., 2001; Lehmann *et al*., 2008). However, the sample size of cub birth rates and seasonal variability are limited in the current study and could be further investigated in future surveys.

The lion population of the KGNP does not appear to be under immediate demographically driven threat to their persistence due to a male biased population. No other populations showing similar shifts to higher proportions of males (Mills, 1995) have experienced significant declines in the population as a result. However, the higher proportion of males in the cub and sub-adult age categories in 2001 (Funston, 2001) and the greater proportion of males observed in 2010 (Ferreira *et al*., 2013), are unexpected (van Vuuren *et al*., 2005; Funston, 2011; Ferreira *et al*., 2013). Explicit investigation of potential drivers both natural

(Celesia *et al*., 2010; Trimble *et al*., 2009) and anthropogenic (Trinkel, 2013; Woodroffe & Frank, 2005) causes of changes in sex ratios are required. The recommended proceeding aim would be to monitor the response of the population to the current demographic parameters. However, this would require robust methods to analyse population trends into the near future. Identifying existing trends in demographic parameters of the lion population in the KGNP requires further investigation and forms the focus of the next chapter.

4.6. References

Abell, J., Kirzinger, M.W.B., Gordon, Y., Kirk, J., Kokeŝ, R., Lynas, K., Mandinyenya, B. & Youldon, D. 2013. A social network analysis of social cohesion in a constructed pride: Implications for ex situ reintroduction of the African Lion (*Panthera leo*). *PLoS ONE*, 8(12): 1–11.

Andresen, L., Everatt, K.T. & Somers, M.J. 2014. Use of site occupancy models for targeted monitoring of the cheetah. *Journal of Zoology*, 292(3): 212–220.

Arsznov, B.M. & Sakai, S.T. 2012. Pride diaries: Sex, brain size and sociality in the African lion (*Panthera leo*) and cougar (*Puma concolor*). *Brain, Behavior and Evolution*, 79(4): 275–289.

Banjerjee, K. & Jhala, Y.V. 2012. Demographic parameters of endangered Asiatic lions (*Panthera leo* persica) in Gir Forests , India. *Journal of Mammalogy*, 93(6): 1420–1430.

Barthold, J.A., Loveridge, A.J., Macdonald, D.W., Packer, C. & Colchero, F. 2016. Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, 53: 295–304.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T., Macdonald, D.W. & Packer, C., 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112(48): 14894-14899.

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2015. *Panthera leo.* The IUCN Red List of Threatened Species 2015: e.T15951A50658092.

Becker, M.S., Watson, F.G., Droge, E., Leigh, K., Carlson, R.S. and Carlson, A.A., 2013. Estimating past and future male loss in three Zambian lion populations. *The Journal of Wildlife Management*, 77(1):128-142.

Bertram, B.C.R. 1973. Lion population regulation. *East African Wildlife Journal*, 11: 215–225.

Bertram, B.C.R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology*, 177(4): 463–482.

Beukes, M. 2016. Unpublished Master's Thesis. Cape Peninsula University of Technology, Cape Town, South Africa.

Bothma, J.D.P., van Hoven, S. & Le Riche, E.A.N. 1993. GPS-corrected and GIS-based remapping of the Kalahari Gemsbok National Park and the adjacent area in Botswana. *Koedoe*, 36(2): 105–108.

Cam, E. 2009. *Contribution of capture-mark-recapture modeling to studies of evolution by natural selection, in* D.L. Thomson *et al*. *(eds.),* Modeling demographic processes in marked populations, Environmental and Ecological Statistics 3, Springer US: 83-129.

Cameron, E.Z., 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism.*Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271(1549):1723-1728.

Caro, T.M., Young, C.R., Cauldwell, A.E. & Brown, D.D.E. 2009. Animal breeding systems and big game hunting: Models and application. *Biological Conservation*, 142(4): 909–929.

Carroll, C., Fredrickson, R.J., Lacy, R.C. & Society, C.Z. 2013. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. *Conservation Biology*, 28(1): 76–86.

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 using a capture–recapture survey. *African Zoology*, 37(1): 27–34.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48(1): 58–71.

Cooch, E.G. & White, G.C. 2015. *Program MARK - A Gentle Introduction (14th edition).* University of Collorado and Cornell University, USA: pp1067.

Davidson, Z., Valeix, M., Loveridge, A.J., Madzikanda, H. & Macdonald, D.W. 2011. Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation*, 144(1): 114–121.

Durant, S.M., Kelly, M. & Caro, T.M. 2004. Factors affecting life and death in Serengeti cheetahs : environment, age, and sociality. *Behavioral Ecology*, 15(1): 11–22.

Eberhardt, A.L.L. 2012. Using Age Structure Data from Changing Populations. *Journal of Animal Ecology*, 25(2): 373–378.

Eloff, F.C., 1980. Cub mortality in the Kalahari lion *Panthera leo* vernayi (Roberts, 1948). *Koedoe*, *23*(1): 163-170.

Eloff, F.C. 1998. The life of the Kalahari lion (*Panthera leo vernayi*). *Transactions of the Royal Society of South Africa*, 53: 267–269.

Fearnbach, H., Durban, J. & Parsons, K. 2012. Photographic mark – recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications*, 22(5): 1689–1700.

Ferreira, S. & Funston, P.J. 2010. Age assignment to individual African lions. *South African Journal of Wildlife Research*, 40(1): 1–9.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables : prey and disease effects in Kruger National Park , South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Frank, K.A. 1995. Identifying cohesive subgroups. *Social Networks*, 17(1): 27–56.

Franklin, S. & Walker, C. 2010. *Survey Methods and Practices* F.S. & W.C., eds. Statistics Canada, Ottawa, Ontario, Canada K1A 0T6, (12): pp408.

Funston, P.J. 2002. *Kalahari Transfrontier Lion Project: Executive Report*. Endangered Wildlife Trust, Upington. South Africa: pp236.

Funston, P.J. 2011. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41(1): 1–10.

Funston, P.J., Mills, M.G.L., Richardson, P.R.K. & van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology*, 259(2): 131–142.

Gardner, B., Reppucci, J., Lucherini, M. & Royle, J.A. 2010. Spatially explicit inference for open populations: Estimating demographic parameters from camera-trap studies. *Ecology*, 91(11): 3376–3383.

Haas, T.C. & Ferreira, S.M. 2015. Federated databases and actionable intelligence : using social network analysis to disrupt transnational wildlife trafficking criminal networks. *Security Informatics*, 4(1): 1–14.

Hanby, J.P., Bygott, J.D. & Packer, C. 1995. Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro crater and the Serengeti plains. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. The University of Chicago Press (A.R.E. Sinclair & P. Arcese, eds*). pp315–331.

Holand, Ø., Mysterud, A., Røed, K.H., Coulson, T., Gjøstein, H., Weladji, R.B. and Nieminen, M., 2006. Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. *Proceedings of the Royal Society of London B: Biological Sciences*, 273(1584): 293-299.

Horton, G.E. and Letcher, B.H., 2008. Movement patterns and study area boundaries: influences on survival estimation in capture–mark–recapture studies. *Oikos*, 117(8): 1131-1142.

Jansen, B.D. & Jenks, J.A. 2012. Birth Timing for Mountain Lions (*Puma concolor*); Testing the Prey Availability Hypothesis. *PLoS ONE*, 7(9).

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33(4): 377–394.

Krebs, C.J. 1995. Two Paradigms of Population Regulation. *Wildlife Research*, 22: 1–10.

Lebreton, J.D., Burnham, K.P., Clobert, J. and Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs*, 62(1): 67-118.

Lehmann, M.B., Funston, P.J., Owen, C.R. & Slotow, R. 2008. Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, 43(2): 230–236.

Loveridge, A.J., Searle, A.W., Murindagomo, F. and 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*(4): 548-558.

Matthews, S.M., Golightly, R.T. & Higley, J.M. 2008. Mark–resight density estimation for American black bears in Hoopa, California. *Ursus*, 19(1): 13–21.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 42(2): 127–137.

Mills, M.G.L. 1995. Notes on wild dog *Lycaon pictus* and lion *Panthera leo* population trends during a drought in the Kruger National Park. *Koedoe*, 38(1): 95–99.

Mills, M.G.L., Wolff, P., le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion *Panthera leo* in the Kalahari Gemsbok National Park. *Koedoe*, 21(1): 163–171.

Mosser, A., Fryxell, J.M., Eberly, L. and Packer, C., 2009. Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, 12(10): 1050-1060.

Mosser, A. & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion , *Panthera leo*. *Animal Behaviour*, 78(2): 359–370.

Orford, H., Perrin, M. & Berry, H. 1988. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). *Journal of Zoology*, 216(4): 717–733.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Mulder, B.M. 1988. *Reproductive success of lions*. In Reproductive success: 363–383. Clutton-Brock, T.H. (*Ed*.). Chicago: University of Chicago Press.

Packer, C. & Pusey, A.E. 1983. Adaptations of female lions to infanticide by incoming males. *The American naturalist*, 121(5): 716–728.

Packer, C. & Pusey, A.E., 1987. Intrasexual cooperation and the sex ratio in African lions. *The American Naturalist*, 130(4): 636-642.

Packer, C. & Pusey, A.E. 1983. Male takeovers and female reproductive parameters: A simulation of oestrous synchrony in lions (*Panthera leo*). *Animal Behaviour*, 31(2): 334–340.

Packer, C. and Pusey, A.E., 1997. Divided we fall: cooperation among lions.*Scientific American*, 276(5): 52-59.

Packer, C., Pusey, A.E. & Eberly, L.E., 2001. Egalitarianism in female African lions. *Science*, 293(5530): 690-693.

Pledger, S., Pollock, K.H., Norris, J.L. & Carolina, N. 2003. Open Capture-Recapture Models with Heterogeneity : I . Cormack-Jolly-Seber Model. *Biometrics*, 59(4): 786–794.

Reisinger, R.R., de Bruyn, P.N., & Bester, M.N. 2011. Abundance estimates of killer whales at subantarctic Marion Island. *Aquatic Biology*,*12*(2), 177-185.

Sheldon, B.C. & West, S.A. 2004. Maternal Dominance , Maternal Condition , and Offspring Sex Ratio in Ungulate Mammals. *The American Naturalist*, 163(1): 40–53.

Smuts, G.L. 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe*, 19(1): 153–164.

Smuts, G.L. 1978. Reproduction and social organisation of lions from the Kruger National Park. *Carnivore*, 1(1): 17–28.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua*, 18(1): 1–9.

Starfield, A.M., Furniss, P.R. & Smuts, G.L. 1981. A modell of lion population dynamics as a function of social behaviour. *Dynamics of large mammal populations*. John Wiley & Sons: 121–134.

Trimble, M.J., Ferreira, S.M. & Aarde, R.J. Van. 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. *Journal of Zoology*, 279(1980): 18–26.

Trinkel, M. 2013. Climate variability , human wildlife conflict and population dynamics of lions *Panthera leo*. *Naturwissenschaften*, 100(4): 345–353.

Trivers, R.L. & Willard, D.E. 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. *Science*, 179(4068): 90–92.

van Vuuren, J.H., Herrmann, E., Funston, P.J., Vuuren, J.H. Van, Herrmann, E. & Funston, P.J. 2005. Lions in the kgalagadi transfrontier park: modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

van Rooyen, M.W., van Rooyen, N. & van den Berg, H.M. 2008. Landscapes in the Kalahari Gemsbok National Park , South Africa. *Koedoe*, 50(1): 99–112.

van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organization (*Panthers, leo*). *Journal of Zoology*, 206(1): 97–112.

White, G.C. & Burnham, K.P. 1997. Program MARK : Survival Estimation from Populations of Marked Animals. *Bird Study*, 46(S1): ppS120–S139.

Whitman, K.L., Starfield, A.M., Quadling, H. & Packer, C. 2007. Modeling the Effects of Trophy Selection and Environmental Disturbance on a Simulated Population of African Lions. *Conservation Biology*, 21(3): 591–601.

Whitman, K.L. & Packer, C. 2006. *A practical guide to aging African lions*. Conservation Force, USA.

Huck, U.W., Labov, J.B. & Lisk, R.D., 1986. Food restricting young hamsters (*Mesocricetus auratus*) affects sex ratio and growth of subsequent offspring. *Biology of reproduction*, 35(3): 592-598.

Woodroffe, R. & Frank, L.G. 2005. Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation*, 8(1): 91–98.

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

Chapter 5:
Trends in the Kalahari Gemsbok National Park lion (*Panthera leo*) population characteristics

5.1. Introduction

Lion (*Panthera leo*) numbers are declining rapidly across their natural range, a trend which is expected to continue into the future (Riggio & Pimm, 2011; Riggio *et al*., 2013; Bauer *et al*., 2015a). The lion population of the Kgalagadi Transfrontier Park (KTP) is one of only four populations in southern Africa that is thought to be stable or increasing (Bauer *et al*., 2015a; Bauer *et al*., 2015b). In light of the vulnerability of lions, and the importance of the KTP as a stronghold of the species (Riggio *et al*., 2013), measuring reliable trends in population size and demography is important (Ferreira *et al*., 2013; Bauer *et al*., 2015a). Reports of changes in the Kalahari Gemsbok National Park (KGNP) lion population's age and sex structures (Funston, 2011; Ferreira *et al*., 2013; Chapter 4), and high rates of human-lion conflict (van Vuuren *et al*., 2005), raised concerns over the population's sustainability (Ferreira *et al*., 2013).

Lion population characteristics are expected to change over time in response to environmental and social constraints (Mills, 1995; Packer *et al*., 2005; Trinkel, 2013). However, quantifying change in population characteristics becomes challenging when observations are made over time, using different techniques (Caro, 1999). Estimates of population characteristics from various methods may not be comparable, or carry margins of error, which makes trend detection imprecise (Gerrodette, 1978). Research design is guided by the objectives of a study (Eberhardt & Thomas, 2008). Research design is seldom conducted with monitoring change over time as an objective and often focusses on determining point estimates of a population rather than a monitoring process that will detect change over time (Pearl, 2000). Research design with the aim of monitoring trends requires a measure of precision to detect directional change from which management decisions can be inferred (Gerrodette, 1978). Even when using a single method consistently, the probability of making an error in deducing population trends persists (Mackenzie & Royle, 2005; Beja *et al*., 2009; Ferreira & van Aarde, 2009). Errors in deducing that a change has occurred in a population when in fact it has not (Type I statistical error), may risk unprecedented effort in further research or interventions, when it is not required. Reacting to the opposite (Type II statistical error), where change has occurred but was not detected, may lead to a lack of response by conservationists when it is actually needed to mitigate change which exists, and thus increases the risk of negative effects to the population due to delayed response (Gerrodette, 1978).

Population size estimates for lions in the KGNP have been determined using various methods with unknown accuracy and varying precision. The methods that have been used to determine population size in the KGNP included closed-population mark-recapture (Mills *et al*., 1978; Castley *et al*., 2002), open-population mark-recapture (Chapter 3), density estimates from known individuals and prides, using radio-telemetry collars (van Vuuren *et al*., 2005; Funston, 2011), and track indices (Funston *et al*., 2010; Funston, 2011; Ferreira *et al*., 2013; Chapter 3). The spatial parameters of the study area in which population size estimates were derived for the KGNP and the GNP to the east, also varied between studies. This is significant because the KGNP in South Africa (9 710 km^2) is an open ecosystem joined to the GNP of Botswana (26 000 km^2). This allows unrestricted spatial movement of lions in the greater KTP (35 710 km^2) and limits the accuracy and precision of mark-recapture estimates constrained to the KGNP exclusively or an undefined area adjacent to the KGNP in the GNP (Mills *et al*., 1978; Castley *et al*., 2002).

In the KGNP, five different studies have described population age and sex structure (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011; Ferreira *et al*., 2010; Chapter 4). The demographic characteristics between the various studies in the KGNP have been derived from variable sample sizes, all of which inferred that the samples were representative of the population (Chapter 4). However, precision is known to increase with sample size, and smaller samples may have misrepresented the true population characteristics (Wintle *et al*., 2004; Chapter 3). The lion demographic studies in the KGNP have been driven by various objectives and numerous logistical, financial and methodological restraints (Pearl, 2000), and challenged by the vast area of the KGNP and the low densities of lions (Mills *et al*., 1978). However, a conclusive framework to quantify population variables for the KGNP and the KTP is required to properly evaluate trends in demographics and population size into the future.

Here the population characteristics of the KGNP lions, over the last 40 years, are compared in an attempt to detect discernible changes in lion population characteristics. The various methods which have been used to derive lion demographic characteristics and population size estimates in the KGNP are assessed. Any discernible changes in population characteristics are discussed with regard to some potential causes and consequences of such changes in demographic and population size characteristics. Challenges associated with comparing population characteristics using various techniques are evaluated and some suggestions are made with regards to future surveys of lions in the KGNP and KTP.

5.2. Data collection and analysis

5.2.1. Data sources

Age and sex structure characteristic information was extracted from four published sources (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011; Ferreira *et al*., 2013) for comparison against the current study (Chapter 4). Population size estimates were obtained from the same four publications, as well as two additional publications (Funston, 2002, Funston *et al*., 2010) for comparison with population size estimates from the current study (Chapter 3).

5.2.2. Analysis of age and sex ratio data

Due to the age categorization of the data obtained from historic studies, age class structure was only comparable for certain age groups. To determine the changes in age class structure across all studies, animals under the age of two years old had to be grouped and are referred to as cubs. "Sub-adults", between the ages of two and four years old were comparable and "adults" over four years old were comparable over all five studies (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011; Ferreira *et al*., 2013; Chapter 4). Comparisons between the various studies are made with reference to the year in which the study ended, *i.e.* the publication of Mills *et al*., (1978), which was conducted between 1976 and 1977 is referred to as "1977".

Each of the studies describing sex and age structure used different sample sizes from which demographic characteristics were derived, but none provided confidence intervals for their estimations. In an attempt to provide an indication of error around the demographic values obtained from different sample sizes in the past, Bootstrap Simulations (with replacement) (Efron & Tibshirani, 1993) were applied to the most recent data set (n =261) of known individuals (Chapter 4). Bootstrap simulations were applied by selecting sub-samples of unique individuals at random from the total reference sample. The simulations were iterated 1000 times at the exact sample sizes used in historic studies from which age and sex structure were obtained. At each sub-sample iterated from the dataset, the proportion of males and females, and the proportions of adults (> 4 yrs), sub-adults (2-4 yrs) and cubs (< 2 yrs) were described for the sub-sample of the "population". From 1000 iterations at different sub-sample sizes, confidence intervals could be calculated at the specific sample sizes related to historic studies (Cortés, 2002). These potential margins of error from the dataset of the current study were assumed to provide an approximation of the potential margins of error, which could have been incurred at the specific sample sizes from which age and sex structures were described in the historic studies. Comparisons between the age and sex structure described in the various studies are made with consideration of the potential bias in the various studies, based on the sample size from which population characteristics were described.

5.2.3. Analysis of population size data

The distribution of the point estimates of the various population size estimates from the various studies were graphically compared, using the published 95% confidence limits to discern any marked changes in the population size over time.

5.3. Results

5.3.1. Sex structure

The sex structure of the lion population in the KGNP, characterized by various age classes, from the various studies, is presented in Table 5.1. The ratio between males and females in the KGNP lion population has fluctuated between 1♂:1♀ to 1♂:2♀ relationship over a 38 year period (1977-2015).

Table 5.1 Data of age and sex structure was derived from historic studies as well as the current study (Chapter 4). The period within which the studies occurred are presented in brackets under the publication. The relationship between males and females in each age class are shown as percentages with sample sizes in brackets for each age class.

	Mills *et al*., 1978; n = 73		**Castley *et al*., 2002; n = 79**		**Funston, 2002; 2011; n = 228**		**Ferreira *et al*., 2013; n = 49**		**Chapter 4; n = 261**	
	(1976-77)		(1996-97)		(1998-2001)		(2010)		(2013-15)	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Cub (0-1 yr)	39 (9)	61 (14)	--	--	--	--	--	--	49 (34)	51 (35)
Juvenile (1-2 yrs)	--	--	--	--	--	--	--	--	50 (15)	50 (15)
Cub & Juv (0-2 yrs)	--	--	--	--	67 (44)	33 (22)	--	--	49 (34)	51 (36)
Sub-adult (2-4 yrs)	42 (8)	58 (11)	31 (4)	69 (9)	61 (32)	39 (20)	75 (9)	25 (3)	54 (16)	46 (13)
Adult & S-adult (>2 yrs)	36 (18)	64 (32)	24 (19)	77 (60)	36 (58)	64 (104)	57 (25)	43 (19)	49 (88)	51 (89)
Adult (>4yrs)	32 (10)	68 (21)	23 (15)	77 (51)	24 (26)	76 (84)	50 (16)	50 (16)	49 (72)	51 (75)
Total	37 (27)	63 (46)	24 (19)	77 (60)	43 (102)	57 (126)	56 (27)	44 (21)	49 (128)	51 (133)

The sex ratios of lions under two years showed a skew towards males (67%) in 2001, but were near parity in 2015 (49% ♂). In 1977, cubs (<1 yr) showed a skew towards females (61%) and were equal in 2015. For sub-adults (2-4 yrs), females were observed in higher proportions in 1977 (58%♀) and in 1997 (69% ♀), but were skewed towards males in 2001 (61% ♂), 2010 (75% ♂) and 2015 (54% ♂). The adult age class (>4 yrs) was biased towards females in 1977 (32% ♂), 1997 (23% ♂) and 2001 (24% ♂) but were observed to be equal in 2010 and marginally skewed to females in 2015 (51% ♀).

The 95% confidence intervals (CI) generated around the overall sex ratios of the respective studies, derived from 1000 simulations for each sample size, from the entire dataset of individuals identified in the current study, (n = 261), are depicted in Figure 5.1. The confidence interval at the specific sample sizes used in each historic study was applied to the respective sex ratio observation. The 95% CI around the sex ratios was ±11% in 1977, with a sample size of 73, and ±11% in 1997, with a sample size of 79. At a sample size of 228 individuals in the KTP, the study in 2001 had the smallest confidence intervals ±6%, whereas the study in 2010 had the greatest confidence intervals (±14%), at a sample size of 49 individuals (Figure 5.1). In 2001 and 2010 there were ≥ 7.7% more males observed in the population than in 1997. In 2015 there were ≥ 13% more males in comparison to observations in 1997. The proportional change in the sex ratios between the observations in 2001, 2010 and 2015 could not be discerned. Similarly, no change in sex ratios could accurately be described between the estimates in 1977, 1997 and 2001 due to analogous confidence intervals.

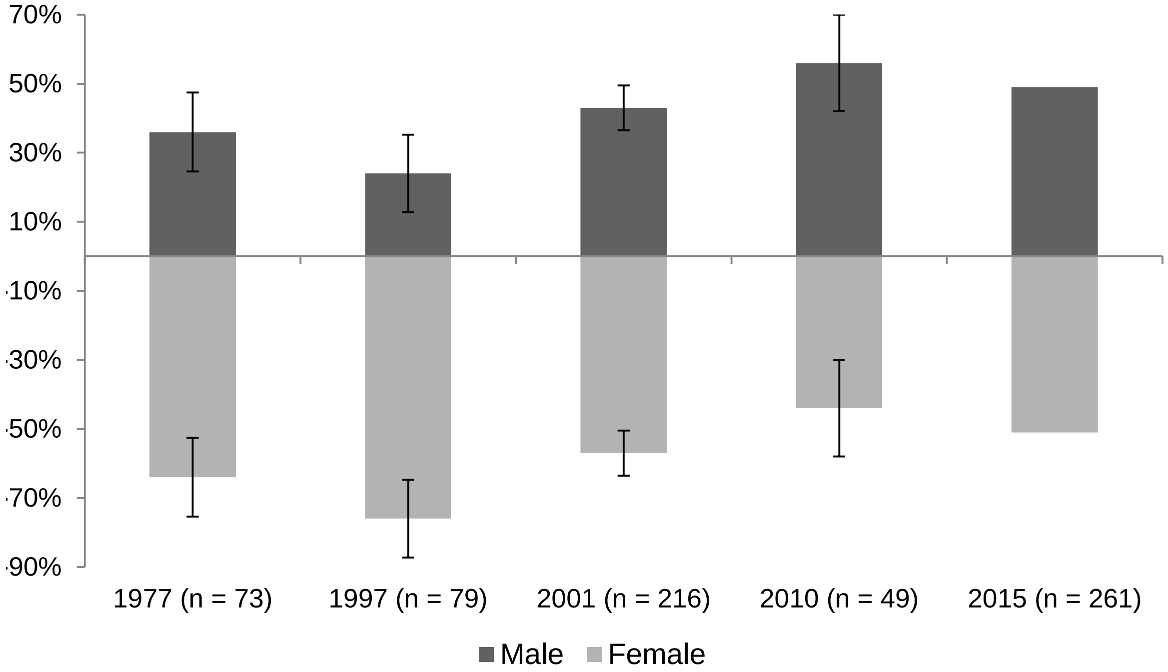

Figure 5.1 Lion population sex ratios in the KGNP derived from historic studies (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011; Ferreira *et al*., 2013) and the current study. These studies are referred to in chronological order on the x-axis according to the year in which the study ended. Error bars represent 95% confidence intervals for the respective sample sizes used in each study. The 95% confidence intervals at the exact sample sizes of each historic study, are derived from the entire database of the current study (n = 261), using 1000 simulation (with replacement) (Chapter 3).

5.3.2. Age class structure

The age class structures observed in the various historic studies and the current study are presented in Table 5.2. The different age classes showed some variability in the proportional margins of error (95% CI) due to their proportional differences in availability of lions of different age classes in the reference sample from which they were drawn (Figure 5.2).

Table 5.2 Age class structure derived from historic studies and the current study. The relationships between cubs, sub-adults and adults are shown as percentages with sample sizes in brackets.

	Mills *et al*., 1978; n = 73 (1976-77)	**Castley *et al*., 2002; n = 102** (1996-97)	**Funston, 2011; n = 223** (1998-2001)	**Ferreira *et al*., 2013; n = 49** (2010)	**Chapter 4; n = 261** (2013-15)
Cub (< 2 yrs)	32 (23)	23 (23)	27 (61)	10 (5)	33 (86)
Sub-adult (2-3 yrs)	26 (19)	13 (13)	23 (52)	25 (12)	12 (31)
Adult (> 4 yrs)	42 (31)	65 (66)	49 (110)	65 (32)	55 (144)

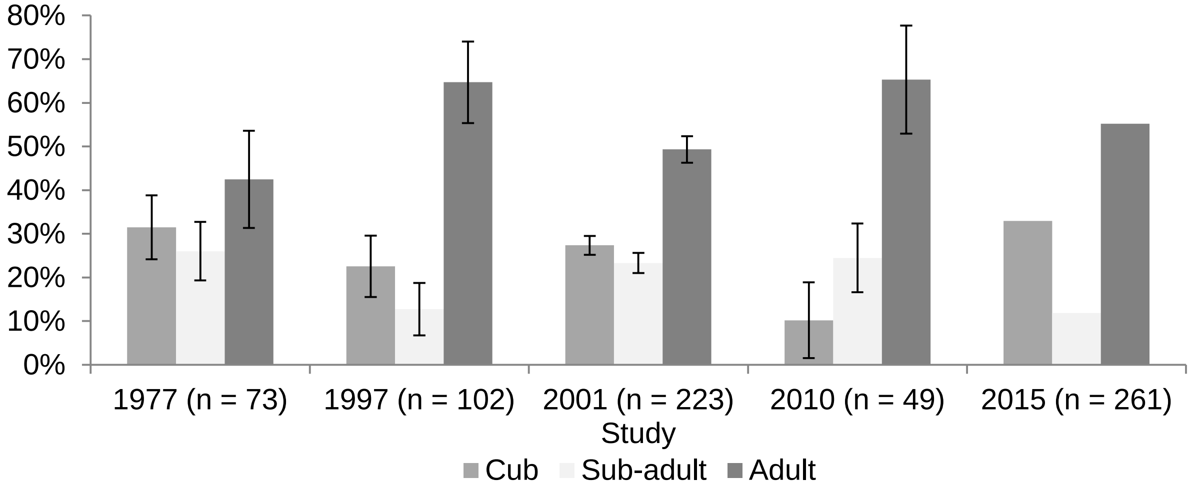

Figure 5.2 Age class structure of lions in the KGNP, derived from historic data (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011; Ferreira *et al*., 2013) and the current study. These studies are referred to in chronological order on the x-axis referring to the year in which the study ended. Margins of error (95% CI) are presented for each age class, and for each study, according to the sample size. The 95% confidence intervals at the exact sample sizes of each historic study, are derived from 1000 simulations of the entire database of the current study (n = 261) (Chapter 3).

The 95% confidence intervals for adults for the respective studies ranged between ±3%, for a sample size of 223 in 2001, and up to 12% from a sample size of 49 in 2010. The 95% confidence intervals for sub-adults for the respective studies ranged between ±2% (n = 223) and ±8% (n = 49). For cubs, the 95% confidence intervals for the respective studies were between ±2% (n = 223) and ±8% (n = 49) (Figure 5.2). The study in 2010 observed ≥ 6.3% less cubs than the observations in 2001 and ≥ 14% less cubs than were observed in 2015. Sub-adults were proportionally less in 1997 (≥ 2%) and 2015 (≥ 4%) than any of the studies in 1977, 2001 or 2010. The proportion of adults in the population was greater in 1997, 2010 and 2015, than that observed in 1977 and 2001.

5.3.3. Population size

The population size estimates and 95% confidence intervals (CI) from the five different studies conducted on the KGNP lion population are presented in Table 5.3. A graphical representation of the population size estimates and 95% CI are presented in Figure 5.3 for a visual interpretation of change in population size over time and between different methods. Mark-recapture estimates excluding cubs showed an increase of ≥ 2 individuals between 1997 and 2015. Including cubs, mark recapture estimates in 2015 showed an increase of ≥ 59 individuals since 1977. Although confidence intervals overlapped for population size estimates from track indices between 2001, 2010 and 2015, the best estimate from the average track density of the respective studies showed an increase in population size of 40 individuals between 2001 and 2015 and an increase of 32 individuals between 2010 and 2015.

Table 5.3 Lion population characteristics in the KGNP derived from historic publications and the current study (Chapter 4). Population size estimates show the best estimates with 95% confidence intervals from each study (CI). The source of the data, the period in which the data was collected and the duration of the studies is presented. The study areas are defined where possible and the techniques used to define population size estimates are presented. KGNP+ indicates that the study occurred in the KGNP and, either a defined area into the GNP, for which area sizes are given, or an unknown area in the GNP, which is stipulated.

Publication	Study period	Duration (months)	Study area	Population size estimate method	Population size N (95% CI)
Mills *et al*., 1978	1976 - 77	6	KGNP+ (Unknown area)	Mark-recapture (Lincoln index)	140 (108-181)
Castley *et al*., 2002	1996 - 97	10	KGNP+ (Unknown area)	Mark-recapture (Lincoln-Peterson)	131 (106-156)
Funston, 2002; 2011	1998 - 2001	30	KGNP (±9 710 km²)	Home range density	138 (113-131)
			KGNP (±9 710 km²)	Track indices	122 (120-128)
Ferreira *et al*., 2010	2010	1	KGNP (±9 710 km²)	Track indices	130 (91-169)
Current study	2013 - 15	26	KGNP+ (14 250 km²)	Registration	261
			3 KGNP+ (14 250 km²)	Minimum-known-alive	145
			KGNP+ (14 250 km²)	Mark-recapture (POPAN)	246 (237-256)
			KGNP (±9 710 km²)	Track indices	162 (120-209)
			KGNP+ (14 250 km²)	Track indices	242 (176-307)

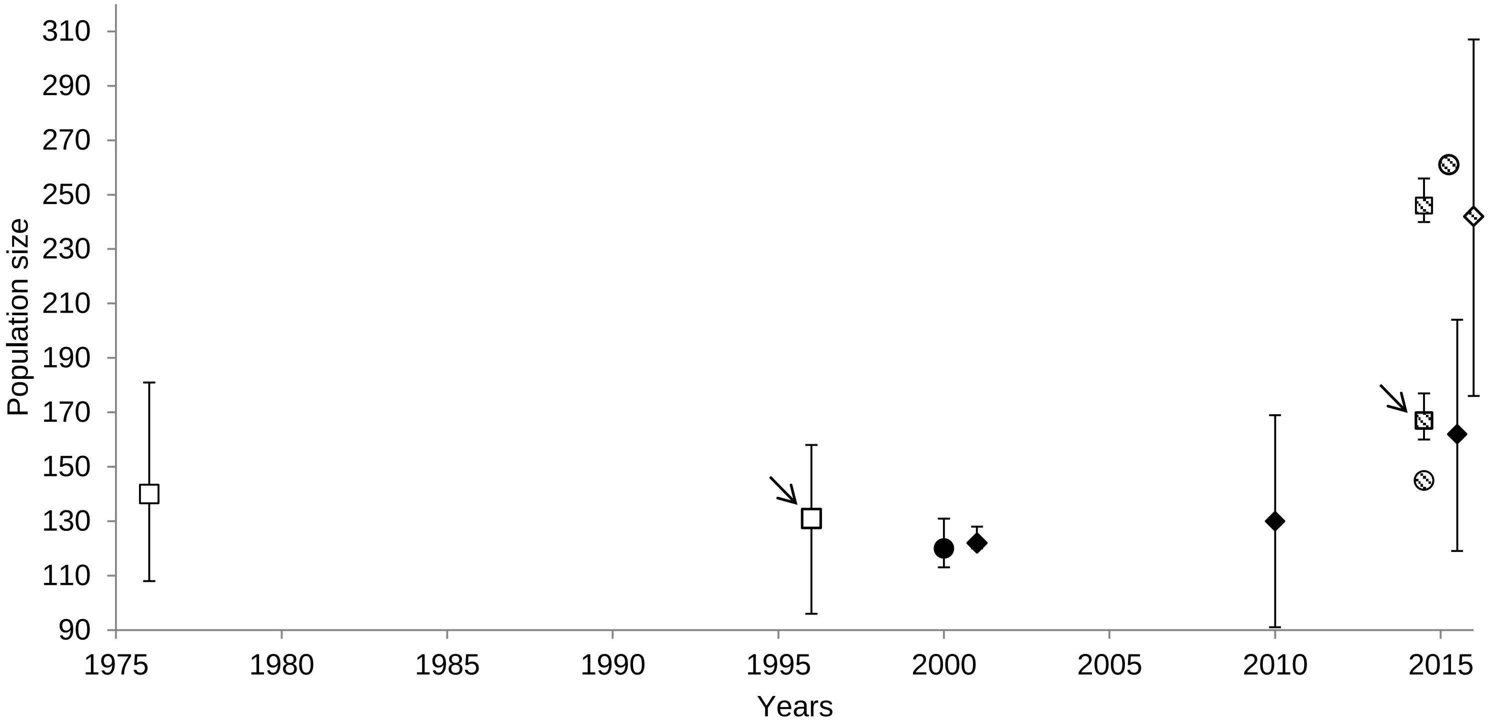

Figure 5.3 Lion population size estimates in the KGNP and immediate area east of the Nossob River in the GNP between 1977 and 2015. Open squares represent closed population mark-recapture in the KGNP and an undefined area to the east of the Nossob River (Mills *et al*., 1978; Castley *et al*., 2002). Closed symbols represent population size estimates for the KGNP exclusively, including home range density estimates (closed circle) and track index density estimates (closed diamonds) extrapolated to the KGNP (±9 710 km²) (Funston, 2002 & 2011; Ferreira *et al*., 2013; Chapter 3). Symbols filled with diagonal patterns represent population size estimates for the KGNP and a defined area to the east of the Nossob River (±14 250 km²), including open population mark-recapture (pattern squares), track indices (pattern diamond), registration and minimum-known-alive (pattern circles) (Chapter 3). Arrows on the graph indicate mark recapture estimates where cubs (< 1 yr) are excluded from estimates.

5.4. Discussion

5.4.1. Sex ratios

Taking into account the potential margins of error (95% CI) which may have been incurred at various sample sizes, it remains apparent that a change in the population sex structure of lions in the KGNP has shifted to a greater proportion of males than recorded historically. Between the estimates in 1977 and 1997, there was no perceptible change in the overall population's sex ratios. A notable change in the sex ratios appears to have occurred after 1996 (Castley *et al*., 2002) towards a greater proportion of males in all following studies. The study in 2010 (Ferreira *et al*., 2013), potentially over-sampled males as a result of a small sample size, therefore no discernible differences can be inferred between the study in 2010 and the study in 2001 (Funston, 2011) or 2015 (Chapter 4). However, a discernible difference is apparent between observations in 1996 (Castley *et al*., 2002) and 2010 (Ferreira *et al*., 2013), showing an increase in the proportion of males.

Due to the imprecision of demographic information obtained from small sample sizes in historic studies, it is not possible to determine the true extent of changes in the sex ratios of lion in the KGNP between every study over the past 38 years. Nonetheless, changes reflected by demographic information over time, detected broader trends in the KGNP lion population. Prior to 2001, all observations found a greater proportion of females in the population, whereas observations after 2001 indicate a population near parity or a slight skew towards males. Lion population sex ratios in other lion populations are predominantly skewed towards females (Bertram, 1973; Smuts, 1978; Stander, 1991; Ferreira & Funston, 2010 Funston, 2011). Equal or male skewed populations in lions are uncommon. The sex ratio in the KGNP is a departure from the ratios expected in lion populations, which fluctuate at a ratio of around two to three females for each male (Bertram, 1973; Smuts, 1978; Stander, 1991; Ferreira & Funston, 2010 Funston, 2011). However, similar shifts in sex ratios to a higher proportion of males have been observed in Mana Pools National Park, Zimbabwe and Kruger National Park, South Africa, in association with changes in prey dynamics and population growth (Dunham, 1992; Mills, 1995).

Changes in sex and age structures within a lion population have also been described as a result of hunting in Hwange National Park, Zimbabwe (Loveridge *et al*., 2007). In the KGNP, hunting of lions may have been replaced with persecution, in the form of retribution killing in response to human-lion conflict (van Vuuren *et al*., 2005). Persecution of lions may have negative impacts associated with lion sociality (Yamakazi, 1996; Elliot *et al*., 2014), human-lion conflict (Funston, 2002; Herrmann, 2004; van Vuuren *et al*., 2005), resilience of a lion population to stochastic environmental events (Celesia *et al*., 2010), and the effects of an outbreak of disease (Ferreira & Funston, 2010; Ferreira *et al*., 2013), which may in turn effect the persistence of the KGNP lion population. When taking into account the increased mortality rates sustained on the persecuted boundary prides in the KGNP, adult female survivability was found to be the greatest influencing factor for the population's persistence (van Vuuren *et al*., 2005). Birth rates and birth sex ratios, with female biased litters increasing the population's resilience, were found to contribute significantly to potential declines in population size (Funston, 2002; Herrmann, 2004; van Vuuren *et al*., 2005).

If the lion population in the KGNP has remained stable in size, an increase in the proportion of males would suggest a decrease in the number of females. However, if the population size has increased, as indicated for some population size estimates in the KGNP (Castley *et al*., 2002; Funston, 2011; Chapter 3), then it is possible that the number of females has remained stable but the number of males has increased. It is possible that the number of males in the population has increased because of higher male survival rates in the current study (Chapter 4) than were observed previously (Eloff, 1980; Funston, 2011). An increase in male numbers was observed in a significant increase in the number of males present within prides from the current study (n ~ 2.42; ±0.49 SD) (Chapter 4) compared with the study concluded in 2001 (n ~ 1.6; ±0.69 SD) (Funston, 2011). Increased male survival rates could be as a result of a recent period of above average ecological conditions in recent history (van Vuuren *et al*., 2005), as well as lower mortality rates due to reduced lion persecution, at least in the past five years (Funston, 2002; Pers. Comm. M. Ferreira[7]). Male lions in other areas generally experience higher age dependent mortality rates than females (Barthold *et al*., 2016). The mortality rate of males in lion populations is largely influenced by competition between males for territory and breeding rights with females, a factor which is also density dependent (Barthold *et al*., 2016).

A greater proportion of males in the lion population can have several consequences. More males can lead to higher rates of coalition turnovers (Yamakazi, 1996), which can lead to increased male recruitment by skewing sex ratios at birth (Packer & Pusey, 1983). A higher recruitment and survival rate of males can also lead to increased dispersal of non-territorial males, searching for residency, which in turn can lead to increased transgressions and heightened human-lion conflict (Funston, 2011; Elliot *et al*., 2014). Increased rates in lion transgressions out of the KGNP would necessitate management interventions, such as capturing and relocating individual

---

[7] Micho Ferreira, Section Ranger, Twee Rivieren, Kalahari Gemsbok National Park, Northern Cape, South Africa. 8800.

lions a substantial distance away from the boundary fence, back into the KGNP (Funston, 2002). The consequences of relocating lions back into the KGNP are unknown. Relocating lions back into the KGNP may have the potential to further exacerbate male recruitment, through increased male-male competition particularly when coupled with stochastic and environmental drivers (Trivers & Willard, 1973; Ferreira *et al*., 2013; Trinkel, 2013). Increased male-male competition could lead to a higher turnover rate of pride tenures by males, resulting in a higher proportion of male cubs being born into the population (Yamazaki, 1996). Once new males take dominance over a pride, the new territorial males are known to kill the cubs, prompting females to come into oestrous. It has been observed elsewhere that the first litters born after a new male has taken dominance over a pride, contain a higher proportion of male cubs (Yamazaki, 1996; Whitman *et al*., 2004; Woodroffe & Frank, 2005).

5.4.2. Age class structure

The margins of error for detecting the proportion of adults in the KGNP lion population were greater than they were for cubs and sub-adults. Within 95% CI's, it is apparent that the proportion of adults showed a marked increase from point estimates obtained in 2001 (Funston, 2011), to estimates obtained in 2010 (Ferreira *et al*., 2013) and 2015 (Chapter 4). The proportion of cubs showed noticeably lower proportions in 2010 (Ferreira *et al*., 2013), than in 1977, 2001 and 2015 (Mills *et al*., 1978; Castley *et al*., 2002; Funston, 2011). Cub proportions did not show obvious differences between 1977, 1997 or 2001, but showed a greater proportion of cubs in 2015 than in 1997, 2001 and 2010 (Mills *et al*., 1978; Castley *et al*., 2002; Chapter 4). Sub-adult proportions were noticeably low in 1996 and in 2015 (Castley *et al*., 2002; Chapter 4).

Attempting to determine age class structures from imprecise data may produce extreme bias in results. As with sex ratios, age class structures are auto-correlated. An increase in the proportion of one age class would influence the proportions of the remaining two age classes. Unlike sex ratios, the relative distribution of the proportional changes in the age classes is unknown. For instance, an increase in adults may result in a decrease in cubs or sub-adults, or both. The proportion of adults in a lion population is expected to remain relatively stable, whereas cubs and sub-adults are expected to fluctuate more significantly over shorter time periods (Mills, 1995; Funston, 2011; Trinkel, 2013). There was a difference in the proportion of cubs noted in the lion population between 2001 (≤ 29%) and 2015 (33%). The proportional representation of adult lions was greater in the current study than in 2001. If the population size has increased, it may be expected that the proportion of cubs may have decreased, as a function of density. Similar differences and fluctuations in proportional representation of cubs and adult lions within a lion population have also been observed in the Kruger National Park (Smuts, 1976).

In addition to the bias and variability related to sample size, observer bias may also affect age classification results. In all the lion population studies that have been conducted in the KGNP, subjective criteria were used to age lion. None of the studies thus far have provided for the possibility of error within age class classification, which may lead to incorrect assumptions of population structure. More objective criteria have recently been developed to classify lion age, such as shoulder height, measured by photogrammetry (Ferreira & Funston, 2010), and proportional nose pigmentation, using GIS software (Whitman *et al*., 2004). However, these objective methods also carry significant margins of error of up to 25%, which could influence conclusions of age class structure. The age class structures of lions observed currently in the KGNP are similar to that which has been observed previously in Kruger National Park (Mills, 1995; Ferreira & Funston, 2010) and Etosha National Park (Stander, 1991).

5.4.3. Survival and recruitment

Of the five studies conducted on lion population demographics in the KGNP, only one study determined birth rates between 1998 and 2001 (Funston, 2011), and two of the studies (Eloff, 1980; Funston, 2011) measured cub survival. A study conducted in 1978 which constrained efforts to a small portion of the northern KGNP, had a limited sample size (n = 16), was conducted during poor ecological conditions and indicated an extremely low (5%) survival rate for cubs (Eloff, 1980). No survival rate estimates existed for lions over one year old (van Vuuren *et al*., 2005) until the current study (Chapter 4). Mortality rates are expected to be higher for males than for females (Ferreira & Funston, 2010; Barthold *et al*., 2016). Higher mortality rates of males than females were also identified in the current study (Chapter 4). Observed survival rates of cubs (61%, Funston 2011; 59%, Chapter 4), differed substantially from apparent survival rates derived from the Cormack-Jolly-Seber models (76%-94%) (Chapter 4). Survival rates of cubs were relatively high in the KGNP in comparison to other lion populations such as Kruger National Park (41-85%; Ferreira & Funston, 2010).

Birth rates of lions in the KGNP have only been determined for the study period of 1998-2001 (Funston, 2011) and the current study (Chapter 4). Between these studies there was a substantial annual variability in lion birth rates in the KGNP (0.3–1.33 cubs, per adult female, per year) (van Vuuren *et al*., 2005; Funston, 2011; Chapter 4). Average birth rates were relatively low in the current study (0.53 per female/year) in comparison to the previous estimate for the KTP population (0.67, Funston, 2011) and in comparison with five boundary prides in the KTP (1.33, van Vuuren *et al*., 2005). The birth rates in the current study (Chapter 4) were similar to those of lions in Etosha National Park, Namibia (0.77; Orford *et al*., 1988) and in the Gir Forest Bioregion of India (0.37; Banerjee *et al*., 2010). Birth rates of lions in Kruger National Park, South Africa are nearly double the birth rate in the current study, producing one cub per female per year (Funston *et al*., 2003).

5.4.4. Population size

Between 1976-1977 a closed population mark-recapture analysis was conducted, using the Leslie's index, from one capture and marking phase (± 2 Months) and one re-capture phase (± 4 Months), over a six month period (Mills *et al*., 1978). Between 1996 and 1997 another closed population mark-recapture survey was conducted, using the Lincoln-Petersen method, with one capture and marking phase (± 2 Months) and two recapture phases (± 1 month each), over a ten month period (Castley *et al*., 2002). Between 1998 and 2001 a study on lion population characteristics was conducted in the KTP, in which the KGNP was included. This 1998-2001 study made use of home range density estimates using known individuals and prides, within defined home-range areas which were calculated from collared individuals (Funston, 2002; Funston, 2011). The study also made use of the density estimates to calibrate track index parameters in the KTP and KGNP (Funston, 2002; Funston *et al*., 2010). The track index parameters from the 1998-2001 study, were used to estimate the population size of lion in 2010 (Ferreira *et al*., 2013), and were used as one of the methods applied in the current study (Chapter 3).

Population size estimates in the current study, were derived using open population mark-recapture analysis, and applying the Cormack-Jolly-Seber derived POPAN model (Chapter 3). A registration study of unique individuals was used as a marking and re-capture/ re-sight method, between May 2013 and June 2015. A "total" count of registered individuals, and minimum-known-alive estimate, were also determined using known individuals and the mark-recapture matrix (Chapter 3). In the current study, 261 individual lions were identified within the boundaries of the KGNP. Eleven of the individual lions that were identified in the current study where known to have died during the study period, and 36 individuals could not be associated with resident prides (Chapter 4). Thus, the resident population in the study area (14 250 km^2) may have included 222 to 250 known individuals in resident prides at the end of the study period, if no more deaths occurred. The identification of known prides further supported the notion of stable residence of lions in the study area. Of the known population in the current study, 87% were expected to remain within the study area, as they were part of resident prides that were defined by collared individual home ranges (van Orsdol *et al*., 1985; Garshelis, 1992).

Open population mark-recapture estimates (POPAN) from the current study gave a population size estimate of 246 (95% CI 238-256). This estimate of 246 individuals was derived from a mark recapture matrix of multiple re-sightings of unique individuals, from which 68% of known individuals were seen more than once (Chapter 3). Open population mark recapture appears to have a high resolution, detecting changes in population size through births. This was demonstrated through changes in population size estimates, including cubs born into the population throughout the study period, but showing little change in estimates when cubs were excluded (Chapter 3). Track indices from the current study, extrapolated to the study area, estimated a population size of 242 individuals (95% CI = 176-307). Track indices inherently include cubs in its estimates. These three estimates from the current study, registration, mark-recapture and track indices within the known study area differ considerably from historic studies.

When cubs (< 1yrs) were excluded from the mark recapture estimates (N = 167; 95% CI = 160-177) and when density estimates from track indices were extrapolated to the KGNP (N = 164; 95% CI = 120-209), estimates from the current study (Chapter 3) did not differ markedly from most historic population size estimates. However, if it is assumed that the mark recapture estimates in 1977, 1996 and those in 2015 sampled the same population, the mark recapture estimates from 1996 (Castley *et al*., 2002) and the mark-recapture estimates from the current study (Chapter 3) indicate a notable increase in the population size when excluding cubs (< 1yrs). Between the study in 1997 (Castley *et al*., 2001) where cubs (< 2 yrs) were excluded and the current mark-recapture estimates, excluding cubs (Chapter 3), the population over two-years may have grown by as much as 81 individuals.

More notable would be the increase in population size between 1977 (Mills *et al*., 1978) and 2015 (Chapter 3), when cubs were included in the estimates. An increase in the population between 1977 and 2015 could be > 59 individuals and as much as 144 lions. These noted changes in population size would be based on the assumptions that in the 1977, 1996 and in the current study, the same roads, in the same areas were surveyed, and therefore sampled the same population. Between the study in 1997 (Castley *et al*., 2001) where cubs (< 2 yrs) were excluded, and the current mark-recapture estimates, excluding cubs (Chapter 3), the population may have grown by as much as 81 individuals over two-years. Abundance estimates from closed population mark-recapture surveys (Mills *et al*., 1978; Castley *et al*., 2002), population size estimates extrapolated from home range density estimates (Funston 2002; 2011), and track indices extrapolated to the KGNP (Funston, 2011; Ferreira *et al*., 2013; Chapter 3), did not reveal any clear changes in population size between 1977 and 2015 (see Figure 5.3).

Some of the effects of methodological variance and imprecise results may be reduced by long time series between estimates (Gerrodette, 1978; Durant *et al*., 2011), as occurs for the KGNP lion population between 1977 and 1996 (Mills *et al*., 1978; Castley *et al*., 2002). However, despite the 20-year interval between 1977 and 1996 estimates, the margins of error were too large to detect meaningful change in population size. The precision of estimates plays a crucial role in determining population trends over time (Gerrodette, 1978; Durant *et al*., 2011). For lion populations, precision in estimates is crucial to detect sudden changes over short periods. For instance, in the Serengeti, the lion population is prone to long periods of stability, with sudden changes in population dynamics (Packer *et al*., 2005). Greater statistical power is required to detect rapid, short-term changes (Gerrodette, 1978). Further mitigation of imprecise estimates through simulation techniques (Caughley, 1976) may aid in determining trend directionality and estimate rates of change with confidence limits, as has been done in the KGNP lion population previously (Ferreira *et al*., 2013). Ferreira *et al*. (2013) randomly simulated population size point estimates within 95% confidence limits, from historic studies, to derive probable population growth directionality, and found that the population did not show apparent directional change between 1977 and 2010 (Ferreira *et al*., 2013).

Another potential source of bias in population size estimates, is the fact that in this, and all the other studies conducted in the KGNP, effort has been biased towards the riverbeds by more than 60% (Mills *et al*., 1978; Castley *et al*., 2002; Ferreira *et al*., 2013; current study), where lion density is highest (Funston, 2011; Ferreira *et al*., 2013). This means that certain remote areas of the dunes, have been under sampled, or excluded completely from the surveys (Mills *et al*., 1978). The probability of detecting individuals or “capture probability” in the case of mark-recapture experiments may be a function of observer bias (vigilance) or subject (lion) behaviour, such as habitat preferences (*i.e.* river or dune habitats) (Jackson *et al*., 2006). Spatial and temporal movement of the subject, in response to stochastic events Horton & Letcher, 2008), or constant influences (Hampton, 2004), may further influence capture probability. For instance, the current study had a lion encounter rate (1.33 lions/100 km, excluding sightings aided by collared individuals) that was 34% greater than the study in 1977, having found 0.7 lions/100 km (Mills *et al*., 1978). Within the current study, encounter rates of lions (n/100 km) varied on a monthly basis (2.65; SD ±1.35; n = 24 months; including collar aided sightings). Inconsistency in such measures can perpetuate variability in results, such as closed population mark-recapture results, which are dependent on constant encounter probabilities for sound estimates (Lettink & Armstrong, 2003). Estimates using mark-recapture may be confounded by immigration through birth, high turnover of the sub-adult and juvenile age class and coalitions of males who are subject to immigration and emigration (Packer *et al*., 2005; Funston, 2011; Marnewick *et al*., 2014).

To detect reliable trends in population size, the most precise method would need to be identified to produce the greatest power in detecting trends (Gerrodette, 1978). Open population mark-recapture, using registration as a means of marking has shown the greatest measure of precision (Gerrodette, 1978; Chapter 3). However, the discrepancy between open-population mark-recapture estimates and historic estimates, begs the question whether the parameters of the observed “population” has changed (Horton & Letcher, 2008). The two previous mark-recapture studies, which present population characteristics for the KGNP (Mills *et al*., 1978; Castley *et al*., 2002), both suggest that the study area includes an undefined portion of the Botswana’s GNP, east of the Nossob riverbed. These two historical studies made use of closed-population mark-recapture estimates to determine lion population size in the KGNP (Mills *et al*., 1978; Castley *et al*., 2002). Considering the unconfined boundaries of the KGNP, perhaps the open-population mark-recapture analysis would better represent the population. Greater sampling effort within the current study, with more equal spatial distribution in the effort, has produced results that are more precise. In addition, due to sampling effort and distribution, current estimates are likely to account for individuals that were missed in previous mark-recapture estimates. Nonetheless, the true extent of the study area, and the population under observation, would require explicit spatial definition to accurately define lion density and not population size in an undefined area (Horton & Letcher, 2008; Penh & Penh, 2012; Chandler & Royle, 2012). Comparisons of lion density estimates would be more comparable between different studies, particularly when the extent of the area and the population being sampled, changes.

Indirect methods of identifying lion population size, based on indices, are dependent on encounter variability for precision (Funston *et al*., 2010; Keeping & Pelletier, 2014). In the current study, broad confidence limits are displayed in lion population estimates using track indices, based on twelve repeated samples (see Chapter 3). Broad confidence limits, in lion population estimates using track indices, were also observed in the study conducted in 2010 (Ferreira *et al*., 2013). This confounds the ability of the track indices technique to detect trends in an efficient manner, as may be expected (Funston, 2002; Funston *et al*., 2010). Therefore, to detect trends in lion population size, it would be unrealistic to use track indices in the KGNP, as too much variability and residual change may occur by the time a trend is detected, which may confound any necessary conservation intervention. Track indices are density based estimates. Therefore, the estimate from track indices for the KGNP is not the same as for the mark recapture estimates, which describe a population outside of the boundaries of the KGNP. However, if density estimates from track indices were extrapolated to the study area of the mark-recapture population in the current study (Chapter 3), the two estimates at the end of the study are similar. However, track indices are less precise (CV = 39%) compared to open-population mark-recapture (CV = 5%) (Chapter 3).

The fission-fusion relationships in prides, which have been described in three of the studies of the KGNP lion population (Mills *et al*., 1978; Funston, 2011; Chapter 4), may confound the ability to accurately determine pride size and therefore density, thus leading to an under estimation (Scheel & Pusey, 1990; Funston, 2011). The average sub-group size which comprised lion sightings in 1996 were on average 2.7 (range: 1-11) individuals (Castley *et al*., 2002). In 2001, sub-group size was 4.2 (±0.4) individuals (Funston, 2011) and in the current study, the average sub-group size was 3.53 (±2.88) individuals (Chapter 4). The study concluded in 2001 (Funston, 2011), had five known prides for which VHF-collar home-range data was available in the KGNP, and a further six prides for which home-range data was not available. Prides showed a smaller pride size in 2001 (11.3 ±1.1), than what was found in the current study (16 ± 8.71) in the KGNP (Funston, 2011; Chapter 4).

Pride size and cohesion is driven by resource availability (Smuts, 1976; Funston & Mills, 2006). The smaller pride sizes, as observed previously in the KGNP, may have been a function of a smaller population or less cohesive prides, where all individuals in the prides were not necessarily accounted for, and thus the pride appeared smaller than it actually was. Pride size increases with an increase in lion density (Packer *et al*., 2001). Not only were prides larger in the current study, there were more prides identified in the study area (n = 14; Chapter 4) than were identified previously in the KGNP (n = 11; Funston, 2011). If pride size has increased, it is possible that resource availability was not a restraining factor on social cohesion during the current study (Celesia *et al*., 2010). Larger pride sizes would also increase the survival probabilities in cubs (Scheel & Pusey, 1990), promote synchronous reproduction within prides, and therefore drive population growth (Packer *et al*., 2001). This would support the notion that the population is currently larger than previous estimates, despite the difficulty in making comparisons between the different surveys.

If the lion population has increased in the KGNP, it would be expected that the population growth rate would start to decline (Trinkel *et al*., 2010), as a function of density dependence and related resource restraints (Kissui & Packer, 2004; Barthold *et al*., 2016), which may explain the low recruitment rate of cubs in the current study (Chapter 4). Several demographic functions may be density dependant, including social interactions such as pride size, mate selection and dispersal and ultimately mating success (Kokko & Rankin, 2006). Smaller litter sizes, longer inter-birth periods and cub survival may all be dependent on lion density (Funston *et al*., 2003). Mortality rates may also be a function of density dependence, not only because of resource acquisition, but also due to changed behaviour in response to increased competition. Sub-adults may disperse earlier due to increased pride size (Funston, 2002), which could have detrimental effects on the success of immigration, particularly in males (Vanderwaal *et al*., 2009; Barthold *et al*., 2016). Not only would males leave their natal prides earlier, but also a greater proportion of females may disperse once the threshold of pride size is reached (±16 individuals) (Scheel & Pusey, 1990). Greater dispersal rates and coalition turnover could exacerbate transgressions of lion out of the park boundaries, leading to increased human-lion conflict, in a system where conflict already has major consequences for lion persistence (van Vuuren *et al*., 2005). Increased coalition turnover due to high rates of competition among a larger number of competing males could further exacerbate male production (Yamakazi, 1996; Packer *et al*., 2005).

5.4.5. Conclusion

The increase in the proportion of males and the decrease in the proportion of the young age classes remains a concern for the persistence of the KGNP lion population. The changes in demographic characteristics of the lion population in the KGNP may be a result of natural ecological factors, but the potential for anthropogenic influences are also apparent. Further investigation into the lion population characteristics of the KTP should be pursued and the potential drivers of demographic change should be addressed more critically. The potential increase in population size of lions in the KGNP, larger pride sizes and a greater proportion of males in the population may lead to increased human-lion conflict.

The open population mark-recapture method, using registration, has provided the highest probability of detecting trends in the KGNP lion population over a relatively short period. However, open population mark-recapture method, using registration as a means of marking individuals, requires a large amount of effort (> 8000 km/ capture event). Due to the high costs involved in identifying lions, as has been done in the current study, using remote or secondary data, such as tourist photographs, from which individual identification and sex and age class can be derived, may be an alternative method for tracking lion demographic signals in the KGNP (Marnewick *et al*., 2014). Similar citizen science projects (Dunham & du Toit, 2012) are being conducted on both leopard and cheetah populations of the KGNP[8]. The existence of a lion identification catalogue, produced through the current study, has formed a large reference catalogue and may further promote the use of this method for deriving lion population characteristics in the KGNP, without the associated costs of a focused registration study. This, along with technological developments in computer program software, which aids in individual identification process, may make remote tracking of demographic parameters feasible (Bolger *et al*., 2012). The data from such studies can then be analysed in a more robust statistical manner, provide more detailed demographic information, have smaller margins of error, be conducted over a larger population (*i.e.* the broader KTP), and ultimately have a greater probability of detecting trends (Bolger *et al*., 2012; Marnewick *et al*., 2014).

The open nature of the ecosystem, and the variability in lion density across various habitats in the KTP (Funston, 2002), calls for similar efforts to be applied in the GNP and surrounding Wildlife Management Areas in the Republic of Botswana. Furthermore, several factors, which may influence demographic characteristics, should be investigated. The effects of human-lion conflict have been addressed in the KGNP previously (Funston, 2002; van Vuuren *et al*., 2005). The effect of lion mortality because of retribution killing has a direct effect on the susceptibility of the population to extinction (van Vuuren *et al*., 2005). However, the effect of human-lion conflict on lion demographics requires further investigation, particularly concerning the effects of management interventions in association with retribution killing (Ferreira *et al*., 2013).

The social dynamics of a greater proportion of male lions in the population and their potential effect on demographic change also requires further attention. Coalition changeovers, infanticide and dispersal (including human aided dispersal), are expected to affect demographic characteristics. Lions on the borders of the KGNP, which have higher probabilities of human-lion conflict, also have greater risks of mortality. Increased mortality risks are associated with direct

---

[8] http://www.ast.uct.ac.za/~schurch/leopards/guide.html

killing of itinerant lions by farmers (van Vuuren *et al*., 2005), or because of lion translocation away from the park boundary (Ferreira *et al*., 2013). Translocation of transgressing lions into the KGNP hinterlands, particularly male lions, may have social repercussions on coalition turnover, fecundity and survival rates, particularly the survival rates of dependent individuals (Yamazaki, 1996; Ferreira *et al*., 2013; Barthold *et al*., 2016).

Considering the importance of the lion population in the KTP to the local and global conservation of the species, their conservation is paramount. Seeking cost effective solutions to detect trends in the KGNP lion population should not be done at the expense of the ability to detect change. Taking into consideration that a comprehensive database of registered individuals in the KGNP now exists, using this as a basis for further surveys could negate some of the effort required in the future. When detecting trends in the population, a highly precise method, such as the Cormack-Jolly-Seber open population mark-recapture method, is preferable. Particularly considering the changes in sex and age structure over the last two decades (Chapter 4), and the variability of population estimates, it is now more important than ever to replicate a highly precise and accurate method in the near future to establish definitive trends in the KGNP lion population. Continuing the use of imprecise or inaccurate methods to determine population size and demographic characteristics could undermine efforts by conservationists to protect the lion population.

5.5. References

Banerjee, K., Jhala, Y.V. & Pathak, B., 2010. Demographic structure and abundance of Asiatic lions *Panthera leo* persica in Girnar Wildlife Sanctuary, Gujarat, India. *Oryx*, 44(02): 248-251.

Barthold, J.A., Loveridge, A.J., Macdonald, D.W., Packer, C. & Colchero, F. 2016. Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, 53: 295–304.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T., Macdonald, D.W. & Packer, C., 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112(48), pp.14894-14899.

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2015. *Panthera leo. The IUCN Red List of Threatened Species 2015: e.T15951A50658092.*

Beja, P., Gordinho, L. & Reino, L. 2009. Predator abundance in relation to small game management in southern Portugal : conservation implications. *European Journal of Wildlife Research*, 55: 227–238.

Bertram, B.C.R. 1973. Lion population regulation. *East African Wildlife Journal*, 11: 215–225.

Bolger, D.T., Morrison, T.A., Vance, B., Lee, D. & Farid, H. 2012. A computer-assisted system for photographic mark – recapture analysis. *Methods in Ecology and Evolution*, 3: 813–822.

Caro, T.M. 1999. Conservation monitoring : estimating mammal densities in woodland habitats. *Animal Conservation*, 2: 305–315.

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 using a capture – recapture survey. *African Zoology*, 37(1): 27–34.

Caughley, G. 1976. Analyses of Vertebrate Populations. *John Wiley & Sons, New York*.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48(1): 58–71.

Chandler, R.B. & Royle, J.A., 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, *7*(2), pp.936-954.

Dunham, K.M. 1992. Response of a lion (*Panthera leo*) population to changing prey availability. *Journal of Zoology*, 227(2): pp.330–333.

Cortés, E., 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation biology*, 16(4): 1048-1062.

Dunham, K.M. & Toit, A.J. 2012. Using citizen-based survey data to determine densities of large mammals : a case study from Mana Pools National. *African Journal of Ecology*, 51: 431–440.

Durant, S.M., Craft, M.E., Hilborn, R., Bashir, S., Hando, J. & Thomas, L. 2011. Long-term trends in carnivore abundance using distance sampling in Serengeti National Park , Tanzania. *Journal of Applied Ecology*, 48: 1490–1500.

Eberhardt, L.L. & Thomas, J.M. 2008. Designing Environmental Field Studies. *Ecological Monographs*, 61(1): 53–73.

Efron, B. & Tibshirana, R.J. (1993). *An Introduction to the Bootstrap*. Chapman and Hall, London.

Elliot, N.B., Valeix, M., Macdonald, D.W. & Loveridge, A.J. 2014. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, 123(9): 1049–1056.

Eloff, F.C., 1980. Cub mortality in the Kalahari lion *Panthera leo vernayi* (Roberts, 1948). *Koedoe*, 23(1): 163-170.

Eloff, F.C. 1998. The life of the Kalahari lion (*Panthera leo vernayi*). *Transactions of the Royal Society of South Africa*, 53: 267–269.

Ferreira, S. & Funston, P.J. 2010. Age assignment to individual African lions. *South African Journal of Wildlife Research*, 40(1): 1–9.

Ferreira, S.M. & van Aarde, R.J. 2009. Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. *South African Journal of Wildlife Research*, 39(2): 181–191.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables : prey and disease effects in Kruger National Park , South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Franklin, S. & Walker, C. 2010. *Survey Methods and Practices* F.S. & W.C., eds. Statistics Canada, Ottawa, Ontario, Canada K1A 0T6, (12): pp408.

Funston, P.J. 2002. *Kalahari Transfrontier Lion Project: Executive Report*. Endangered Wildlife Trust, Upington. South Africa: pp236.

Funston, P.J. 2011. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41(1): 1–10.

Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A. & Ferreira, S.M. 2010. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281: 56–65.

Funston, P.J. & Mills, M.G.L. 2006. The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *South African Journal of Wildlife Research*, 36(1): 9–22.

Funston, P.J., Mills, M.G.L., Richardson, P.R.K. & van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology*, 259(2): 131–142.

Gerrodette, T.I.M. 1978. A Power Analysis for Detecting Trends Author. *Ecology*, 68(5): 1364–1372.

Hampton, S.E. 2004. Habitat overlap of enemies : temporal patterns and the role of spatial complexity. *Oecologia*, 138: 475–484.

Herrmann, E. 2004. *Modelling the effect of human-caused mortality on a lion sub-poulation using spreadsheets*. University of Stellenbosch.

Horton, G.E. & Letcher, B.H., 2008. Movement patterns and study area boundaries: influences on survival estimation in capture–mark–recapture studies. *Oikos*, 117(8): 1131-1142.

Jackson, R.M., Roe, J.D., Wangchuk, R., Hunter, D.O. & Jackson, R.M. 2006. Estimating snow leopard population abundance using photograpy and capture-recapture techniques. *Wildlife Society Bulletin*, 34(3): 772–781.

Keeping, D. & Pelletier, R. 2014. Animal density and track counts : Understanding the nature of observations based on animal movements. *PLoS ONE*, 9(5): 1–11.

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*, 271: 1867–1874.

Kokko, H. & Rankin, D.J. 2006. Lonely hearts or sex in the city ? Density-dependent effects in mating systems. *Philosophical transactions of the Royal Society B*, 361: 319–334.

Lettink, M. & Armstrong, D.P. 2003. An introduction to using mark-recapture analysis for monitoring threatened species. *Deparment of Conservation Technical Series*, 28A: 5–32.

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(4): 548-558.

Mackenzie, D.I. & Royle, J.A. 2005. Designing occupancy studies : general advice and allocating survey effort. *Journal of Animal Ecology*, 42: 1105–1114.

Marker, L.L., Dickman, A.J., Jeo, R.M., Mills, M.G.L. & Macdonald, D.W. 2003. Demography of the Namibian cheetah , *Acinonyx jubatus jubatus*. *Biological Conservation*, 114: 413–425.

Marnewick, K., Ferreira, S.M., Grange, S., Watermeyer, J., Maputla, N. & Davies-mostert, H.T. 2014. Evaluating the status of and African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PLoS ONE*, 9(1): e86265. doi:10.1371.

Mills, M.G.L. 1995. Notes on wild dog Lycaon pictus and lion *Panthera leo* population trends during a drought in the Kruger National Park. *Koedoe*, 38(1): 95–99.

Mills, M.G.L., Wolff, P., le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion *Panthera leo* in the Kalahari Gemsbok National Park. *Koedoe*, 21: 163–171.

Orford, H., Perrin, M. & Berry, H. 1988. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). *Journal of Zoology*, 216(4): 717–733.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., Sinclair, A.R.E. & Journals, P.S. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science (New York, N.Y.)*, 307(5708): 390–393.

Packer, C. & Pusey, A.E. 1983. Male takeovers and female reproductive parameters: A simulation of oestrous synchrony in lions (*Panthera leo*). *Animal Behaviour*, 31(2): 334–340.

Packer, C., Pusey, A.E. & Eberly, L.E., 2001. Egalitarianism in female African lions. *Science*, 293(5530): 690-693.

Pearl, M.C. 2000. *Research Techniques in Animal Ecology: Methods and Cases in Conservation Science*. L. B. & T. K. Fuller, ed. Columbia University Press, New York. pp. 442.

Penh, P. & Penh, P. 2012. Leopard density in post-conflict landscape , Cambodia : Evidence from spatially explicit capture–recapture. *Journal of Wildlife Management*, 76(1): 163–169.

Pullin, A.S. & Stewart, G.B. 2006. Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, 20(6): 1647–1656.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*, 22(1): 17–35.

Riggio, J.S. & Pimm, S.L. 2011. *The African lion (Panthera leo leo): A Continent-wide species distribution study and population analysis*. Masters project submitted in partial fulfillment of the requirements for the Master of Environmental Management degree, Nicholas School of the Environment, Duke University.

Rollett, A.D. & Manohar, P. 2004. The Monte Carlo Method. In L.-Q. C. C. Dierk Raabe, Franz Roters, Frederic Barlat, ed. *Continuum Scale Simulation of EngineeringMaterials: Fundamentals–Microstructures–Process Applications.* Wiley-VCH Verlag: 56–78.

Scheel, D. & Pusey, A.E. 1990. Why lions form groups: Food is not enough. *The American naturalist*, 136(1): 1–19.

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. 1978. Reproduction and social organisation of lions from the Kruger National Park.pdf. *Carnivore*, 1(1): 17–28.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua*, 18(1): 1–9.

Trinkel, M. 2013. Climate variability , human wildlife conflict and population dynamics of lions *Panthera leo*. *Naturwissenschaften*, 100(4): 345–353.

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C. & Slotow, R. 2010. Inbreeding and density-dependent population growth in a small , isolated lion population. *Animal Conservation*, 13: 374–382.

Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068): 90–92.

Vanderwaal, K.L., Mosser, A. & Packer, C. 2009. Optimal group size , dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, 77(4): 949–954. http://dx.doi.org/10.1016/j.anbehav.2008.12.028.

van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, 206(1): 97–112.

van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the kgalagadi transfrontier park: modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171

Whitman, K.L., Starfield, A.M., Quadling, H. & Packer, C. 2007. Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology*, 21(3): 591–601.

Wintle, B.A., McCarthy, M.A., Parris, K.M. & Burgman, M.A. 2004. Precision and bias of methods for estimating point survey detection probabilities. *Ecological Applications*, 14(3): 703–712.

Whyte, I.J., Biggs, H.C., Gaylard, A. & Braack, L.E.O. 1999. A new policy for the management of the Kruger National Park's elephant population. *Koedoe*, 42(1): 111–132.

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

Young-Overton, K.D., Funston, P.J. & Ferreira, S.M. 2014. Rainfall driven changes in behavioural responses confound measuring trends in lion population size. *Wildlife Biology*, 20: 344–355.