

**HABITAT QUALITY EFFECTS ON
THE ECOLOGY OF LEOPARD ON A
SMALL ENCLOSED RESERVE**

By

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As the candidate's supervisor, I have approved this thesis for submission

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ABSTRACT

Although the leopard (*Panthera pardus*) is one of the more successful large carnivores, challenges for leopard conservation emulate those of other more endangered carnivores, and they are a model species for investigating issues affecting carnivore persistence worldwide. This thesis represents a six-year study of leopard on the Karongwe Game Reserve, South Africa, which provided a unique opportunity to observe various aspects of behavioural ecology in the absence of prey availability constraints or human persecution. Small, enclosed reserves such as Karongwe make up 16.8% of the total land in South Africa and undertaking sound ecological research in these areas provides valuable data for evidence-based conservation and management. The leopard is notoriously shy and difficult to study and I used free darting and habituation to enhance visual observation, in order to understand the ecological processes influencing leopard reproductive success and survival. My results show that leopard in the high prey area studied, consume almost double the number of ungulates as leopard in similar habitats elsewhere. This generalist predator improved its hunting success by selecting vulnerable prey and selectively hunted in habitats of intermediate density, where preferred prey were most abundant. Ample nutrition played a key role in reproductive health and reduced the duration of reproductive parameters below that previously recorded in the literature. Any additional nutritional input could not translate into increased population growth as females were already reproducing optimally. Female territorial size and habitat selection were determined by the availability of riparian habitat and resources of their preferred prey. Territoriality however was governed by prey biomass. Neighbouring leopards were territorial, sharing little space (average 11% territorial overlap) and hunting five times more often in the core than in the rest of their territory. During periods of prey richness, females became more territorial and there was a positive “bottom up” effect through subadult recruitment. Density-dependent intraspecific and interspecific competition for limited space regulated the population around carrying capacity, and constrained population growth. These results provide fundamental baseline data about leopard in the absence of human disturbance, or prey constraints. They highlight that, although the influence of optimal nutrition is important in the reproductive health and territoriality of leopard, habitat quality and quantity are ultimately what govern leopard carrying capacity and population size. I provide baseline reproductive, carrying capacity and territorial data for agencies developing policy, and for setting priorities in conservation and management, as well as habitat protection and restoration, for not only this species but other threatened species as well.

PREFACE

The experimental work described in this thesis was carried out in the Karongwe Game Reserve from September 1999 to September 2005, under the supervision of Prof. Robert Slotow and co-supervision of Abi Tamim Vanak (University of KwaZulu-Natal).

These studies represent original work by the author and have not otherwise been submitted to any tertiary institution in any form for a degree or diploma. Where use has been made of the work of others it is duly acknowledged in the text.

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DECLARATION 1 – PLAGIARISM

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Details of contribution to publications that form part and/or include research presented in this thesis (include publications in preparation, submitted, in press, and published and give details of the contributions of each author to the experimental work and writing of each publication).

Publication 1: In preparation for submission.

Owen, C., Vanak, A.T., Niemann, S. and Slotow, R. Principle prey of leopard and their hunting habitat selection in a small, enclosed reserve

Author contributions:

CO conducted fieldwork, processed and analysed all the data, and designed and wrote the paper. SN conducted research. ATV provided valuable input on data analysis and provided valuable comments on the manuscript. RS provided valuable comments on the manuscript.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 Carnivores

Human sentiment towards carnivores is a complex combination of fascination, reverence, fear and loathing which has led to a multifaceted situation where they are both protected and persecuted. Large carnivores require huge areas of space and often end up directly competing with humans for natural key resources (Woodroffe & Ginsberg 1998, Azevedo & Murray 2007, Balme 2009). As human populations expand, conservationists throughout the world are increasingly faced with declining carnivore populations, as a result of overkill (persecution and hunting) and habitat degradation (Caughley & Sinclair 1994, Woodroffe 2001). Globally, 22 of the 30 large carnivore species are endangered and all 36 Felidae species, with the exception of the domestic cat (*Felis catus*), have been classified as either threatened or endangered (IUCN 2008). Therefore, in our modern crowded world, complex conservation and management strategies are needed if the persistence of large carnivores is to be ensured (Mech & Goyal 1995, Linnell *et al.* 2001).

1.2 Why are carnivores important?

Large carnivore species are an integral part of a functioning ecosystem, fulfilling a multitude of crucial roles, including regulating mesopredators (Crooks & Soulé 1999), provisioning for scavengers (Wilmers *et al.* 2003), moderating intra-guild competition among similar prey species (Miller *et al.* 2001) and top-down regulation of ungulate populations (Hopcraft *et al.* 2010). Their presence in an ecosystem can therefore influence the flora and fauna, and help keep it in a more natural and diverse state than areas where there are no predators (Estes 1996, Terborgh *et al.* 1999). The disappearance of large carnivores from an ecosystem can result in a cascade of effects and changes through all trophic levels, reducing biological diversity, simplifying ecosystem structure and function, and interfering with ecological processes (Pace *et al.* 1999, Terborgh *et al.* 2002).

1.3 The importance of collecting baseline data

Historical data reference conditions against which current changes can be assessed (Dietl & Flessa 2011); however, this cannot serve as an exact template for restoration in a changing world. Ecologists need to be forward thinking, and manage and develop ecosystems that will best function in the ever changing, human dominated conditions of the future. The use of relatively undisturbed reference sites, with similar historical ecology features to a disturbed site, can be used to create comparative baseline data used for gauging progress towards restoration targets and goals (Alagona *et al.* 2012). This

establishes a basis on which to compare the situation before and after an intervention, allowing inferences to be made about project efficacy or success (Dietl & Flessa 2011).

Baseline data for large carnivores are severely lacking throughout their ranges. Their naturally low densities, and their nocturnal, shy and wide ranging behaviours, make them extremely difficult to study (Balme 2009). Without easily accessible research-based evidence, conservation managers rely on limited experience-based information, developed from traditional land management practices (Pullin *et al.* 2004).

1.4 Principal ecological data

Conservation goals are determined by two main scales, at fine filter (genes, species and population) and coarse filter (community, ecosystem and landscape) levels (Schwartz 1999). Fine scale research can be expensive and complicated when trying to conserve a multitude of species, and coarse filter approaches make it difficult to assess the value of ecosystems for conservation (Hunter 2005). Using flagship and umbrella species, a multi-scale conservation approach of integrating fine and coarse-filter designs, can be effective (Hunter 2005). Researching keystone or flagship species is a tool that provides conservation protection not only to the study species but numerous co-occurring species as well, while concurrently protecting large tracts of land (Roberge & Angelstam 2004). Having complete knowledge about the ecological requirements of keystone species as well as ecosystem processes has significant implications for ecosystem management and biodiversity enhancement (Simberloff 1998, Roberge & Angelstam 2004).

1.4.1 Nutrient requirements

The study of resource selection is a complex ecological area, because of the range of selection decisions reflecting the variation in resources on which each species depends (Sih 1987, Lima & Dill 1990). What carnivores select to eat determines their fitness (Pyke 1984), population density (Boyce 1989), reproductive success (Owen *et al.* 2010) and territoriality pattern. However, disproportionate selection pressures by predators can have an alarming impact on both prey biomass, and the system as a whole (Johnson 1980, Thaker *et al.* 2011).

Depending on what prey predators select, and how they respond to changes in prey abundance, the effects on prey dynamics may be stabilising or destabilising (Fryxell & Lundberg 1994). Predators with a strong preference for specific prey (specialists) can destabilise a predator-prey system (Eubanks & Denno 2001), while predators consuming a wide variety of prey (generalists) can be generally stabilising (Lidicker 2000). If generalists continue to consume rare species this could lead to local species extinction, which has greater risk in small, enclosed reserves where resident prey

populations are often at low densities, and where predators can regulate and even limit prey (Power 2002). It is important to understand the variables that determine how carnivores select and capture prey, which can have a dramatic positive or negative influence on community stability and prey diversity (Snyder & Wise 2001).

1.4.2 *Reproductive systems*

Reproductive mechanisms are little understood in most felids due to their secretive behaviour, and difficulty in obtaining visual observations (Holt *et al.* 2003). Reproductive behaviours and mechanisms underlying reproductive success are particularly important because fitness is fundamentally a function of fecundity (Purves & Turnbull). The study of reproduction is therefore a crucial understanding to conserving species, populations, and indirectly to the vitality of entire ecosystems (Holt *et al.* 2003).

1.4.3 *Population ecology*

Population ecology studies the dynamics of species populations and how these populations interact with the environment (Kunkel *et al.* 2005). The rate at which animal populations increase is a result of several factors which vary widely among species. Abundance of environmental resources such as food, water and space determines how population abundance changes over time, in an inherently density-dependent bottom-up process (Sibly & Hone 2002). As populations increase, density-dependent factors intensify, affecting individuals more strongly by decreasing reproduction and increasing mortality in overcrowded populations (Turchin 1999).

Other density-independent, top-down processes e.g. abiotic events, density-independent social interaction (e.g. infanticide), natural enemies such as predators, parasites or human-caused mortality (Bowers & Harris 1994, Gomez & Zamora 1994, Kissui & Packer 2004, Moore *et al.* 2010), unrelated to population density, can reduce population size before density-dependent resource factors become important (Sinclair & Pech 1996). All else being equal, population size generally remains stable, close to carrying capacity, through a combination of both density-dependent and independent factors (Campbell 1993).

1.4.4 *Habitat requirements*

Habitat loss is a major driver of species loss worldwide (Foley *et al.* 2005). Given this, it is essential to establish how much habitat is needed to meet the definitive conservation objectives. The spatial extent of a conservation reserve determines its capacity for habitat support (Smallwood 2001). Large reserves are favoured because they meet conservation goals for species with large home ranges, are more resistant to disturbance and have increased habitat diversity and landscape heterogeneity,

thereby reducing the risk of species extinction (Schwartz 1999). Although large reserves provide many advantages over small reserves, reserve size does not accurately predict population size or diversity, because large, disturbance-prone sites may have lower diversity than smaller, higher quality sites (Schwartz 1999). High quality habitat (i.e. suitability) is one in which individuals can experience high survival and reproduction and, thus, the population has the potential for a high growth rate (Mitchell & Hebblewhite 2012). In a human dominated landscape there are often no alternatives to small reserves due to a high degree of habitat loss and fragmentation (Tschardtke *et al.* 2002). Understanding availability of prey resources and habitat selection within these small areas is vital to our ability to correlate habitat selection with population processes (Miquelle *et al.* 1999).

Habitat selection has become the key factor in the life cycle of animals because it can affect most components of fitness and relates resources to survival and reproduction (Morrison *et al.* 2006). Understanding all four orders of habitat selection for a species; geographical range, home range, usage of habitat components within the home range (i.e., a feeding site), and the procurement of elements available within habitat components (i.e., food from the feeding site) provides a broad picture for species and ecosystem management and conservation (Johnson 1980).

Carnivore spatial organisation is largely associated with key resource availability (Litvaitis *et al.* 1986); however, where these resources are not limiting, the population is controlled by intraspecific territorial competition through territorial behaviour, mutual avoidance and aggression (Pierce *et al.* 2000, Adams 2001). How organisms establish and use home range, although not a parameter of population ecology, is important for managing habitat for populations. Understanding the factors that can influence home range size and habitat selection facilitates an understanding of the optimisation process that involves habitat selection of food, density of conspecifics, body size and competitors, which have important management implications about habitat quality (Morrison *et al.* 2006).

1.4.5 Resource limitations

It is important to understand why carnivores live where they do and what resources contribute to and which limit their fitness. A limiting resource, or factor, is one in short supply among those that affect an organism's growth, survival and reproduction (Kaiser *et al.* 1994). A limiting factor, (i.e. nutrition, water and space), inevitably has the potential to limit an organism. However, only one will be the active constraint at a given point in space and time, and vital to ecology (Kaiser *et al.* 1994, Mitchell & Hebblewhite 2012). Understanding the functional links between limiting resources and species fitness is fundamental in conservation ecology.

Although small enclosed reserves offer great opportunities for conservation ecology, there are very real concerns about population genetics (Trinkel *et al.* 2011), dynamics, and risk extinction (Caughley & Sinclair 1994). A metapopulation approach will ensure that these can be avoided, and enable effective management practices to be implemented (Akçakaya *et al.* 2007, Kettles & Slotow 2009).

1.5 Challenges of managing small reserves

Over the past few decades wildlife tourism has increased significantly in South Africa, with the establishment of thousands (± 9000) of game-fenced small reserves ($<100 \text{ km}^2$) whose primary objectives are to use natural resources to generate an income from ecotourism (Barnes 2001). These reserves accounts for 20.5 million hectares (16.8 %) of the total land in South Africa (Cousins *et al.* 2008). The role of these private reserves could therefore be invaluable to conservation efforts in the country.

Reserves that are too small to simulate nature and allow natural processes to function need to be managed to maintain a balanced bio-diverse ecosystem, through the regulation of population growth (Kettles & Slotow 2009), genetic integrity (Trinkel *et al.* 2008) and structure, and balancing predator-prey relationships (Van Dyk & Slotow 2003), in a financially sustainable way (Grubbich 2001, Riley *et al.* 2002). These challenges are compounded by strict fencing standards, substantially higher reproduction rates (Druce *et al.* 2004) and the immense pressure of tourists' expectations of seeing the charismatic species (Swarbrooke 1999).

An ecosystem has a limit to the number of individuals that it can support, and species need to be managed around their carrying capacity in order to address long-term sustainability and avoid impacting negatively on the ecosystem and its biodiversity (Sinclair 1989, Kettles & Slotow 2009). Especially important in small reserves are the genetic risk factors of inbreeding depression and loss of genetic variability (Trinkel *et al.* 2010), as a result of closely related individuals mating and producing offspring with reduced fitness, thereby increasing the population's risk of extinction (Lande *et al.* 1999, Trinkel *et al.* 2011). Unless numbers and inbreeding of top predators and mega fauna such as elephant are controlled, they have the potential to change the habitat and prey community composition (Peel & Montagu 1999).

Game fences prevent natural ecological processes, which adversely affects population dynamics within a reserve (Lindsey *et al.* 2012). Practical tools which managers have, to manipulate population size and inbreeding, are translocation, culling/ hunting and contraception (Kettles & Slotow 2009). Translocation, although difficult due to recent legal changes and expense, is an effective management strategy used to regulate numbers, enhance genetics in wildlife populations (Trinkel *et al.* 2008), and

establish new populations (Griffith *et al.* 1989 428, Trinkel *et al.* 2008). The primary predator population regulation measure used in small reserves is the capture and removal of subadults (usually two years old) from the population, with older individuals occasionally being hunted (Vartan 2001, Kettles & Slotow 2009, Slotow & Hunter 2010). Having a metapopulation management plan between fenced reserves can ensure closed populations stimulate natural conditions in processes such as group dispersal (Gusset *et al.* 2006). Negative aspects of translocation include increased stress and mortality of relocated animals, negative impacts on resident animals at release sites, increased conflicts with human interests, and the spread of diseases (Chipman *et al.* 2008). Leopards are not constrained by fences, and edge effect from anthropogenic mortalities is high outside of reserves reducing the leopard conservation potential of conservation areas (Balme & Hunter 2004, Balme *et al.* 2010). Conservation corridors are needed between isolated populations to ensure safe emigration and immigration (Daly *et al.* 2005).

Culling or hunting, for population control and for balancing male and female ratios, is common on wildlife reserves but raises serious ethical issues when directed at endangered and charismatic species, setting dangerous precedents when our intention should be to protect living creatures and their habitat (Slotow *et al.* 2008, Kettles & Slotow 2009). Culling at times may be the only option and managers are expected to make these difficult decisions.

Contraception might provide an alternative to culling and a long term solution for limiting numbers on Game Reserves (Orford *et al.* 1988, Delsink & Kirkpatrick 2012). What makes this solution attractive is that it is both practical and humane and has been very successful in controlling both lion and elephant populations (Orford *et al.* 1988, Delsink & Kirkpatrick 2012). Furthermore it seems to cause less disruption of biological processes, is reversible, and prevents genetic loss – especially useful in endangered species (Orford *et al.* 1988).

Baseline ecological information from small reserves is essential for managers to be able to assess population fluctuation (Lande *et al.* 1999), prevent inbreeding (Packer *et al.* 1991, Trinkel *et al.* 2010) and manage genetic flow (Grubbich 2001, Moehrenschrager & Somers 2004, Kettles & Slotow 2009, Trinkel *et al.* 2010). In the absence of historical baseline data, relatively undisturbed sites with similar ecological features to disturbed sites can be used as reference sites, providing a control in which we can measure human disturbance (Moehrenschrager & Somers 2004), justify recovery and restoration programs for endangered species, and recreate conditions that allow for ecological processes to follow a similar evolutionary path (Van Andel & Aronson 2006).

1.6 Leopard

The leopard (*Panthera pardus*) is the most widely distributed and adaptable of the big cats, inhabiting much of sub-Saharan Africa and Asia, Middle East and Northern Africa (Nowell & Jackson 1996), and is the only large feline occupying habitats from rainforest to desert and all habitats in between (Skinner & Smithers 1990, Nowell & Jackson 1996) (Fig 1.1).



Figure 1.1. A general geographic distribution of leopard (www.bbc.co.uk/nature/life/Leopard)

They achieve this through highly adaptable generalist habitat (Bailey 1993) and feeding practices (Hayward *et al.* 2006), varying their behaviour according to the habitat occupied (Seidensticker & Lumpkin 1991, Bailey 1993).

Despite their incredible ability to adapt, of the nine subspecies of leopard three are listed as “Critical” and almost extinct, and two are listed as “Endangered” (IUCN 2008). In 2008, leopard in South Africa were classified as “near threatened” by the IUCN (IUCN 2008). Although common in some areas, their populations are fragmented and numbers continue to decline outside large government reserves, because of persecution (Balme 2009), habitat loss, fragmentation (Wilcove *et al.* 1986) and degradation (Rojas *et al.* 2011), and may soon be listed as “Vulnerable” if numbers continue to decline (Henchel 2008).

Leopards are a top predator and the most adaptable, and hence the most widespread, wild representative of the family felidae (Nowell & Jackson 1996). They, are also the most elusive and

least studied of all the large African felids, and visual behavioural information essential to their effective management and conservation is sorely lacking throughout their range (Daly *et al.* 2005). A large number of studies using non-invasive study methods such as camera traps (Balme & Hunter 2004, Kawanishi & Sunquist 2004, Soisalo & Cavalcanti 2006), spoor analysis (Schaller & Crawshaw 1980, Bothma & le Riche 1984, Stander *et al.* 1997, Kerley *et al.* 2003) and faecal analysis (Mizutani & Jewell 1998, Hayward *et al.* 2006) have been conducted, and although they provide useful information, the diversity of emerging ecological information is nominal.

Because of the difficulties of monitoring species of cryptic nature, inhabiting extensive areas in difficult terrain, relatively few studies on leopard have been carried out where continuous visual observations were possible (Eibl-Eibesfeldt 1970, Balme & Hunter 2004). Bertram (1982) wrote that “the quality and quantity of information obtainable in an ecological study is directly related to sample size and the number and regularity of visual observations.” Although these criteria present relatively few challenges with predators such as lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*), which are often unconcerned by vehicles, for example, the locating of the elusive leopard is a daunting task. The leopard relies on concealment to survive, and because of its inaccessible habitat, attempts at in-depth studies have been avoided, and the management of leopards, especially in small enclosed reserves where they have the potential to regulate prey, is often not tackled or tackled without sound baseline data.

Like their relative the lion, leopard are capable of realising that vehicles are non-threatening in areas where they are only viewed (Hes 1991). Through reduced capture-stress and correct habituation techniques, visual observations can be improved (Herrero *et al.* 2005). The Karongwe Reserve, where my study was conducted, supports a healthy population of leopard and many of their key prey species. It offers an excellent opportunity to examine leopard ecology and biology in the absence of human persecution.

Ongoing habitat fragmentation has led to concerns regarding minimum viable populations, and the number of individuals that will ensure the survival of isolated populations is the key factor challenging leopard conservation in South Africa (Daly *et al.* 2005). Leopards are so successful because, unconstrained by fences, they move freely, ensuring a metapopulation flow between populations (Balme & Hunter 2004, Swanepoel 2008). Unfortunately, while protected in wildlife reserves, they continue to be persecuted on the boundaries and outside these sanctuaries by legal hunters, poachers, farmers with destruction permits and often by indiscriminate inhumane illegal methods (Balme & Hunter 2004).

A 2005 population habitat viability assessment of the leopard population in South Africa concluded that, although the overall leopard population was likely to persist, it was the small, isolated populations, with low genetic flexibility and reduced ability to cope with any additional human-related mortalities, that were likely to become locally extinct (Daly *et al.* 2005, Whittaker & Fernandez-Palacios 2007). Eliminating illegal hunting would have a significantly positive impact on survival of local populations, all of which would then have zero risk of extinction in the next 100 years (Daly *et al.* 2005).

The key to ensuring the future of the leopard in this fragmented environment lies in an interdisciplinary approach to conservation, requiring the integration of data and information with the experience and perspectives of different stakeholders (Marzano *et al.* 2006). Understanding leopard resource requirements, habitat size, quality, and connectivity, along with issues of conflict, land use, and the needs of local people, will be vital (Swanepoel 2008).

Leopard conservation challenges mirror those of other more endangered carnivores and are an excellent ecological model for understanding the issues that affect the persistence of not only large carnivores but felids in general (Cousins *et al.* 2008). The conservation of carnivores can only be effective if protection programs and specific initiatives are based on baseline research information of how they utilise, share and compete for available habitat and other resources (Jackson 1996). Even though ecological parameters may vary among species in response to different climates, habitats, prey densities, and other environmental factors, the detailed results presented in this thesis could assist in developing effective world-wide conservation strategies for the long-term survival of carnivores (Kerley *et al.* 2003).

1.7 Research objectives

The Karongwe Game Reserve supports a healthy population of leopard, and abundant and diverse prey species. The reserve's extensive road network offered an excellent opportunity to visually examine leopard ecology in high quality habitat, in the absence of human disturbance and forage limitations. Overall study objectives were to successfully habituate leopards, thereby making it possible to visually gather detailed data, and examine aspects of their ecology including feeding, reproduction, sociality and territoriality.

1.8 Research questions

1) How best to go about studying leopard; how to improve visual observations for research purposes; and what is the relative effectiveness and efficiency of different techniques?

- 2) How does prey richness influence leopard foraging ecology, and what are the management implications in a small, enclosed reserve?
- 3) How does prey richness influence leopard reproduction parameters?
- 4) How does prey richness influence leopard population growth? Is the leopard population able to limit itself in the absence of forage limitation and human persecution? If so, what limits the population?
- 5) How do forage availability and population density influence, territory size and overlap; and does territoriality regulate population density?

1.9 Overview of the thesis

This thesis was divided into nine chapters, an introduction, study site description, description of general methods, five data chapters and a general discussion. Chapters 4 to 8 were independent papers structured for journal publication. Chapter 6 has already been published. A complete description of the study area can be found in Chapter 2. References are available at the end of each section and paper chapter. The individual chapters were collated into a comprehensive document of baseline data that together answer the questions being asked about leopard conservation and management in a fragmented environment.

The objectives of the specific chapters were as follows:

In Chapter 4, I examined the costs of free darting, collaring / implanting and habituating leopard, I assessed the pros and cons of collars and implants and investigated habituation, for the enhancement of data collection and management purposes.

In Chapter 5, I investigated how resource richness influenced leopard foraging ecology in a small enclosed reserve and the ecological ramifications that affect leopard conservation and management. Using belly scores and kill data, I investigated foraging behaviour as follows: (1) I identified the principal prey species of leopard and calculated prey biomass removal, (2) quantified kill frequency in each habitat, (3) identified leopard prey selection with respect to species, size, age and sex, (4) determined habitat selection of principal prey species and (5) ascertained whether leopard hunting-habitat selection matched the habitat selection of their principal prey.

In Chapter 6, I investigated the reproductive biology of free-roaming leopards. Reproductive and copulatory behaviour was studied to understand the mating system of leopards, and how reproductive parameters influenced population growth. I examined the different aspects including, copulatory behaviour, reproductive rate, seasonality, birthing intervals and natal dispersion.

In Chapter 7, I investigated leopard population biology as follows: (1) I calculated population size, (2) defined the density-dependent and independent processes that stabilised the population, and identified the causes of fluctuation and instability, (3) identified the bottom-up resources responsible for population limitation and (4) ascertained which age groups were most influenced by these stabilising or destabilising processes.

In Chapter 8, I investigated prey biomass, population density and seasonal influence on intraspecific territorial size and overlap, in order to understand how territoriality regulated population density. I (1) calculated home range size and overlap of all adult breeding females, (2) determined how prey biomass, population density and season influenced territorial size and overlap and (3) investigated prey use within territories.

In Chapter 9, A final chapter to the thesis linked the results from the chapters together, and indicated gaps in our knowledge, and directions for further research.

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CHAPTER 2

STUDY AREA

2.1 Location and topography

Karongwe Game Reserve is 8500 ha in area (Longitude 30°64'; Latitude 24°30') and lies at the foot of the Drakensberg Mountains in Limpopo Province, South Africa. Created in 1999, Karongwe consists of six farms with common internal fences removed. The landscape combines riverine, undulating terrain and rocky outcrops. Elevations range from 480 m above sea level in the northeast, on the Makhutswi River, to 520 m at Beacon Rock in the central southern area. Karongwe is drained by the perennial Makhutswi River in the north, the annual Mafunyane and Kuyvenami Rivers in the central section and the Karongwe and Matumi Rivers in the south. All these rivers flow west to east, with the Mafunyane and the Kuyvenami eventually flowing into the perennial Makhutswi, which roughly forms the northern boundary of the reserve (Fig 2.1).

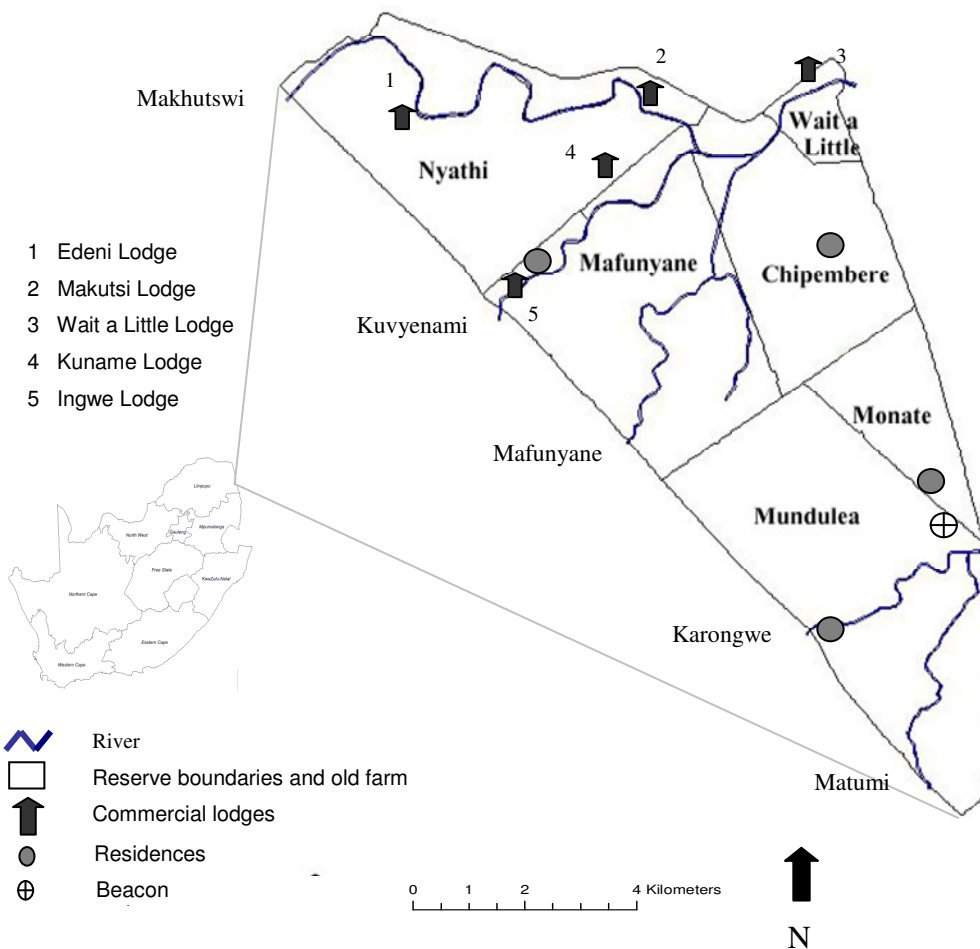


Figure 2.1 Karongwe Game Reserve map, of lodges, residential areas, rivers and reserve boundaries.

2.2 Geology and soils

The soils are predominantly derived from biotite gneiss in the north and coarse grained, quartz rich biotite-Muscovite in the south (Peel & Peel 2000). The substratum is characterised by well drained inferior nutrient sandy soils in the uplands and high nutrient clayey soils with high sodium content in the bottomlands (Low & Rebelo 1998).

2.3 Vegetation

Karongwe is found within the savannah biome of southern Africa, with mixed Lowveld bushveld (Type 19) and Mopane bushveld (Type 10) as the dominant vegetation types (Low & Rebelo 1998). Mixed Lowveld bushveld is characterised by a large number of tree species including *Combretum apiculatum* and *Combretum zeyheri*, *Sclerocarya birrea*, *Acacia nigrescens*, and within the scrub layer by species such as *Cissus cornifolia*, *Dichrostachys cinerea*, *Acacia exuvialis* and *Dalbergia melanoxylon*. The Mopane Bushveld is characterised by a fairly dense growth of *Colophospermum mopane* trees and mixtures of *C. mopane* and *C. apiculatum* (Low & Rebelo 1998). The vegetation is classified as sweet woodland savannah (Acocks veld type II) and supports a large variety of ungulate species (Acocks 1988). It is characterised by a grassy ground layer and a distinct upper layer of woody plants (Low & Rebelo 1998). The tree layer usually consists of a discontinuous crown cover of 2-10 m, which overlies a grassy layer 0-2 m tall. There may be an intermediate layer of small trees or scrubs present, and the grass layer may be temporarily absent or replaced by dicotyledonous herbs during drought or other disturbance (Kunstler *et al.* 2009). Habitat on Karongwe consists of the following physiognomic classes: Closed riverine (1.6%) consisting of gallery forests along rivers; Open riverine (15.8%) consisting of open canopy forest with thick under story along rivers and drainage lines; Closed woodland (54.4% of area) consisting mainly of *Combretum* and *Mopane* woodlands with closed tree canopies; Open woodland (24.1%) consisting mainly of *Acacia* with separated tree canopies; and Open scrub (4.1%) consisting of old agricultural lands now reverting to open scrub habitat.

2.4 Climate

The area is characterised by hot, rainy summers and warm dry winters with an annual average precipitation of 487 mm. The first rains typically fall in September or October and the majority of the reserve's precipitation occurs during November and March. Annual precipitation recorded during the study varied from a low of 170 mm in 1997 / 1998 to a high of 952 mm during 1999 / 2000, an

exceptionally wet year (Appendix A-1). The daytime temperatures range from 3 °C in the winter months to as high as 40 °C in the summer months (Climate information office, 2000, pers. Comm.¹)

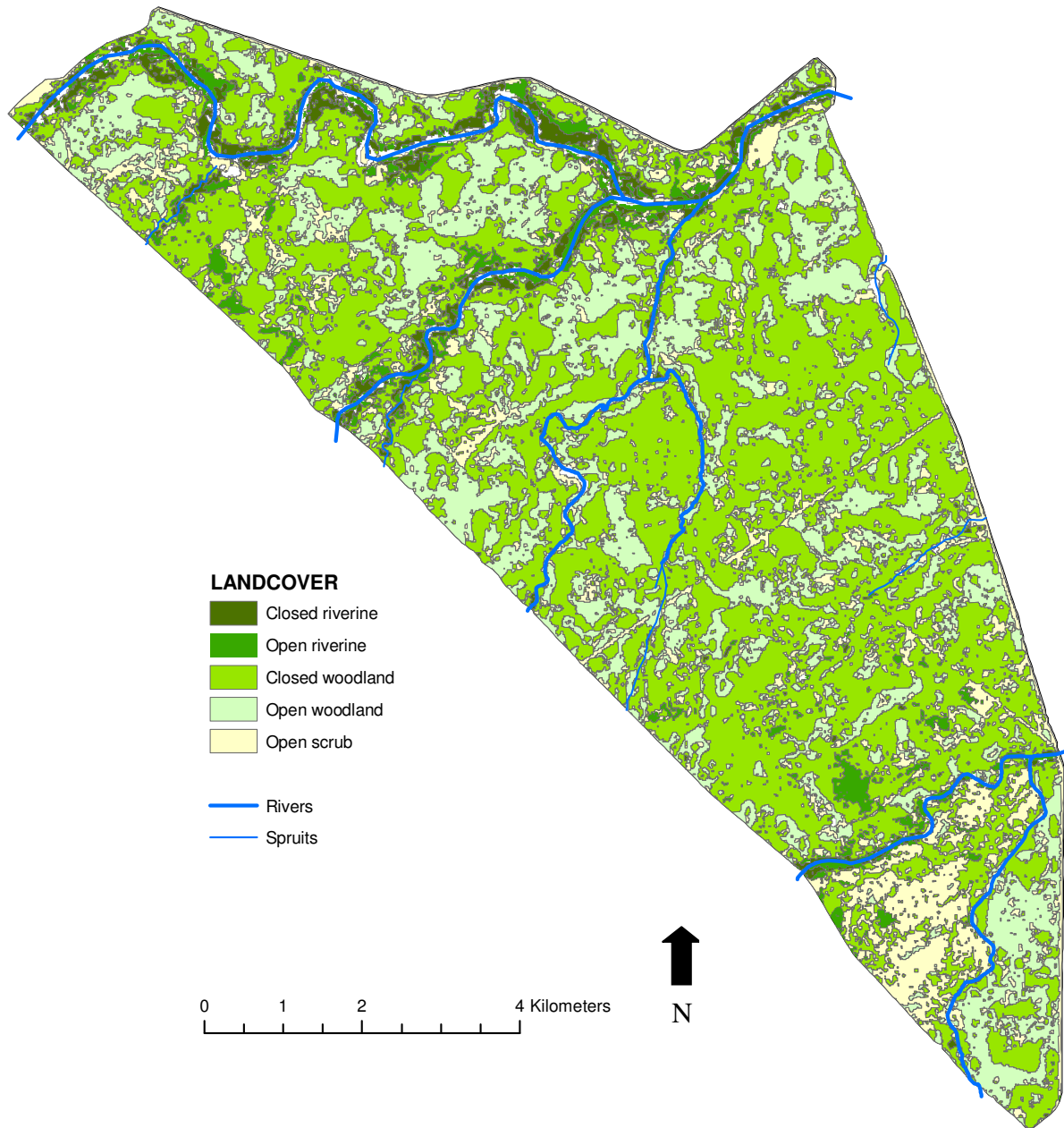


Figure 2.2 Habitat types of Karongwe Game Reserve

¹ Climate information office, 082 233 8484

2.5 Water

Water availability is not limited, as animals have access to natural rivers as well as artificial waterholes across the whole reserve throughout the year (Fig 2.3).

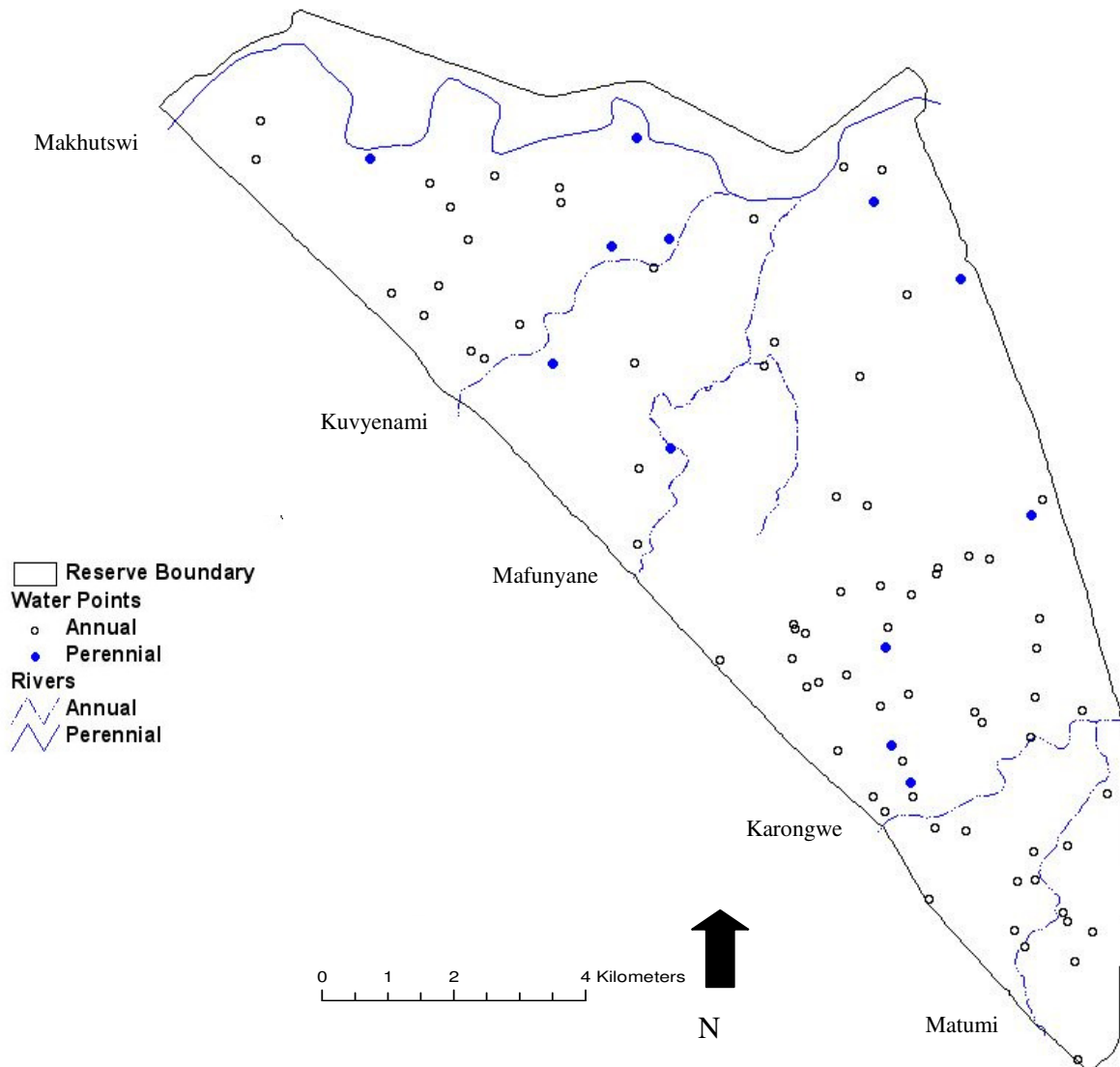


Figure 2.3. Map of Karongwe Game Reserve indicating the positions of annual and perennial rivers and water points.

2.6 Fauna found on Karongwe during the study

Prior to 1999, ungulate species already occurred in large numbers and only 20 zebra were reintroduced (Table 2.1). Following the reintroduction of elephant (*Loxodonta africana*), lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), wild dog (*Lycaon pictus*), serval (*Felis serval*), white rhino (*Ceratotherium simum*) and hippopotamus (*Hippopotamus amphibius*), almost all the medium and large mammal species that were historically indigenous to the area had been reintroduced (Table 2.2). Leopards were naturally occurring, and none were reintroduced.

The following guilds were present on the reserve:

1. **Bulk grazers:** white rhinoceros, hippopotamus, zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*) (only present in an isolated 150 ha disease free buffalo breeding project).
2. **Selective feeders:** blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*), warthog (*Phacochoerus aethiopicus*), gemsbok (*Oryx gazella*), eland (*Taurotragus oryx*).
3. **Mixed feeders:** impala (*Aepyceros melampus*), elephant, grey duiker (*Sylvicapra grimmia*), steenbuck (*Raphicerus campestris*).
4. **Browsers:** giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), nyala (*Tragelaphus angasii*), klipspringer (*Oreotragus oreotragus*).
5. **Carnivores:** lion, cheetah, leopard (*Panthera pardus*), black backed jackal (*Canis mesomelas*), side striped jackal (*Canis adustus*), serval, wild dog, African wild cat (*Felis lybica*), caracal (*Felis caracal*), spotted hyena, brown hyaena (*Hyaena brunnea*).
6. **Other smaller species** including chacma baboon (*Papio ursinus*), vervet monkey (*Cercopithecus pygerythrus*), pangolin (*Manis temminckii*), scrub hare (*Lepus saxatilis*), greater canerat (*Thryonomys swinderianus*), porcupine (*Hystrix africae australis*), Cape clawless otter (*Aonyx capensis*), honey badger (*Mellivora capensis*), African civet (*Civettictis civetta*), small-spotted genet (*Genetta genetta*), large-spotted genet (*Genetta tigrina*), yellow mongoose (*Cynictis penicillata*), slender mongoose (*Galerella sanguinea*), white-tailed mongoose (*Ichneumia albicauda*), water mongoose (*Atilax paludinosus*), banded mongoose (*Mungos mungo*), dwarf mongoose (*Helogale parvula*), Aardvark (*Orycteropus afer*), rock dassie (*Procavia capensis*), lesser bushbaby (*Galago senegalensis*), and thick-tailed bushbaby (*Galago crassicaudatus*).

2.7 Human activities

Prior to the removal of internal fences in 1999, the land was principally utilised for game farming and hunting and was already well stocked with ungulates. Karongwe was initially established to create a reserve large enough to sustain large predators and mega herbivores to enable the reserve to receive “Big Five” status. Of the six major landowners and nine minor landowners (1ha stands), only two of the major landowners possessed commercial lodges, Edeni Lodge on Nyathi which was predominantly hunting, and Wait a Little Lodge, a horseback safaris lodge on Wait a Little. Three minor landowners possessed commercial lodges from which landowners received income through traversing rights across the reserve (Figure 2.1).

Today, the reserve, with Big Five status, is primarily orientated towards tourism which is its main source of income. The Karongwe Game Reserve consists of five main lodges. Ingwe Lodge is capable of sleeping 60 people and has game viewing vehicle rights for six ten-seater vehicles, Kuname Lodge can sleep 10 people (one vehicle right), Edeni Lodge can sleep 120 (six vehicle rights) and Makutsi Lodge can sleep 120 (three vehicle rights). Wait a Little is a horseback safari lodge sleeping eight, and traverses the reserve on horseback (fig. 2.1). Driving rights are charged per vehicle, with unrestricted travel in the reserve. An individual lodge, such as Edeni Lodge, may put as many vehicles as they require on their own farm, Nyathi, however their allocation of vehicle rights means they may only use up to six vehicles to traverse the rest of the reserve. Makutsi Lodge specialises in long staying guests and uses minibuses to take tourists to local tourist attractions. They only put three vehicles on the reserve at any one time. Apart from the lodges Karongwe has 10 residential establishments, in four residential areas (Fig. 2.1). Each residential owner receives the right to one non-commercial game-viewing vehicle, after having undertaken training to become an honorary field guide. In 1999, only two commercial game viewing vehicles traversed the reserve. Today (2012) up to 16 such vehicles view the wildlife daily, and an additional 10 non-commercial vehicles may be on the reserve, particularly on weekends and holidays.

The Karongwe Game Reserve has no 1 km² block without an accessible road (Fig 2.4). The reserve utilizes a radio communication system that controls vehicle activity around the vicinity of large predators, elephants and rhinoceroses. The vicinity of the animal is defined as an estimated 500 m radius area around the location of the individual. A maximum of three vehicles are allowed at the sighting, to obtain visual contact, and an additional two vehicles in the vicinity may wait on standby to enter the sighting itself at any particular time. As soon as a vehicle leaves the area of visual observation another one can enter. The first vehicle at a sighting usually assesses the status and direction of movement of the animal before contacting other game drives in the vicinity, and before

specifying the direction of approach for the rest of the vehicles towards the sighting, so as not to block the animal's path, or cut off its escape route, or to encircle animals by approaching from all directions at once. Off road driving is permitted for a confirmed visual sighting and while following one of the Big Five. The main game drive times are during the morning periods between 6:00 and 9:00 and during the afternoon periods between 15:30 and 19:30.

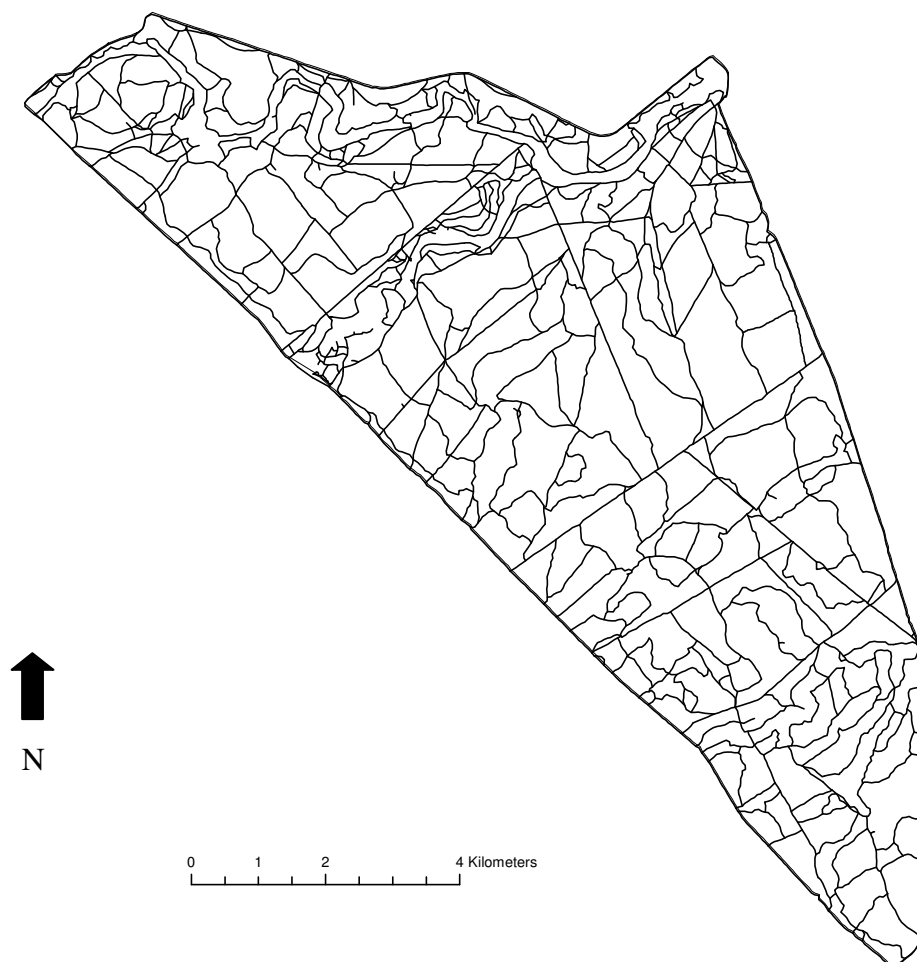


Figure 2.4. Map of Karongwe Private Game Reserve displaying the extensive road network

2.8 Reserve aims

The reserve's main aims were to manage and conserve wildlife and their habitat, and enhance the wildlife viewing experiences in order to generate enough economic benefits to sustainably run the reserve (Swarbrooke 1999). This was achieved by considering all aspects of biodiversity and by making balanced decisions derived from practical experience as well as continuous research and monitoring. Economic benefit was derived from tourism and game sales, and, in order to increase wildlife viewing opportunities, the reserve was restored as far as possible to its natural state. In

addition, programmes aimed at rehabilitating the habitat were implemented, for instance the control of bush encroachment that had resulted from overgrazing (Smit 2004), and the removal of alien plant species (Nel *et al.* 2004), internal fences and disused buildings. These programmes were a crucial part of the process of achieving the reserve goal of providing the desired wildlife viewing experiences to visitors.

Management actions in the Karongwe Game Reserve were directed towards maintaining wildlife populations and habitats. These included annual aerial game counts (Jachmann 2002), patch mosaic burning (Parr & Andersen 2006), elephant impact studies (Guldmond & Van Aarde 2008), vegetation surveys (Peel & Peel 2000), ground counts (Hirst 1969) and culling of excess animals when necessary.

Annual aerial ungulate counts in September were undertaken using a Bell Jet Ranger helicopter for an eight-hour period starting at 8 am. Using a GPS-aided computer to guide the helicopter pilot, 300 m wide strips were flown throughout the reserve. A computer-mapping program was used to plot the location of the animals, which reduced the chances of replicate counting. Weather conditions, dense vegetation, spotting, counting problems and drought can all impact on the accuracy of the game count (Jachmann 2002) (Table 2.1). Quarterly ground counts were undertaken in which five circuits of a set route were carried out over five days to assess the age and sex ratios of the ungulate population (Hirst 1969).

Fires are a determining factor in the dynamics and structure of almost all terrestrial ecosystems (Bond *et al.* 2004). Controlled burning was dependent on seasonal rainfall, and the decision to burn was made on an annual basis. Patch mosaic burning was undertaken to remove moribund and/or unacceptable grass material, eradicate or prevent encroachment of undesirable plants and to create fire-breaks, to limit the damage of unplanned fires (Parr & Andersen 2006) (Appendix A-2).

Culling was used to redress any imbalance in the ungulates' sex ratio, with carcasses being supplied to predators in holding pens or sold for meat. Annual vegetation surveys (Peel & Peel 2000) were carried out to assess the grazing quality and the ecological carrying capacity of the reserve. Additional vegetation surveys were designed to assess the impact elephants were having on the reserve. Daily monitoring on selected species: elephant, white rhinoceros, lion, cheetah, leopard, spotted hyaena and wild dog were carried out.

Table 2.1: Ungulate game count figures undertaken annually on Karongwe from 1999 – 2005, and their mean biomass weights (Bothma 1996).

Species	1999	2000	2001	2002	2003	2004	2005	Mean biomass (kg)
Bushbuck	178	58	96	127	56	14	21	2318
Common Duiker	32	11	16	18	22	29	17	228
Eland	4	4	0	0	0	0	0	2200
Gemsbok	10	3	0	0	0	0	0	1430
Giraffe	65	85	79	80	90	66	73	57643
Red Hartebeest	42	21	17	7	4	2	0	1528
Impala	1816	1953	2140	1782	1252	930	1124	64254
Kudu	161	183	166	144	140	154	118	20772
Nyala	27	19	20	27	30	11	15	1547
Steenbok	8	1	3	2	3	1	2	29
Warthog	146	244	261	266	119	113	138	5332
Waterbuck	278	254	231	205	185	149	185	43463
Blue Wildebeest	289	282	239	321	298	219	203	48073
Zebra	172	195	171	206	190	159	152	38417

Table 2.2: Large predator and large herbivore numbers on Karongwe at the beginning of each study year from 1999-2005.

	1999- 2000	2000- 2001	2001- 2002	2002- 2003	2003- 2004	2004- 2005	2005- 2006
Large Predators							
Cheetahs	5	13	9	15	12	9	8
Hyaena	-	-	-	5	7	11	11
Leopards	13	16	24	25	19	12	4
Lions	-	6	8	10	8	10	8
Wild dogs	-	-	4	9	13	4	0
Large Herbivores							
Elephant	-	10	12	13	15	15	16
Hippopotamus	3	11	12	15	16	16	17
Rhinoceros	-	5	5	4	4	5	6

- Indicates that the species was not present on the reserve and the year of introduction is indicated by the appearance of a number.

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CHAPTER 3

STUDY METHODS

3.1 Introduction

This thesis is prepared in such a way that each chapter may be read as an independent paper. Methods and techniques are described in the relevant chapters (papers). This chapter thus serves as a comprehensive methodology, not possible to describe in all chapters due to word restriction for publication.

During the first year, all fieldwork was successfully undertaken without the need for a field assistant. During the following years field assistance was provided by Keri Research, an ecological research organisation operating on the Karongwe reserve where the study was carried out. Sophie Niemann joined the project in the second year for one year, when it became evident that an additional assistant was required. Sophie was replaced by Ivan Killian who was in turn replaced by Lorna Struthers. On Lorna's departure in 2003, Monika Lehmann, and Brigitte De Coriolis joined the project for the last two years, when two field assistants were necessary. From October 2001 four field researchers were also provided by Global Vision International, to assist with reproductive data collection. This ensured that from 2003 at least three vehicles were on the reserve daily, collecting data. Philip Owen, the reserve manager, dedicated a large portion of his time to habituating leopards, and was instrumental in ensuring immobilisations were undertaken in a manner that would improve habituation and increase wildlife viewing.

3.2 Road map construction

A map of Karongwe detailing road positions, koppies and waterholes was created using the Cartalinx GIS programme (Clark Labs, Clark University, Worcester, USA). Using a Garmin legend GPS datum WGS84, linked to a laptop computer, each road on the reserve was driven and recorded via the Global Positioning System into a laptop computer. Junctions were marked so that, once the data collection was complete, the map could be tidied by snapping the nodes of each road crossing a junction together. Koppies, water points and dams were marked as waypoints and labelled while driving. The Cartalinx road map and the aerial photograph were brought into the Global Information System ArcGIS (ESRI), where rivers and drainage lines were digitized from an underlay of the photograph as accurately as possible.

3.3 Habituation additional methods

Karongwe is a tourism destination and it was necessary to ensure that research conduct did not conflict with the main income and objectives of the reserve. There are various ways of studying leopards, and this chapter highlights methods that could improve the chance of both habituating leopards and enhancing visitor's experience, through sensitive capture and handling techniques, discreet tracking devices and a post immobilisation habituation. People can, need to, and are co-existing in close proximity with leopards. This occurs at a variety of places, with acceptable safety for both people and leopards. Maintaining safe environments for leopards and people viewing them requires active management, of people and leopards. Managers need to develop plans that specify the extent to which leopard-to-people habituation will be encouraged or discouraged. These management plans need solid scientific underpinnings and a broad understanding of habituation and other processes that may lead leopards to accept people at close distances. This is the first study that I am aware of where habituation of a focal species was a management objective. Habituation of wildlife is normally considered a management problem (Burger 1981, Henson & Grant 1991, Fernandez & Azkona 1993, Holmes *et al.* 1994, Steidl & Anthony 1996, 2000, Swarthout & Steidl 2001, Mann *et al.* 2002, Swarthout & Steidl 2003, Johnson *et al.* 2005). In areas that are changing from agriculture to nature-based ecotourism, and where wild animals may have been historically persecuted and have become secretive, habituation may be critical to the success of commercial ventures. Specific research objectives were to describe free darting as a capture method of leopards and highlight elements that could influence the ability to habituate leopards.

3.3.1 Capture and immobilisation

Immobilisation equipment

The immobilisation darts were reusable, accurate and reliable. Needles were made from stainless steel and available in lengths ranging from 20-100 mm with or without collars and barbs. The smallest needles (20 mm) without barbs were opted for, as the dart dislodged readily, reducing distress. The entry wound was also minimised and no surgery was required to remove the dart. A collared needle was used if leopards were darted harder and from a further distance. The flat end of the collar was filed-down, making it more rounded and easily dislodged. This ensured that the dart stayed in just long enough to inject but did not remain in long, which prevented it from flapping against the leopard's body as the subject fled.

The dart gun had the capacity to fire over a range of 10-60 m for difficult subjects; however, to prevent accidents or undue distress, a short distance of 10-20 m and soft penetration were selected. Soft penetration was achieved by reducing the pressure on the gun at least 2 bars lower than that recommended by the manufacturer. For example, if five bars at 10 m were recommended, then the gas

was set to three bars. Darts were fired into the rump or shoulder of the leopard. Visual surveillance of the darted leopard was maintained until the drugs took effect and then the vehicle's engine was switched off.

Immobilisation drugs

All leopards were immobilised with Zoletil 100 (Virbac, Republic of South Africa), a mixture of tiletamine hydrochloride, an analogue of ketamine in a 1:1 combination with zolazepam. It was used because of its wide margin of safety and dissociative properties (Dr. P. Rogers 2000, pers. comm.²). In leopards, 4-6.5 mg/kg were used by intra-muscular injection. Occasionally leopards required an additional injection if, for example, a dart syringe failed to discharge properly, if it was deflected by the leopard's movements, if weight was underestimated or if the animal had recently consumed a sizeable meal.

Immobilisation procedure

When leopards were located by researchers or game drive vehicles, Dr. P. Rogers was contacted to undertake the darting. Once visual of the leopard was obtained by the veterinarian the time, location and odometer reading was recorded. The leopard was followed in a vehicle until an opportunity presented itself and the vegetation type was open enough to ensure that the darted leopard could be followed and located easily post-darting. When darting without a collared needle the dart was fired from 10 m at three bars or less. When darting softly the darter needed to aim higher as the dart travelled in a flatter trajectory and lost height more quickly. In order to dart softly, the darter needed to be experienced and practice regularly because the dart was slow travelling, and anything from wind to a branch could change the course of the dart. If a dart was fired hard and at speed, the dart was more likely to bounce out before discharging and a collared dart was then used. Barbed darts were avoided because the flapping motion of the dart against the leopard's body as it ran caused the animal to flee further. Once the leopard was immobilised, the time, location and odometer reading were re-noted. Visual was maintained of the immobilised leopard until the subject became stationary (Appendix A-3). Vehicle engines were switched off and noise kept to a minimum until 10 min had elapsed and the subject was fully sedated.

Immobilising females consorting with a male

The same method was used when female leopards were immobilised while mating with a male. Once the female was darted, a vehicle was driven between the male and the female to prevent him causing injury to her while the drugs took effect. The female was then loaded onto a vehicle and driven a safe

² Dr. P. Rogers, Wildlife Veterinarian, Hoedspruit.

distance away (+/- 1km), where she was processed. The effect the presence of a habituated male had on the ease with which a female was immobilised was examined.

Processing immobilised subjects

An immobilised leopard's eyes remained open with the pupils dilated and therefore an ophthalmic ointment, IC ointment (Virbac, Johannesburg, South Africa) was used to protect the cornea from desiccation. The eyes were then covered with a cloth throughout the remaining handling to protect them from bright light and dust (Dr. P. Rogers 2000, pers. comm.³). To prevent excess salivation, 0.5 - 0.75 mg Atropine sulphate (Centaur Laboratories, Mumbai, India) was administered via intramuscular injection. An ampoule of Frontline® (Pfizer, Johannesburg, South Africa) was applied to the skin for the eradication of external parasites. Ampoule sizes 0 - 10 kg = 0.67 ml, 10 - 20 kg = 1.34 ml, 20 - 40 kg = 2.68 ml, 40 - 60kg = 4.02 ml. An injection of 1 ml / 50 kg body mass of Dectomax® (Pfizer) was administered subcutaneously for internal parasites. For the treatment of stress, 2 - 3 ml of Kyrovite® B Co-Super (Kryonlabs, Johannesburg, South Africa) was administered intra-muscularly. Bovaclox®DC (Schering-Plough Coopers, Johannesburg, South Africa) ointment 4.5 g was inserted into the dart wound and any other small open wounds found on the body to prevent infection. If the animal was moved, it was rolled carefully onto a blanket, being sure to support the stomach to prevent the intestines twisting. While the subject was sedated the facial, neck and body markings were photographed and measurements were taken (Appendix A-4 and A-5).

Measurements taken

Leopards were examined for the presence of external parasites and general body condition, by looking at the state of the fur, body wounds, tooth structure and wear, and muscle fat ratio.

Morphological measurements were taken of the neck and chest circumference, length from nose to base of tail, tail length, shoulder height, length of canine teeth and distance between teeth. The underside of the paw was measured and any unusual structures on the paw were recorded to help identify individuals from their tracks. Length was measured from toe to pad across the longest part. The width was measured from toe to toe across the widest part of the paw and the pad was measured from the top to the bottom (Appendix A-6). Measurements do vary by a few millimetres depending on the person performing the technique and therefore only one person was responsible for measuring at each immobilisation. In an attempt to standardise, at least two other individuals observed, and trained to measure in the same way should the main measurer not be available. If a leopard was immobilised a second time the original measurements were taken to compare with current measurements, to ensure

³ Dr. P. Rogers, Wildlife Veterinarian, Hoedspruit.

measurement repeatability. Any changes in measurements were re-measured and checked to ensure an actual change rather than human error.

The subject was sexed, reproductive status noted, and an estimate of age based on both body characteristics (Turnbull-Kemp 1967) and dentition and tooth wear (Stander 1997) was made. Where possible the animal was weighed using a flat surface with digital scales. Weighing was performed twice to ensure accuracy. Where it was not possible the weight was estimated by the reserve manager by physically lifting the subject and so noted in the data. Larger males were weighed using a net and meat scales hung on a pole, the leopard being lifted by two strong people and the scales read (Appendix A-4 and A-5).

Leopard age classes

Four different age classes could be distinguished during the study, namely cubs 0-12 months, subadults 12-36 months, mature adults 3-8 years, or old adults >11 years (Stander 1997). These were as follows:

Old leopard would have yellow, badly worn and missing teeth (Stander 1997), tattered ears, facial and body scars, and males would have large dewlaps. In the wild, leopard that live ten to eleven years are probably old (Turnbull-Kemp 1967).

Prime adults were smaller with bright coats. Teeth were slightly yellowed and the tips of canines only slightly worn (Stander 1997). Females had darkly pigmented nipples longer than 9 mm and males had the largest scrotum at this age (Turnbull-Kemp 1967).

Subadults had a slender delicate appearance with sharply pointed, white teeth (Stander 1997). Females had short pink nipples, and males' behaviour and movements like scent marking, vocalisation, territorial expansion and courtship were used in assessing when they become prime leopards (Bailey 1993).

Cubs were usually lighter than 20 kg, lacked permanent teeth (Stander 1997) and still associated with an adult female (Turnbull-Kemp 1967).

3.3.2 Telemetry equipment and radio-tracking procedures

Radio transmitters

All the radio transmitters originated from Telonics (Arizona, USA) and were constructed into radio collars or implants by Africa Wildlife Tracking (Pretoria, South Africa). Continuous signals were used, as triangulation locations are more accurate with these than with pulse signals (Sargeant 1980). Transmitters needed to be large, with a larger power supply, so as to reduce the interval between replacements. Transmitters were replaced every 12 – 18 months to ensure no loss of capacity before recapture of all the leopards. The transmitting frequency range chosen for transmitters was 148 – 152

MHz, which provided maximum although more variable range and allowed the use of small, easily transported antennae (Sargeant 1980).

The model of transmitter used for radio collars was an SB2 transmitter powered by a single D-Cell battery. The transmitter and battery were embedded in a waterproof matrix of fibreglass and epoxy resin with the antennae running on the inside of the collar belting. A magnetic switch, embedded within the transmitter collar, was used to turn it on and off. Belting of 3.5 cm breadth and 0.5 cm thick was cut to fit from the original length of 65 cm. The weight of the collar with a single D-Cell was in the region of 400 g (0.8%). The transmitter and battery housing were 8.5 cm x 4 cm x 5 cm. The cost of a new collar in 2003 was \$ 431.25, and the cost to refurbish the collar in 2003 was \$ 194.38.

Radio transmitter implants with a single D-Cell battery, weigh in the region of 200 g (0.4%), and are 14 x 4 cm in size. The cost of a new radio transmitter implant in 2003 was \$ 431.25, and the cost to refurbish the implant in 2003 was \$ 194.38. They were handled with care to prevent damaging the inert wax coating.

Fitting radio collars

A tape measure was placed around the neck and then enlarged so that three or four fingers could be inserted comfortably underneath. The tape was then pulled towards the nose over both ears and then over each ear individually and it became apparent if a collar would stay on or not. Pop rivets were used to secure the collar; as any bracket near the internal antenna may have caused interference in very wet weather (Dr. M. Hofmeyer 2000, pers. comm.⁴). Once a collar was fitted, the head was lifted to ensure the collar moved freely but was not too loose. The collar was pulled at an angle over each ear and then straight over the head to ensure that it could not be dislodged. As the leopard started to awake the collar was checked again.

Radio transmitter implantation

Once on the operating table the animal was placed dorsal recumbent in a steel cradle for surgical implantation by a veterinarian and was given 7 – 8 ml of procaine and benzathamine penicillin (Lentrax®, Rhone Poulenc) intramuscularly. The leopard's head was placed in such a way as to prevent inhalation of saliva and connected to an intravenous drip containing 800 – 1000 ml ringers lactate (Adcock Ingram Critical Care (Pty) Ltd, Johannesburg). Additional anaesthetics were administered via this route as required.

⁴ Dr. M. Hofmeyer, 2000, Skukuza Veterinarian, Kruger National Park.

The abdomen was shaved from the xyphoid process to the pubis, disinfected and prepared for surgery. The peritoneal cavity was entered through the linea alba to reduce bleeding. A 6 cm incision through the skin was made caudal to the umbilicus and the muscle layers were parted by blunt dissection until the peritoneal cavity was entered. The transmitter was sterilised by submersion in Hibitane® (ICI Pharmaceuticals, Johannesburg, South Africa) for 15 min prior, and then rinsed thoroughly in sterile physiological saline before implantation. The transmitter was inserted through the incision towards the ventral abdomen and left to fall into the cavity. Prior to suturing, the wound was filled with 5 ml of Lentrax® to prevent infection. The peritoneum, individual muscle layers and subcutaneous fascia were sequentially sutured using simple interrupted sutures of no.1 chromic gut. Skin wounds were closed with loose mattress stitches to prevent the animal from taking them out even when licked. Sutured wounds were topically treated with Necrospray® (Bayer, Johannesburg, South Africa). The time taken per surgical implant was approximately 1.5 h. The transmitter implants were recovered with a similar surgical procedure to the implanting procedure. During sedation, the animal was unable to control its body temperature and required monitoring with a thermometer via the rectum.

Post immobilisation recovery

Noise and bright light were avoided during the recovery stage. Post immobilisation, the leopard was always returned to the point of darting to ensure it was returned to its own territory. If it was not too cool, the animal was placed lateral recumbent in an open area, under a bush, near the point of darting. If it was cold, a high ridge nearest the point of darting was chosen where air temperature was observed to be warmer. If it was particularly cold (<5°C) or other large predators were present the leopard was allowed to recover fully in a wooden crate (1 m wide x 1.2 m high x 2 m long) and released early the following morning or when the leopard was responding normally to stimuli. One leopard was allowed to wake up in an open crate however, a vehicle remained present until the leopard was responding normally to external stimuli and walked out. If a female was darted out of her territory because she was mating with a male, she was returned to her own territory. If she was mating with a male and her territory was not known, she was put in a crate or observed until alert. The Global Positioning System location of the recumbent leopard was noted. Recovering leopards were observed from a vehicle 30 – 40 m away, until they were standing but not yet reacting to external stimuli. The following morning the leopard was relocated using the radio telemetry and the distance moved from point of recovery was calculated. If a leopard was particularly difficult to get close to during the darting, or had undergone an implant operation, meat was left the following day and then every three days for nine days to prevent them moving too far or having to hunt.

Radio receiving equipment

The radio receiver used for locating the leopards was a TR4 Telonics portable receiver with a two-element rubber Yagi antenna connected by a 1.5 m BNC/BNC connection and coaxial cable (Telonics Inc, Arizona, USA). Direction of the leopard from the observer was easily determined with a co-directional hand-held Telonics antenna, and the distance was accurately calculated by using the intensity of the signal (squelch) and by reducing the volume.

Transmitter detection

Measurement of the receiving distance of radio transmitters was undertaken when the animal was located recumbent in a flat open area. The vehicle odometer was checked and the GPS point noted at the leopard. The vehicle was driven away in a straight line on the same plane and when a signal could only just be heard by the person standing on the back of the vehicle the odometer was rechecked and the GPS point taken. The GPS points were then entered into ArcGIS (ESRI, California, USA) and the distance calculated. After the maximum distance had been measured, the vehicle was driven back to the leopard to ensure that it had not changed location during the trial. Each transmitter was checked on two different occasions resulting in a total of 28 samples. Average transmitting distance was calculated from the resultant data.

Monitoring radio tracked leopards

Using discontinuous radio tracking, collared and implanted leopards were located twice daily from the ground using Toyota Hilux 4x4 vehicles, at discrete time intervals throughout the study period. On days where lightning posed a hazard, or if heavy rain resulted in excessively wet conditions that would result in researchers becoming stuck, research was not conducted. Research was undertaken by 1 – 4 vehicles for 8 h a day in the morning from 05:00 – 09:00 and in the afternoon from 16:00 – 20:00.

Away from the rivers, radio-collared leopards were located by stopping every kilometre and using the roof of the vehicle and high elevation points to locate a signal. This method, coupled with continuous sweeping (driving with the telemetry on all the time) was used along rivers. The perimeter of the reserve was checked daily at kilometre intervals. Once a signal had been located and the direction established, the animal was tracked to a distance where the signal indicated that the leopard was within visual distance (Cochran 1980). A visual was always attempted: however, when this was not possible it was noted that only a signal was possible.

Whenever an exact location of the leopard could be determined or a visual obtained, reference was made to the following factors to describe the immediate environment around the leopards:

- (1) GPS co-ordinates of the location and the location in words
- (2) Date
- (3) Time observation starts and ends
- (4) Leopard status:
 - (a) Visible (V) – one or more leopards visible enabling observation of behaviour
 - (b) Audible (A) – no leopard visible but close enough to observer for identification of sounds of feeding and vocalizations produced by the leopard (within a hearing range of 30 m from the observer)
 - (c) Not observable (S) – leopard location only confirmed through a clear signal from the telemetry equipment
- (5) Estimated distance of leopard from observer in meters using visual assessment, radio telemetry equipment and sounds produced by the leopard
- (6) Number and identity of leopards present at the location
- (7) Other predator species present at the leopard sighting closer than 40 m from the leopard (IG)
- (8) Behaviour, including copulation data and territorial movements
- (9) Feeding behaviour including kill species or any sign of feeding, and belly score between 1 – 5, one being the thinnest and five being the fullest (Appendix A-7).

Data were recorded on data sheets and by using a camera and digital video camera to capture leopard identities and behaviour. Once the required data were collected, the subject was left. Each radio-tracked leopard was generally located twice a day every day during the study. Observation periods following location lasted between 15 min and 24 h of continuous following, depending on the activity of the animal and how many other subjects still needed to be located that day. If leopards were engaged in interesting unusual behaviour, the researcher remained with them for as long as it took to acquire all the data. All-night observations were also undertaken when leopards were located copulating (Chapter 6).

3.3.3 *Habituation*

Habituation is defined as a process whereby continual exposure to a neutral situation such as people in vehicles viewing them in a non-threatening manner results in a muting of the subject's reactions (Herrero 1985, Aumiller & Matt 1994, Whittaker & Knight 1998). Consequently, the target individual gradually relaxes to viewing from a close distance. The distance at which an animal reacts to a person is called a flight initiation distance (Runyan & Blumstein 2004). When approached within this distance stress related overt reactions occur, which include change in body position, staring at the

approaching vehicle, changing course or moving away and on occasion attacking (Herrero *et al.* 2005). Overt reaction describes behaviour that can be observed, yet does not preclude the possibility that important, unobserved internal reactions may occur without overt response. This has been demonstrated using heart-rate telemetry in bighorn sheep (*Ovis canadensis californiana*) and studying their heart rate change in response to potential stressors such as dogs and helicopters (MacArthur *et al.* 1982). Energetically costly increases in heart rate often occurred before any overt reaction from the bighorns. Hence we surmise that leopard may be stressed without overt response to a person. This implies a conservative approach distance to leopard, and stopping before an overt reaction would be anticipated during the habituation process is imperative (Blumstein *et al.* 2003). Habituation of leopard to people is not an all-or-none response and may vary widely among individuals (Herrero *et al.* 2005). It will occur to the extent that the benefits of not reacting outweigh the perceived risks (costs) to the leopard. If, however, the leopard is wrong in its assessment, it may be injured or killed. (Herrero *et al.* 2005). For the purpose of this study, habituation was measured as the amount of time it took a leopard to relax sufficiently to allow a vehicle to approach to 20 m and remain in view for 20 min without showing an overt reaction (Swarthout & Steidl 2001). This distance was necessary due to the dense nature of the leopard's habitat, and a visual was often not possible at a further distance.

Initially, visual observations from the road of recently immobilised leopards in the bush were only attempted at the onset of darkness. The tracking vehicle was driven along the road towards the strengthening signal. When the vehicle was within 80 m, the leopard was approached at about 10 km/h. If the leopard concealed itself in the grass, the vehicle would drive past slowly on the road without stopping. This method of viewing continued until the leopard remained relaxed when the vehicle was driven past without stopping, and the leopard remained in view and showed no overt reaction. Once a leopard showed confidence when being viewed with the vehicle driving past, the vehicle was stopped on the road and the leopard viewed. The leopard's behaviour indicated the distance that it was comfortable being viewed from. Worked slowly and sensitively, the viewing distance became shorter with time, and the leopard relaxed enough to be followed. Initially the leopard was only followed along the road at a distance of 40 m, or a distance that did not elicit an overt reaction (look around, move forward at a quicker pace or leave the road due to pressure from the vehicle). If the leopard left the road, the vehicle would stop until the leopard re-emerged and resumed its natural behaviour. If the leopard became stationary or stopped to mark its territory, the vehicle would approach slowly trying to get to 20 m, watching for any overt reaction. At the slightest sign of an overt reaction, the vehicle would stop and the engine would be switched off.

Once the leopard was comfortable with being followed on the road it could be followed off road. The vehicle always approached in low range 4 x 4 at an oblique angle, aiming at a point to the leopard's side, and thereby drawing closer, being sure not to break large branches or make excessive noise.

Engaging 4 x 4 low range ensured the vehicle moved slowly but kept the engine beat at a steady rate. If the subject moved a short distance and settled, the vehicle would follow slowly. Often, when located in the open, the leopard would move to an elevated point such as a termite mound. Once located visually the leopard was approached to a distance that did not illicit an overt reaction. When the observer was ready to leave a sighting, the vehicle was started and allowed to idle for 15 – 20 s before the vehicle reversed out slowly. At no point during a reverse-out manoeuvre did the vehicle get closer than its initial position. If the subject moved a considerable distance through the bush, it was not followed. Instead, the vehicle returned to the road, and waited with the engine switched off at the expected point of exit from the bush onto the road.

Distance of visual observations depended on the individual. On every occasion, the behaviour of the leopard was observed, and when the leopard showed any overt reaction because of the observer, the vehicle was switched off and the subject observed from that position. Once the subject relaxed, it was often possible to move closer or alter positions. Females with cubs could be aggressive and were given a wider berth. Apart from the consideration accorded to the mother, it was essential that the cubs be given very particular treatment during the early months.

Use of a habituated male to habituate females

Once the resident male leopard was habituated, he was used to habituate females (n = 5) during the copulatory period. The pair were followed continuously on and off-road, trying to maintain visual observation until the pair split after 2 – 4 days (Chapter 6). Whenever the pair were mobile along a road or in open habitat, the vehicle remained in the comfort zone of the female. When the pair were stationary, the vehicle approached to a distance of 20 m and switched off. If the female was reluctant to approach the male, the vehicle pulled back to a distance that permitted the female to approach comfortably and mate. If the male became mobile the vehicle was not started until the female was out of sight and then the pair were relocated using telemetry. In thick bush the vehicle followed the male, maintaining visual observation. As soon as purring was heard or the female began to wasp in front of the male the vehicle was switched off to allow the female to approach the male and mate without being disturbed by the vehicle.

Measuring the effect different elements of the immobilisation have on habituation

In order to assess the effect the different elements of the darting had on the ease of habituation the following were recorded and ranked against the number of hours taken to habituate individual leopards. The darting experience (hard or soft), type of recovery (open, crate or in a crate with the door open), type of transmitter used, age of the leopard and the habitat type in each leopard's territory (riverine, open or a combination of both).

3.4 Reproduction

3.4.1 Data collection

Radio tracked leopards were located twice daily using radio telemetry techniques and directly observed from a 4 X 4 vehicle in the standard way used in other predator studies (Schaller 1972) (Chapter 4). When leopards were located copulating, a vehicle was dedicated to the leopard pair and remained with them 24 hours a day until the end of the copulatory period when the pair separated. This allowed two vehicles to carry out daily monitoring of other leopards. The vehicle dedicated to the copulating leopards would check for the presence of other predators and therefore assisted the general data collecting researchers with locations of other radio tagged subjects.

3.4.2 Reproductive data

Females with radio transmitters were visited twice daily for a minimum of 15 min to establish if they were close to or consorting with a male. Vocalisation (a sawing call) was an indication of the onset of oestrus (Smith & McDougal 1991) and usually began several days prior to association with a male. Males replied with the same call, which is also used when patrolling their territory (Hancock 2000). During copulatory periods, six researchers were required to enable 24-h surveillance of copulating pairs throughout the courtship period. At the beginning of the study, each shift during a copulatory period lasted 4 h. The shifts were later extended to 6 h to reduce the number of researchers needed, as there was sufficient time between shifts to sleep. Each shift required two researchers, one to drive and operate the spotlight at night and the other to operate the stop clock and record time, observational and Global Positioning System information.

Copulatory data collected during nineteen copulatory periods studied 24 hours a day

From 2001 to 2003, intensive copulatory data were recorded during 2449 h (24 h a day) on eight adult leopards (seven females and one male) located copulating in 19 copulatory periods. Five copulatory periods which were interrupted when females were immobilised were not included, and entailed a further 58 h of study.

Once a male and female were close to each other, monitoring was intensified and researchers remained with them 24 hours a day until the pair separated 2-4 days later. It was possible to determine when mating had begun even when visual observations were not possible, as the post-copulatory roar was audible (See copulatory definitions below).

During the copulatory period, the following were noted: the number of copulations in the copulatory period, initiator of the copulation, the length of each copulation from the purr and the time of

mounting, start and end times of the roar, and whether the female rolled post-copulation. Additional comments about the mating included post-mating aggression, unusual vocalisation such as snarls and calls (Hancock 2000), false copulations, distances moved after copulation and any other interesting behaviour. Interruptions to the mating were also recorded as human related (immobilisations), as due to other female leopards when copulation took place in another female's territory, or as due to other predators. One adult male (M1) undertook all the copulations on the reserve and covered all seven adult females. M1, the only breeding male on the reserve, was therefore deemed to be the father, of all the cubs. There were no other behavioural data to suggest non-resident males ever fathered cubs.

Copulatory data collected during regular monitoring times

A further 27 copulatory periods were studied less intensively from 2003 until M1 died in August 2004. The leopard pair were located twice a day, in the morning and evening during regular monitoring times (Chapter 4). Information was only collected on the start and end of the copulatory period, and on the identity of the male.

3.4.3 Definitions of copulatory terminology

- Start purr:** As the female approaches a male to initiate copulation, she begins to purr while wasping. The male joins in the purring as he mounts the female. This purring continues until the end of the post-copulatory roar, undertaken by the male.
- Waspings:** The female moves back and forth in front of the male, enticing him to mate.
- Lordosis:** The female is crouched down with her tail up and forward towards her face
- Time of mounting:** The point where the male climbs onto the female in lordosis.
- Copulation:** The male would perform a series of penetrating thrusts with his pelvis, during which he bared his teeth and gently grabbed the back of the female's neck.
- Post-copulatory roar:** The roar occurs just prior to the male dismounting the female post-copulatory.
- Dismount:** Males have a barbed penis which causes pain to the female when the male dismounts (Apps 2000). The female is therefore usually aggressive during the dismount, and the male will jump clear of the female, who rolls onto her back swiping at the male with her front paws.
- Post-copulation roll:** Once the male has dismounted the female, post-copulatory, the female may roll on her back.

- Post-mating aggression:** After the dismount is over the female may snarl, hiss or swipe the male with her paw.
- False copulation:** The male mounts the female as usual but climbs off without penetration or a post-copulatory roar.
- Copulatory period:** A period of time that male and female leopards are together copulating, from when they meet until they part several days later. This is during the female's oestrus period and may also be described as oestrus association.
- Inter-copulatory interval:** The period of time in between consecutive copulations.

3.4.4 *Reproductive parameters*

Litters

The birth date of cubs was estimated as the day after the female became localised for a period longer than a week, approximately 90 days after the last oestrus with no further matings (Smith & McDougal 1991). The average was 95.5 days ($SE = 0.9$, range 89 - 98, $n = 10$) in this study. The female would leave and return regularly to the same location, ruling out death or a kill. Data on litter size and survival were obtained by daily monitoring of the females and their cubs (Chapter 4). From approximately two months old, cubs began to move with their mother and tracks of females with their offspring were monitored. It often took repeated observations to determine the litter size, which was approximated as the number of cubs first seen unless their tracks suggested otherwise or more cubs were seen at a later date. Cubs were sexed as they matured. It was decided against searching the den when the females were away so as not to precipitate cub mortality or to force a female to move her cubs to a less favourable den. On a single occasion, the reserve manager searched the area where a female was presumed to have her cubs. He found nothing (Bailey 1993) and, on her return, the female moved her cubs.

Inter-oestrus intervals

Leopard are polyestrous (Bailey 1993) and in this study inter-oestrus intervals were measured from the last day of copulation to the first day of the next copulation period.

Gestation period

Gestation length was measured from the second to last day of mating to the day the female became localised. This was not a precise estimation of gestation as it cannot be established which copulation in the copulatory period resulted in conception. The first day cannot be considered because mating need not continue once a leopard has conceived. Nor can the last date of mating be used as the starting point of the gestation period, because it would take at least 24 to 36 h for the fertilisation physiology to function and to produce the behavioural reaction in the leopard female (Herron 1986). If the

average of copulatory periods was taken as a fixed date, this too would be unrealistic as the oestrus period ranges from 4 – 96 days (Bailey 1993) during which time the pair may split and resume copulation days later, and no female would tolerate a male for 10 to 12 days once she has become pregnant (Herron 1986). I therefore considered the date of fertilisation to be a day before mating ceased. This date was satisfactory as it included the short copulatory periods of two days. Associations within five days of a previous copulation were not included in the calculations as the females were likely to be entering into oestrus but not yet receptive to mating.

Reproductive success

Reproductive success were calculated as the number of courtship associations until conception. Human interrupted copulations (when a female was darted during copulation) were not included in the calculations. Lion (*Panthera leo*) and other leopard did disturb courtships, and these natural disruptions were included. Inter-birth intervals was calculated as the number of days between consecutive births. Inter-birth intervals were only calculated for those litters where cubs dispersed, and not when cubs died prematurely.

Reproductive success

Females typically have their first litter at three years old (Bailey 1993) and are reproductively active until 8.5 years (Eaton 1977) in a captive population, or up to 19 (Bailey 1993) years in a wild population. Assuming the females in this study are reproductively active for nine years from 3–12 years (Eaton 1977) of age, total lifetime productivity can be calculated. Reproductive success is the number of cubs that survived to dispersal or one year of age (Clutton-Brock 1988). Youngsters that disappeared prior to 10 months old were assumed dead. Reproductive success was calculated by dividing the number of cubs born to each female by the number of months between their first litter and either the end of the project in September 2005 or the date that they died.

Seasonal influences

For seasonal analysis, the year was divided into spring (September & October), summer (November to February), autumn (March & April) and winter (May to August). Copulatory periods that fell over two months, were scored as the month with the greater number of copulatory days in it. On this basis the number of copulatory periods, conceived copulatory periods and births were plotted according to the month in which they occurred.

Probability of encounter with other predators

To assess the impact other predators had on litter mortalities, data concerning other predator-population dynamics and distance from the leopards was recorded. The probability of leopards encountering other predators was calculated from the combined location data (n = 551 days) of three

leopards (M1, F1 and F2). This was only undertaken on three of the four radio tracked leopards as F3 encountered no other predators when researchers were with her during the study. An encounter with another predator was recorded if there was visual observation of another predator species in the same location as the leopard, and the leopards' behaviour was affected by, or the leopard moved away from the approaching predator.

3.5 Population

3.5.1 Population dynamics

A leopard database was maintained from 1999 – 2006. The females were numbered in the order that they were either captured or discovered consorting with M1 and a positive identification could be made. Individuals were identified by the spot pattern on the face and neck as well as facial features such as scars and ear tears. Video footage and photographs were used to assist in the accurate construction of identikit. In the database an identity number, name, sex, age, date of birth, date of death, the origin of each leopard and translocation details if leopards were removed was recorded (Chapter 7). The sire of cubs was assigned to the resident male present on Karongwe during this study (i.e. the male observed copulating) (Chapter 6), while the age of the cubs (Chapter 4) and their association with a female were used to determine their mother if she was not known.

Method for population estimate

We used the minimum count method with recognizable individuals. The most accurate density estimates of large carnivore populations are obtained when individuals can be recognized either through natural markings or unnatural marking such as ear tags or radio collars. Using a combination of territory mapping using radio telemetry, natural markings and tracks it was possible to calculate the total population.

3.5.2 Data collection

Ecotourism guides, trackers and researchers monitored the roads for tracks to obtain additional information about leopard that were not radio tagged. Due to the high vehicle activity a large majority of the roads were traversed daily, and any fresh leopard tracks located by trackers on game viewing vehicles were reported to the researchers via the radio. Researchers would then relocate and measure the tracks. Tracks were only measured in firm soil with a light covering of dust, anything softer and the spoor size appeared to be larger than it actually was, and was not measured. Only those tracks that could be identified as a front or back foot, and left or right, were measured. This allowed the same tracks (e.g. front-left track) of any two leopards to be compared. Length was measured from toe to pad across the longest part. The width was measured from toe to toe across the widest part of the paw

and the pad was measured from the top to the bottom using callipers accurate to a millimetre. The pugmarks of an adult male could be distinguished from those of adult females by their size and their rounder shape and greater spread of the toes (Liebenberg 1990). The pugmarks of a subadult were smaller than those of an adult, and they were sometimes either with or near those of a female (Liebenberg 1990). It was often possible to identify individuals who had already been darted and had their paws measured. Any unknown spoor was placed into a database of sizes, in an attempt to identify any regular patterns. Since the study population was small and relatively isolated we seldom had problems identifying tracks of specific leopards.

Young leopards

There was reluctance by the reserve manager to collar or implant young leopards, which were likely to leave the confines of the reserve. If they dispersed with the collar they may be choked as they matured. It was found that the collars on a young leopard needed to be made larger after a year and a half. An implanted tracking device retained in the peritoneal cavity for an extended period could wear over time at the corners, leaking battery acid into the animal, causing death (pers. comm, Martin Haupt 2000, ⁵) advice from manufacturers and Dr. Henk Bertschinger 2001⁶). The majority of subadult leopards were therefore identified from natural markings and subsequent encounters involved re-sighting, track identification, or recovery of dead animals.

Mortalities

Leopard mortality was divided into two categories; confirmed and suspected. Mortality was confirmed with the recovery of a carcass, radio tracking device or remains of a leopard. When cubs younger than eight months disappeared they were also classified as confirmed mortality. Mortality was suspected when old leopards were never seen again or adult females that had been seen regularly and copulated previously ceased to be seen or to re-copulate with the resident male. Adult males and subadults of both sexes were always assumed to have emigrated rather than to have been killed, unless there was a confirmed mortality.

Causes of confirmed leopard mortality were established by direct observation, measuring bite marks if death was due to another predator, and evidence collected from tracks around the site and other animals with transmitters nearby. Dead leopards (48%) were found within 24 h unless death occurred in the thick reeds of riverbeds. In such cases sufficient time was allowed to elapse to ensure that the stationary leopard was not on a kill or injured.

⁵ M. Haupt, 2000, Africa Wildlife Tracking, Pretoria

⁶ Dr. Henk Bertschinger, 2001, Onderstepoort, Pretoria

Other immobilisations used only for population data

As subadult females F8 and F9 of previously habituated females' matured, they were also collared, however, as they were already habituated, they were not included in the immobilisation and habituation chapter (Chapter 4). They were also not yet sexually mature and did not mate. F8 was immobilised and collared in June 2004 and F9 was immobilised and collared in December 2004. In October 2004, two months after M1 died, M4 arrived on the reserve and was immobilised in December 2004. F2 was the last remaining adult female and had two two-month-old cubs from M1 which M4 killed before copulating with her, resulting in two cubs which were still alive at the end of the study (Chapter 7, Fig 7.1).

3.6 Territorial behaviour

How most appropriately to represent an animal's home range is a persistent problem. The four different approaches to the estimation of the home range include the Minimum Convex Polygon method, which fits the original definition of home range, while Harmonic Mean method, the Fourier Transform method and the Kernel method give an index of use within that (Worton 1989). Historically, a prominent method used was convex polygon (Mohr 1947), while the kernel home range is the one of the most robust, best-known methods and will be utilised in this study (Seaman & Powell 1996, Laver & Kelly 2008). This method calculates utilisation distribution describing the relative intensity of an animal's use of areas within a defined space and then specifies the home range boundary by the contour that encompasses a selected percentage of the total space used (Samuel *et al.* 1985). Geographical information systems provide a useful tool for preparing and manipulating datasets in a spatially explicit manner.

The kernel method is a nonparametric method for smoothing the two dimensional locations. Since the method makes no assumption about the utilisation distribution, the various factors, which influence the animal, can be investigated and interpreted with ease (Seaman & Powell 1996). The kernel UD method is a probability density estimation which calculates the home range of an animal based on the relative amount of time that an animal spends in different areas of its range. Nonparametric methods typically need at least 30-100 independent locational observations for an animal (Worton 1989). Each kernel is a density, and therefore the distribution range estimates that the result is a true probability density function. It is possible to investigate and interpret the various factors that influence an animal, since this method makes no assumptions about the form of the utilisation distributions (Worton 1989). A leopard followed would have several GPS points and often several from the same location. To avoid autocorrelation and prevent any errors in the estimation of core and home range, only two GPS point were used each day, the first one and the last one of the day.

In order for the description of environmental variability and predictability to make sense, it is necessary to refer to the range of scales relevant to the organism under study (Worton 1989). A manual grid of 20 cells was used to calculate band width as it produced the most accurate home range estimate. Kernel estimates are less biased than other estimates of home range, with fixed kernel method performing better than adaptive kernel method. The smoothing parameter of 250 m for individuals provided the least biased estimate of home range for the volume of data being tested. Most studies define the home range as the smallest area containing 95% of the utilisation distribution and the area of greatest activity within the home range is known as the activity radius (Seaman & Powell 1996). Sample sightings smaller than 50, generally lead to an overestimation of the home range size (Seaman & Powell 1996). Thus while it is important to include as many individuals as possible for statistical purposes, there was a trade off between sample size and accuracy.

Home ranges are estimates of where an animal may be found based on where the animal has been seen and these often overlap the borders of the reserve. The reserve is fenced and in reality most of the animals did not utilise the area outside the reserve (e.g., tracks did not cross fences, radio-locations were not detected outside the reserve). The home ranges were therefore clipped for those leopards not leaving the confines of the reserve according to the border, and the area of the kernel contours recalculated.

The individual animals' home ranges were plotted on maps of the area in which they were found, ensuring all sightings fell within the border. Each GPS point was checked to ensure its accuracy in relation to the written location. Suspected errors and duplicate records were deleted. On many occasions the vehicle could not get to where the leopard was, so GPS points were taken directly in line with the leopard and an estimated distance was given from the vehicle to the leopard. This was usually the case when the leopard was on a koppie or in a river or drainage line. The correct GPS point was obtained from ArcGIS and corrected on the original data.

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CHAPTER 4

METHODS OF RADIO TAGGING AND OBSERVING SECRETIVE LEOPARD FOR RESEARCH

4.1 Abstract

Studies of secretive and historically persecuted species are difficult and, in particular, direct observational data are rare. Radio tagging for location data is commonplace but, in order to obtain visual observation, a degree of habituation to enhance scientific research is necessary. We describe and cost immobilising and radio tagging leopard (*Panthera pardus*), and assess factors that promote habituation for study. Nine leopards were darted from a vehicle and fitted with radio transmitters. The average time it took to dart leopard was 130 ± 46 min and the average cost of immobilising and fitting a radio transmitter, costing US\$531, was $\$1060 \pm 132$ (range = \$732 – \$2748, n = 15). Five adult female and two adult male leopard were habituated, to a predetermined distance and length of time (20 m for 20 min), which was achieved after on average 17.3 ± 6.3 h (range 3- 43, n = 7) of interaction post immobilisation, spread over 13 ± 5 days (range 1 – 37), and cost on average was $\$593 \pm 222$ (range = \$45 - \$1651). Habituation made it possible for researchers to watch key behaviours including copulation and kills. Although the habituation of wildlife is usually perceived as a management problem, the habituation of wildlife to vehicles, at a safe distance for both the researcher and the leopard, is beneficial for research purposes.

4.2 Introduction

Radio tracking is a widely used tool for efficiently locating and studying free ranging animals. Several comprehensive accounts on methods, and the benefits and problems of radio tracking animals have been compiled (Sargeant 1980, Bertram 1982, Millsbaugh & Marzluff 2001). Because of its wide application, radio tracking has transformed field studies, and can provide answers to a multitude of behavioural and biological questions. Radio transmitters have been used to track leopards (*Panthera pardus*) in several studies; however, these studies primarily yielded data on territorial movements (Schaller & Crawshaw 1980, Norton & Henley 1987, Bothma *et al.* 1997, Mizuntani & Jewell 1998, Marker & Dickman 2005, Simchareon *et al.* 2008, Grant 2012), feeding (Muckenhirn & Eisenberg 1973, Mizuntani 1999, Fröhlich *et al.* 2012), population ecology, and predator human conflict (Myers 1976, Nowell & Jackson 1996, Balme & Hunter 2004, Swanepoel 2008). Bailey's (1993) study, the most comprehensive to date, undertaken in the Kruger National Park, produced a large quantity of data. However, a considerable amount of circumstantial information was collected, as visual observations were for the most part not possible. It is clear that radio tracking of leopards has seldom been exploited to its full potential in behavioural studies. Such shortfalls may be expected for

secretive and persecuted species like the leopard (Schaller & Crawshaw 1980, Sunquist 1983, Jackson 1996).

When wild animals encounter humans, they may show one of three responses: habituation, attraction or avoidance (Knight & Cole 1991). Habituation (a waning of response to repeated, neutral stimuli) can be described as the process whereby an animal becomes accustomed to non-threatening environmental stimuli and learns to ignore these stimuli, resulting in a muting of reactions (Herrero 1985, Aumiller & Matt 1994, Thompson & Henderson 1998, Whittaker & Knight 1998). Consequently, the target individual gradually relaxes to viewing from a close distance. Attraction is a response to positive reward characterized by the strengthening of an animal's behaviour as a result of positive reinforcement, and indicates movement toward stimuli (Knight & Cole 1991, Thompson & Henderson 1998). Wildlife attraction is often referred to as food-conditioning, but is equally applicable to behaviours that attract wildlife to shelter or security (Knight & Cole 1991). Avoidance behaviour is a response exhibited from fear and previously experienced painful stimuli (Brush 1971, Davey 1981, Domjan 2003, Rauer *et al.* 2003).

Capture methods have the potential to cause aversive conditioning by establishing a link between a pain and fear-inducing unconditioned stimulus (such as, dart, confinement, leg snare), and some environmental cue as the conditioning stimulus (vehicle or human presence) (Hunt 1984). One way of improving wildlife viewing for research is through sensitive capture and habituation techniques.

The aim of this study was to capture, attach transmitters to, and habituate leopards as part of an extensive behavioural ecology study. The study was designed to use methods with minimal impact on study animals. It provides descriptive methods for reducing stress associated with capture and research to achieve successful habituation, and highlights the economic costs of darting, radio tagging and habituation. This study emphasizes the suitability of habituation for increasing effectiveness and efficiency of research at collecting unbiased data. Vegetation and terrain is likely to influence the probability of observing leopards and may have a large impact on how quickly and easily each leopard is habituated. Our specific objectives were to: (1) describe free darting as a capture method of leopard, (2) highlight elements that could influence the ability to habituate leopard, and (3) calculate the costs of such immobilisation and habituation.

4.3 Methods

4.3.1 Study area

Fieldwork was conducted on the 85 km² Karongwe Private Game Reserve, Limpopo Province, South Africa (24°13'S; 30°36'E). The reserve was formed in 1998 and a 2.4 m electrified game-fence was

erected around the reserve perimeter. The triangular shaped reserve is bordered on two sides by commercial game farms and by trust lands (a tract of land with associated dwellings, set aside for wildlife) on the remaining border. Karongwe falls within the savannah biome (Rutherford & Westfall 2003) and lies within the Mixed Lowveld Bushveld (Low & Rebelo 1998). The study area is characterised by hot, rainy summers and warm dry winters with an average annual precipitation of 487 mm.

The reserve's main function is eco-tourism and many animal species are present. Carnivores that were reintroduced include lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*) and spotted hyena (*Crocuta crocuta*). Twelve ungulate species support them. Leopards occur naturally in the area, and persisted during years of heavy persecution preceding the formation of the reserve.

4.3.2 Capture method

The study began in September 1999 and ended in August 2005. The preferred capture method was free darting (darting from a vehicle). Eight leopard were free darted (five adult females, three adult males) (Table 4.1) and aged as in Owen *et al.* (2010). Subsequent immobilisations of leopard (six leopards) were undertaken on average 500 ± 15 days (range = 476 – 557 days, $n = 6$) after the initial immobilisation for transmitting device replacements. F1 underwent a third immobilisation a month later when the dart failed to inject on the second immobilisation (Table 4.1).

Leopards were captured by free darting from a vehicle using a Dan-inject rifle JM Spl.CO₂ (Dan-Inject, ApS Sellerup Skovvej, 116 DK, 7080, Børkop, Denmark) with Zoletil 100 (Virbac), a tiletamine hydrochloride in a 1:1 combination with zolazepam at 4-6.5 mg/kg. Needles were 20 mm and barbless. Darting was undertaken from 10-20 m at least 2 gas bars lower than that recommended by the manufacturer (soft penetration) (exceptions detailed in results) in open habitat to ensure easy leopard recovery post darting. Females immobilised during consortship were moved +/- 1 km from the male for processing to avoid harassment from the male.

4.3.3 Telemetry equipment

VHF radio transmitters (SB2 transmitter, Telonics (Arizona)) were constructed by AWF (Africa Wildlife Tracking, Pretoria). The weight of the collar powered by a single D-Cell was ~ 400 g. The transmitter and battery housing were 8.5 cm x 4 cm x 5 cm. Radio transmitter implants had a single D-Cell battery, weight ~ 200 g, and were 14 x 4 cm in size. Implant operations (McKenzie *et al.* 1990), both insertion and removal, took ± 90 min. Implantation was used in instances where a collar

had previously been removed by the leopard or where it was calculated that the neck was bigger than the head, reducing the chance of the collar remaining on.

4.3.4 *Post immobilisation*

Post immobilisation, leopards were returned to the location of darting. Females immobilised outside their known territory during mating, were returned to their territory. Where the territory was unknown, females were placed in a crate or observed until alert. Recovering females were vulnerable to attack from territorial owners as they negotiated their way back to their own territory. We observed recovering leopards from a vehicle 30 – 40 m away until they were starting to stand (noise and bright light were avoided). If a leopard had been implanted and it was particularly cold ($< 5\text{ }^{\circ}\text{C}$), or if other large predators were present, the leopard was allowed to recover fully in a wooden crate (1 m wide x 1.2 m high x 2 m long) and released early the following morning. One leopard was allowed to wake up in an open crate.

We noted the location and GPS (Global Positioning System) position of the recumbent leopard. An audio distance of 20 m (visual distance) was calculated and recorded for each transmitter using the intensity of the signal (squelch) and by reducing the volume on a TR4 Telonics portable receiver with a two-element rubber Yagi co-directional hand-held Telonics antenna. Leopards were re-located the following morning and distance moved from the point of recovery was calculated. Leopard that had undergone an implant operation, were provisioned with meat the following day, and then every three days for nine days to enable visual monitoring and ensure their well-being, and to prevent them moving too far or having to hunt. Leopards particularly difficult to get close to during the immobilisation, or which remained stationary the day following immobilisation, were provisioned with meat to enable a post darting visual to monitor for potential adverse effects.

Using three vehicles and nine researchers, radio tagged leopard were located twice daily (05:00-9:00 and 16:00-20:00) where possible throughout the study period. Location was recorded to the nearest 20 m using a handheld GPS (Garmin International, Kansas, USA) or by radio triangulation when close approach was not possible.

4.3.5 *Habituation*

Post initial immobilisation, five adult females and two adult male leopards were habituated. Habituation occurred through daily monitoring and during the concurrently running reproductive study where leopards were followed throughout the copulatory period (Owen *et al.* 2010). For the purpose of this study, habituation was measured as the amount of time in hours it took for a leopard to relax sufficiently to allow a vehicle to approach to 20 m and remain in view for 20 min without

showing an overt reaction (Swarthout & Steidl 2001). This distance was chosen due to the dense habitat and a visual observation was often not possible at a further distance whether a collar or implant was used. When a leopard is approached, stress related overt reactions occur which include change in body position, staring intently at the approaching vehicle, changing course or moving away, and if approached too closely the leopard could attack (Herrero *et al.* 2005). Overt reaction describes behaviour that can be observed, yet does not imply that important, unobserved internal reactions may occur without overt reactions (Blumstein *et al.* 2003). Hence, we surmised that leopards may be stressed without overt response to a person or vehicle. This implies that during the habituation process it was imperative that a conservative approach distance was maintained, and that the approaching vehicle stopped before an overt reaction was seen (Blumstein *et al.* 2003).

When starting habituation, visual observations of recently immobilised leopard in the bush were only attempted at the onset of darkness, from the road, using a spotlight with a red-filter. The vehicle never stopped or left the road to view the leopard. Once a leopard showed confidence with being viewed, the vehicle was stopped on the road for viewing with the engine on. As it moved, the leopard was followed along the road at a distance that did not elicit a reaction. If the leopard left the road, or became stationary, the vehicle would approach on the road slowly, trying to get to within 20 m, watching for any overt reaction. If an overt reaction was observed the vehicle was switched off, and the subject observed from that position. Once the leopard was comfortable with being followed on the road it could be followed off-road in low range 4 x 4 at an oblique fashion, aiming at a point to the leopard's side. When the observer was ready to leave a sighting, the vehicle was started and allowed to idle for 15 – 20 seconds before being reversed out slowly. Habituation time per session was calculated from when the signal indicated the leopard was within 50m until the sighting was left. Once habituation of the resident breeding male leopard was complete, female (n = 5) habituation was undertaken during copulatory periods.

Statistical assessment – We used a Mann – Whitney U – test to determine the relationship between the presence of a habituated male leopard during initial immobilisation and the length of time taken to immobilise females. Evaluations between initial and subsequent immobilisations were made using the Wilcoxon signed ranks test. We assessed the relationship between leopard age and habituation time using Pearson's correlation.

In order to assess the effect different elements of the darting process had on the ease of habituation, the following were recorded and correlated with the number of hours taken to habituate individual leopards: the darting experience (hard or soft), type of recovery (in the open, closed crate, or in a crate with the door open), type of transmitter used (collar or implant), age of the leopard, the habitat type in each leopard's territory (riverine, open or a combination of both) and presence of an habituated male.

The time taken to immobilise each individual provided an indication of temperament prior to habituation.

We estimated the costs of habituating a leopard to 20 m for 20 min by multiplying the daily cost of US \$ 44.62 per day (\$ 15 salary, and 80 km.day⁻¹ at \$ 0.37 km⁻¹, which covers vehicle maintenance and fuel) by the number of days spent trying to habituate each leopard. The conversion rate at the time of writing was calculated at ZAR 7 to US\$ 1.

4.4 Results

The average overall time taken across all immobilisations combined was 130 ± 46 min (range 15 – 720, n = 15), and average distance travelled while trying to dart was 1.9 ± 0.6 km (range 0 – 10, n = 15). Immobilisation results are summarised in Tables 4.2 and 4.3.

Female F1 was the only female darted with a barbed telemetry dart, which had to be fired with a higher pressure, resulting in a hard impact (Table 4.4). Female F3 could not be approached closely, and after 300 min following was also darted with a higher-pressure setting and a collared dart (Table 4.4). M1, F2, M3, F4 and F5 were darted with a low-pressure settings (soft immobilizations), and had shorter habituation times than the two individuals darted harder, or cage captured (Table 4.4).

F1 and M1 were allowed to recover in closed crates. F1 was given a light dose of Zoletil, and was fully alert for many hours in the crate prior to her release; her habituation took longer than expected (Table 4.4). F5 was allowed to recover in an open crate; she was habituated quickly (Table 4.4). F2, M3, F4 and F5 experienced open recoveries; they all had short habituation times. F3 was allowed to recover in the open, but while recovering she began retching, and we had to move closer to check on her state, including leaving and returning on two occasions later in her recovery; resulting in her habituation taking a longer time (Table 4.4).

Age did not affect habituation time (Pearson Correlation: $r = -0.231$, $n = 6$, $p = 0.659$). The last three leopard habituated were amongst the oldest and quickest to habituate. Whether a collar or implant was used did not affect habituation time (Mann-Whitney: $z = -1.528$, $n = 3$, $P = 0.2$).

Vegetation and terrain is likely to influence the probability of observing leopard and should have had a large impact on how quickly and easily each leopard was habituated. This, however, was not reflected in the results as habituation was accelerated during consortship with the habituated male when the pair was followed continuously for up to 4 days (Table 4.4). Leopard in dense riverine vegetation were difficult to get close enough to view, while leopards followed in more open habitat

were more likely to be seen, as they could be observed from greater distances. However, they were more skittish and would initially seek the refuge of drainage lines and thicker vegetation and elevated positions like termite mounds. Once relocated, they could be approached slowly and viewed. Statistical analysis was not possible as only two of the seven leopards had mainly open vegetation in their territories.

Visual observation of leopards was obtained on average 1 ± 0.8 day (range 0 – 6, $n = 7$) post immobilisation. The effort expended to obtain visual was 134 ± 96 min (range 15 – 708, $n = 7$). During habituation, direct observation was achieved on 5 ± 1.4 days (range 1- 12, $n = 7$) of the 13 ± 5 days (range 1 – 37, $n = 7$) that leopards were followed (as described in the habituation method). Direct observation of leopards was obtained on average 41 % of the time (Table 4.5). The average time (following and viewing) from immobilisation for a leopard to become habituated to being viewed from 20 m for 20 min was 17.3 ± 6.3 h (range 3- 43, $n = 7$) during 13 ± 5 days (range 1 – 37, $n = 7$) (Table 4.5). However, leopard at the beginning of the study which underwent more stressful immobilisations took longer to habituate. If F1 and F3 were excluded, the average time to habituation was 7.7 ± 1.5 h (range 3 – 11.8, $n = 5$).

The presence of a habituated male during initial immobilisation had no significant effect on darting time (mins) (Mann – Whitney U – test: $z = -0.318$, $n = 5$ single and $n = 5$ with male, $p = 0.750$). The time taken to immobilise a leopard a second time post habituation was significantly lower (Wilcoxon signed rank test $z = -3.411$, $n = 5$, $p = 0.001$). The average distance travelled for the second immobilisation was half that of initial immobilisations, but this was not significantly different (Wilcoxon signed rank test $z = -0.177$, $n = 6$, $p = 0.860$). Leopards tended to be significantly closer to the vehicle when darted a second time (Wilcoxon signed rank test $z = -3.413$, $n = 5$, $p = 0.001$). The distance that the leopard had moved from its place of recovery post immobilisation to the following morning was significantly shorter for second immobilisations (Wilcoxon signed rank test $z = -3.071$, $n = 4$, $p = 0.002$).

Veterinary costs of darting leopards was on average $\$370 \pm 132$ (range = $\$43 - \2059 , $n = 15$) (Table 4.6). This cost depended on the ease with which the leopard was darted (see Table 4.6). The average cost to habituate a leopard to 20 m for 20 min was $\$593 \pm 222$ (range = $\$45 - \1651 , $n = 7$) (Table 4.6).

4.5 Discussion

Our results illustrate that free darting leopard is achievable, and that it is possible to habituate leopard in an area where they were previously persecuted, over a relatively short period. The success of the

free darting method was the result of immobilising, radio tagging and habituating the male first. Females attracted to males during consortships lasting 68 h (Owen *et al.* 2010) could then be followed using the signal from the male, allowing the pair to remain in view until the vet arrived, and enable a soft and quiet immobilisation. The same could be achieved if a female was darted first to capture a male. Although the presence of the habituated male had no significant effect on darting time, a crucial element was to be able to follow the un-habituated leopard to an open area attempting to get within 20 m to immobilise softly and safely. This took from 60 - 300 min for females, and 720 min for M3 over four separate nights using traditional tracking methods. M2 was quick as he was located in a thicket surrounded by open area where he stayed until darted. Free darting can be achieved in a variety of conservation areas as well as areas where leopards were previously persecuted. More time and patience may be necessary in some areas than others.

To prevent aversion conditioning and to decrease habituation time, it is imperative to avoid any negative or painful stimulus during the capture, handling and habituation process (Eibl-Eibesfeldt 1970, Hunt 1984, Domjan 2003, Rauer *et al.* 2003, Kloppers *et al.* 2005). Elements of immobilisation that negatively affected habituation were any negative incidents occurring while the leopard was not under the disassociative effect of Zoletil (Janovsky *et al.* 2000). Note that radio tagging is not necessary for habituation of leopard, as this has been successfully achieved through regular viewing over an extended period in tourism destinations in South Africa without the use of radio tags (Hancock 2000). For this research study, radio tagging was essential to allow the concurrent ecological study to progress, and to impact minimally while enabling leopards to be followed for extended periods. By doing so we were able to not only locate the leopard using the radio signals, but could visually observe them continuously, for example over the entire courtship period, thereby providing a unique dataset for understanding leopard biology and management (Owen *et al.* 2010).

Although generalisation of our results is constrained by the small sample sizes and confounding variables, our study highlights certain elements that may affect the ease with which habituation occurs. The components important to the habituation process included: the capture method, recovery, and post-capture monitoring. Habituation of leopard handled sensitively can be achieved in less than 8 h of follow-up investment.

Wildlife habituation has two facets, the negative, associated with the problems society and wildlife accrue, presented in abundant professional and popular literature. These include human wildlife conflict and the dangers associated with habituation (Hunter 1998, Herrero *et al.* 2005, Michalski *et al.* 2006, Cahill *et al.* 2012), the effects of recreational activities on wildlife (Burger 1981, Henson & Grant 1991, Fernandez & Azkona 1993, Holmes *et al.* 1994, Steidl & Anthony 1996, Steidl & Anothy 2000, Mann *et al.* 2002, Johnson *et al.* 2005, Steven *et al.* 2011), the effect increasing tourism has on

increased energetic stresses (Bélanger & Bédard 1990, Houston *et al.* 2011, Thiel *et al.* 2011), changes in activity budgets (Steidl & Anothy 2000, Swarthout & Steidl 2001, Mann *et al.* 2002, Swarthout & Steidl 2003, Johnson *et al.* 2005, Houston *et al.* 2011), displacement from preferred environments (McGarigal *et al.* 1991, Velando & Munilla 2011), and reduced productivity through abandonment and decreased survival of young (Tremblay & Ellison 1979, White & Thurow 1985, Müllner 2004). There is also concern that leopard movements are not restricted by fenced boundaries and they rely on their elusive behaviour to survive outside protected areas. The consequence of habituation on long-term survival has not been studied, and should be discouraged in threatened or endangered leopard populations, such as in high hunting or livestock farming areas (Balme & Hunter 2004). These aspects are worthy of further investigation.

The positive benefits of habituation are represented by the numerous research studies of animal behaviour that have been hugely augmented by the use of habituated wildlife (Packer *et al.* 1990, Clutton-Brock *et al.* 1999, Stokes & Parnell 2003, Herbst. & Mills 2010). Habituation is often beneficial to animals, as it allows them to focus more strongly on stimuli that are associated with actual positive or negative effects (Whittaker & Knight 1998). Habituated wildlife promotes viewing which, in turn, may promote conservation of their populations, habitats, and ecosystems (Herrero *et al.* 2005, Debruyne and Smith 2009).

When considering an immobilisation and habituation programme wildlife researchers need to assess each situation carefully to ensure the conservation and protection of the target species and evaluate human safety (Riley *et al.* 2002, Juarez *et al.* 2011). With increasing human/wildlife interaction, wildlife conflict is becoming a major concern in many countries and wildlife habituation has frequently been maligned as dangerous (Herrero *et al.* 2005, Michalski *et al.* 2006). Human-wildlife conflicts are ascribed to habituation, when in reality, over-habituation and attraction behaviour with food conditioning are the causes of most of these predator-human conflicts (Aumiller & Matt 1994, Hile 2003, Kloppers *et al.* 2005). This, combined with humans approaching leopard too closely, results in predator-human conflict (Aumiller & Matt 1994, Olliff & Caslick 2003) and occasionally to tourists being killed (Hunter 1998, Olliff & Caslick 2003). We do caution against over-habituation where the natural barriers between animals and humans are broken, and, for example, contact with vehicles occurs. We recommend that where habituation of leopard does take place, a distance no closer than 20 m be maintained as the habituation goal to prevent over-habituation. While further distance would be preferable, where vegetation is dense this may not be possible. Habituation as such is neither good nor bad. Rather, the value (negative or positive) of habituation to both people and wildlife depends upon context and perception. The need to capture and habituate wild animals to facilitate research can be justified, provided the benefits do not exceed ethical, ecological, social and economic costs (Gill 2002, Juarez *et al.* 2011).

Table 4.1. A summary of leopard immobilisations on Karongwe Private Game Reserve

Initial immobilisation	End of subject's study	ID code	Comments
Feb-00	Aug-04	M1	Darted and implanted
Jun-01	Feb-04	F1	Darted and collared
Aug-01	Aug-04	F2	Darted and collared
Oct-01	Aug-04	F3	Darted and collared
Jan-02	Aug-03	F4	Darted but could not find her
Feb-02	Mar-04	F5	Darted and implanted. Reception poor
Oct-02	Aug-03	M3	Darted and implanted

Subsequent immobilisation	ID code	Comments
Feb-02	F4	Re-darted and collared. She removed her collar
Jul-02	M1	Re-darted and implanted
Nov-02	F1	Re-darted, dart failed to inject
Dec-02	F1	Re-darted and collared
Dec-02	F2	Re-darted and collared
May-03	F3	Re-darted and collared
May-03	F4	Re-darted and implanted

Table 4.2. The effort required and the reaction of leopards when first-time free-darting immobilisations were undertaken on the Karongwe Game Reserve from February 2001 to October 2002.

First immobilisation	M1	F1	F2	F3	M2	F4	F5	M3	Average \pm SE	Median
No. nights spent trying to dart	1	1	1	1	1	1	1	4	1.4 \pm 0.4	1
Distance travelled from initial visual until immobilisation (km)	1	1.5	2	3	0	2	1	10	2.6 \pm 1.1	1.75
Time spent following leopards until darted (min)	60	120	90	300	15	60	120	720	186 \pm 82	105
Amount of Zoletil used (mg)	250	200	200	250	300	250	250	300	250 \pm 13.4	250
Distance darted from (m)	15	20	20	30	15	20	10	30	20 \pm 2.5	20
Time spent recovering subject post darting (min) ^a	0	0	0	0	55	*	0	0	7 \pm 7.9	0
Distance leopard moved once darted (m)	40	100	100	200	100	*	20	100	82.5 \pm 21.7	100
Direction of leopard movement once darted	S	C	N	S	S	C*	N	S	-	-
Distance moved post recovery to location the following day (m)	900	2500	?	1000	2000 #	*	800	500	962.5 \pm 350	950

0= visual was maintained and therefore no searching was required

^a if visual was lost after immobilisation, searching only began after 10 min and the zoletil had taken effect

* Individual could not be located once darted, no further information available

distance moved until the collar came off

Movement: (S) after darting the leopard travelled in the same direction as it was originally travelling,

(C) circled and came back to the point of darting, (C*) the leopard circled but was never located, (N)

no movement, ? unknown as the leopard was not located the following day.

Table 4.3. The effort required and the reaction of leopard during subsequent immobilisations on the Karongwe Game Reserve from February 2002 to May 2003. Data for F0 were excluded from the table due to dissimilar capture method.

Second immobilisation	F4	F4	M1	F1	F1	F2	F3	Average \pm SE	Median
No. nights spent trying to dart	1	1	1	1	2*	1	1	1.1 \pm 0.1	1
Distance traveled from initial visual until immobilisation (km)	1	2	0	0.3	0.1	4♦	1	1.2 \pm 0.5	1
Time spent following leopards until darted (min)	128	60	15	15	60	45	135	65.4 \pm 18.5	60
Amount of Zoletil used (mg)	200	200	300	250	250	250	300	250 \pm 15.4	250
Distance darted from (m)	20	25	10	15	15	12	20	16.7 \pm 2	15
Time spent recovering subject post darting (min) ^a	0	30	0	>	0	0	0	4.3 \pm 5	0
Distance leopard moved once darted (m)	80	130	2	>	100	50	40	57.4 \pm 18.7	65
Direction of leopard movement once darted	S	S	N	S	S	K	S	-	
Distance moved post recovery to location the following day (m)	1000	0 #	300	>	1500	N	50	407 \pm 331	650

* the female was followed for 2 nights as she was not with her cubs and it was the cubs that were required for veterinary purposes while her collar was changed

◆ hunting and difficult to get close to but when she caught a wildebeest she was easy to dart

0= visual was maintained and therefore no searching was required

^a if visual was lost after immobilisation, searching only began after 10 min and the zoletil had taken effect

distance moved until the collar came off

> dart failed to discharge therefore no recovery data available

Direction: (S) after darting the leopard travelled in the same direction as it was originally travelling,

(N) no movement, (K) feeding on a kill and therefore no movement.

Table 4.4. The effect of the darting process, recovery, territorial habitat type, age of the leopard and transmitter type, on the ease of leopard habituation. Data for F0 were excluded from the table due to dissimilar capture method.

Leopard	Time taken during immobilisation: an indication of initial habituation	Time taken from first visual post immobilisation to habituation (hours)	Elements affecting habituation					
			Ease of habituation ranked according to the no. of hours taken to habituate	Type of darting experienced by the leopard	Type of recovery	Habitat type territories located in	Age (years)	Type of radio transmitter
F1	120	43	7	Hard *	Crate	Riverine	2	Collar
F3	300	40	6	Hard^	Open □	Riverine	5	Collar
M1	60	11.75	5	Soft	Crate ◇	Both	3	Implant
F2	90	9	4	Soft	Open	Open	2.5	Collar
M3	720	9	3	Soft	Open	Riverine	3.5	Implant
F4	60	5.5	2	Soft ≠	Open	Riverine	3	Implant
F5	120	3 +	1	Soft	Crate open	Riverine	4.5	Implant

Leopards were ranked by hours to habituation. One hour was the quickest time and seven the longest

* Telemetry dart used with a barbed needle

^ Darted with high gas pressure

≠ Darted three times

□ Vehicle activity while waking up

◇ Was still under the effect of the drugs while in the crate

+ F5 was followed for 26 h30 during the reproductive study prior to being darted as the veterinarian was unavailable.

Table 4.5. Effort required when habituating seven leopards to 20 m for 20 min post immobilisation on the Karongwe Game Reserve

	Leopard							Average ± SE
	F5	F4	M3	F2	M1	F3	F1	
Time spent with the leopards to achieve habituation (h)	3	5.5	9	9	11.75	40	43	17.3 ± 6.3
No. of days spent with the leopards to habituate post immobilisation	1	2	9	12	7	25	37	13 ± 5
No. of days followed before first visual #	0	0	1	0	0	6	1	1 ± 0.8
No. of days visual observation was obtained during habituation	1	2	4	6	5	8	12	5 ± 1.4
Percentage of those days visual observation was obtained during habituation	100%	100%	44%	50%	71%	32%	32%	41%

A value of 0 indicates the individuals were seen on the first day they were followed

F1 was darted hard with a barbed dart and recovered in a crate

F3 recovered with a vehicle and people around her

F4 was darted three times before we could begin habituation

+ F5 was followed for 26h30 during the reproductive study prior to being darted as the veterinarian was unavailable.

Table 4.6 Costs of darting, fitting transmitters and habituating leopard on the Karongwe Game Reserve.

Leopard	Time to dart leopard from first visual by the veterinarian (min)	Veterinarian darting fees ^(a)	Costs of darting and consumables	Darting transmitter and consumables	Costs of darting, transmitter, consumables, implantation ^(b) and post operative feeding	Habituation costs ^(c)	Total cost
M1	60	\$172	\$330	\$861	\$1,325	\$312	\$1,637
F1	120	\$343	\$502	\$1,032	-	\$1,651	\$2,683
F2	90	\$257	\$416	\$947	-	\$535	\$1,482
F3	300	\$858	\$1,016	\$1,547	-	\$1,116	\$2,663
M2	15	\$43	\$201	\$732	-	-	\$732
F4	60	\$172	\$330	\$861	-	\$89	\$950
F5	120	\$343	\$502	\$1,032	\$1,454	\$45	\$1,498
M3	720	\$2,059	\$2,218	\$2,748	\$3,154	\$402	\$3,555
F4	128	\$366	\$525	\$1,055	-	-	\$1,055
F4	60	\$172	\$330	\$861	-	-	\$861
M1	15	\$43	\$201	\$732	\$1,145	-	\$1,145
F1	15	\$43	\$201	\$732	-	-	\$732
F1	60	\$172	\$330	\$861	-	-	\$861
F2	45	\$129	\$287	\$818	-	-	\$818
F3	135	\$386	\$545	\$1,075	-	-	\$1,075
Average	130	\$370	\$529	\$1,060	\$1,769	\$593	\$1,450
± SE	± 46	± 132	± 132	± 132	± 466	± 222	± 221

^a Veterinarian time per hour: \$171.60

^b Surgery costs include professional time per hour: \$171.60 and surgical consumables: \$71.37
(\$ 328.77 for an hour and a half surgery)

Darting consumables (Total = \$158.46): Sedative (\$68.50); Dart (\$33.33) when not reused; Front line (\$15.44); Dectomax (\$0.65); Kyrovite B co (\$3.00); Bovaclox DC (\$2.55); Rabies vaccination (\$1.76); Fel-O-Vax (\$1.88); Atropine sulphate (\$24.38); Eye cream per tube (\$5.35); Syringe and needle (\$1.62).

Transmitter costs \$ 531

Costs exclude veterinarian travel to the reserve (\$0.68 per km: \$43.35), travel to and from each leopard, actively looking for the leopard in the reserve and staff costs.

^c Habituation costs per = \$ 44.62 per day and calculated as \$ 15 salary, and 80 km a day at \$ 0.37 per km which covers vehicle maintenance and fuel.

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CHAPTER 5

PRINCIPAL PREY OF LEOPARD AND THEIR HUNTING HABITAT SELECTION, IN A SMALL ENCLOSED RESERVE

5.1 Abstract

Foraging ecology is fundamental in determining predator fitness, population density, reproductive success, territoriality, and impacts on prey, all of which affect overall ecology, and wildlife conservation and management. Here we examine the feeding ecology and hunting habitat selection of leopard on Karongwe, a small (85 km²), enclosed game reserve with super-abundant prey. Using ungulate kill data (364) from seven leopards, collected over a four-year period, we examine leopard prey consumption, prey species selection, and their prey preference. The prey-rich environment translated into leopard consuming double the amount of kills, compared with similar habitats elsewhere. Although leopards are generalist feeders, they did select for prey vulnerability by species (common duiker, bushbuck and warthog), age (juveniles), group size (solitary, pair and small groups) and sex (females). Impala, the most abundant prey species on the reserve, were the principal prey (53%), but only had a low preference rating. Leopard on KGR were hunting habitat generalists, hunting in all available habitats. Their hunting distribution matched their prey resources; hunting preferably in riverine habitat, where prey was most abundant or easier to hunt. Feeding generalists can stabilise an ecosystem, but their selection pressure, combined with heavy consumption, is likely to reduce species richness in a small, enclosed reserve, and needs to be carefully managed.

5.2 Introduction

Foraging ecology of large carnivores explains predator survival and success, and has important ecological consequence for other species, making it important for both wildlife conservation and management (Bekoff *et al.* 1984, Kruuk 1986, Sunquist & Sunquist 1989, Glen & Dickman 2005). What predators select to eat improves their fitness (Pyke 1984, Steven 2012), determines reproductive success (Owen *et al.* 2010), influences population density (Boyce 1989), and impacts on the life histories of their prey (Mills 1992, Gervasi *et al.* 2012, Mejlgaard *et al.* 2012). The study of resource selection is a complex ecological area because of the range of selection decisions by both predators and prey, reflecting the variation in resources on which each species depends (Sih 1987, Lima & Dill 1990).

Strategies by large carnivores aim to maximise nutrient intake, selecting prey by their size (Hayward & Hayward 2009, Ramesh *et al.* 2012), age, sex, abundance (Sunquist & Sunquist 1997, Mejlgaard *et*

al. 2012), temporal and spatial distribution (Abrams 2007), and anti-predator tactics (Hopcraft *et al.* 2005, Balme *et al.* 2007). Drivers for ungulate habitat selection are meeting resource requirements (Ben-Shahar & Skinner 1988, Compton *et al.* 2002, Shannon *et al.* 2013), and reducing predation risk by avoiding high-risk habitats (Lima 1998, Valeix *et al.* 2009, Thaker *et al.* 2011).

Predators have been shown to exert disproportionate selection pressures on prey biomass, and can have a disturbing effect on both individual species and the system as a whole (Johnson 1980, Thaker *et al.* 2011). Specialist predators consuming a single prey species are able to improve prey coexistence by impacting the abundance of one species, thereby enabling non-target species to exploit the available resources (Payton *et al.* 2002). Generalist predators have a varied and extensive influence on ungulate communities (Snyder & Wise 2001). A single generalist acts like a group of specialists in enhancing prey coexistence, so long as the predator ignores the prey species which are temporarily the rarest (Estes *et al.* 2001). If rare species are not ignored this could lead to local species extinction, of which there is a greater risk in small, enclosed reserves where resident prey populations are often at low densities, and where predators can regulate and even limit prey (Power 2002).

Leopards (*Panthera pardus*) are solitary, generalist, opportunistic predators (Skinner & Smithers 1990, Nowell & Jackson 1996) and their catholic diet suggests they are largely unselective. However, they do select prey species weighing 10–40 kg (Hayward *et al.* 2006), as well as selecting their hunting habitat (Balme *et al.* 2007).

Spatial distribution in animals is seldom homogenous, and understanding predators' hunting distribution, and their prey's habitat selection, is crucial in small, enclosed systems where movement is restricted. Predators have been shown to select hunting habitats where energy intake requirements can be met while expending minimum energy (Balme *et al.* 2007), while Lima (2002) suggests that predator distributions should match their prey's resources, and prey distributions should reflect their habitat riskiness (Hugie & Dill 1994, Sih 1998, Thaker *et al.* 2011).

Predators fulfill a vital role in influencing prey numbers; however, this needs to be managed on small, enclosed reserves where certain species of prey are at low densities and where predators can regulate and even limit prey (Power 2002). Large predators fill several crucial roles of regulating mesopredators (Crooks & Soulé 1999, Johnson & Vanderwal 2009), provisioning for scavengers (Wilmers *et al.* 2003) and herbivore regulation (Hopcraft *et al.* 2010), and the disappearance of apex predators from an environment can result in trophic cascades (Pace *et al.* 1999, Sergio *et al.* 2008).

Karongwe Game Reserve is a small reserve with superabundant resources, and its well-studied leopard population (Owen *et al.* 2010) provides an ideal context to assess predation patterns of large

predators. I hypothesized that leopard would select to hunt small, young, vulnerable prey in dense vegetation as they are generally perceived as ambush predators. This paper aims to provide insight into leopard foraging ecology in a small, enclosed reserve, and the ecological ramifications that affect their conservation and management. Our specific objectives were to: (1) identify the principal prey species of leopard and calculate prey biomass removal, (2) quantify kill frequency in each habitat, (3) identify leopard prey selection with respect to species, size, age or sex, (4) determine habitat selection of principle prey species and (5) ascertain whether leopard hunting habitat selection matched selection by their principal prey. I hypothesized that leopard would select to hunt small, young vulnerable prey in dense vegetation as they are generally perceived as ambush predators.

5.3 Methods

5.3.1 Study area

Field work was conducted on the 85-km² Karongwe Private Game Reserve, Limpopo Province, South Africa (24°13'S; 30°36'E) (see Thaker *et al.* 2011 for a vegetation map and waterholes on the reserve). The reserve was formed in 1998 as an ecotourism reserve. A 2.4-m-high electrified perimeter fence was erected to contain several charismatic wildlife species such as lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), spotted hyaena (*Crocuta crocuta*), elephant (*Loxodonta africana*), and 12 ungulate prey species, but was permeable to leopard (Owen *et al.* 2010). Leopard on Karongwe persisted during years of persecution preceding the formation of the conservancy in 1999, following which they were fully protected while in the reserve. Karongwe is located within the savannah biome (Rutherford & Westfall 2003) and lies within the Mixed Lowveld Bushveld (Low & Rebelo 1998). The study area was characterized by hot, rainy summers and warm dry winters, and received an average annual precipitation of 487 mm. We used a habitat map of Karongwe that consisted of the following physiognomic classes: Closed riverine (1.6% of area), consisting of gallery forests along rivers; Open riverine (15.8%), consisting of open canopy forest with thick under story along rivers and drainage lines; Closed woodland (54.4%), consisting mainly of *Combretum* and *Mopane* woodlands with closed tree canopies; Open woodland (24.1%), consisting mainly of *Acacia* with separated tree canopies; and Open scrub (4.1%), consisting of old agricultural lands now reverting to open scrub habitat (Thaker *et al.* 2011).

5.3.2 Ungulate presence

Ungulate species were censused annually in the dry season September (2001- 2005) by aerial counts undertaken in a Bell Jet Ranger helicopter with four observers (including the pilot) and one data capturer. Using a GPS-aided computer, 300m wide strips were flown throughout the reserve. Counts began in the early morning (between 7:30 and 9:00), and were completed within a day. A data capture

program “Capture”, written by Mark Schormann, was used to plot the location of the animals, reducing the chance of duplicate counting. Wet season (summer) ungulate presence and distribution was determined using road strip census procedures in summer months (Hirst 1969). Each of the five drive counts were sampled for five consecutive days: 26 – 30 April 2004, 29 November – 3 December 2004, 16 – 20 March 2005, 3 – 7 December 2005, 12 – 16 December 2005 (Thaker *et al.* 2011). Ungulate locations were georeferenced, and intersected with the habitat map using ARCGIS 9.3 (Environmental Systems Research Institute, Redlands, California) (Hooge *et al.* 1999), thereby assigning a habitat to each ungulate location.

Herbivore mean biomass was calculated according to Coe *et al.* (1976), for the survey years 1999-2005. Karongwe herbivore mean biomass was 4064 kg/ km² (*SE*= 938, range 3703- 4532). Mean biomass across years was above the Coe *et al.* (1976) predicted mean for Karongwe (2789 kg/ km²) at which the herbivore biomass should be stocked, and, even at its lowest density, was greater than the maximum recommended (3681 kg/ km²) for that area (Coe *et al.* 1976).

Ungulate biomass killed was calculated using live body mass of prey species obtained from the literature (Bothma 1996). The edible percentage of carcass mass was estimated from live prey body masses (<50 kg: 80%; 50–150 kg: 75%; 151–250 kg: 70%; 251–500 kg: 65% (Viljoen 1993), and the inedible portion subtracted. Annual biomass consumption was calculated using, edible weight (kg) killed per leopard per year (Mills & Biggs 1993).

5.3.3 Field data collection

We studied seven radio-collared leopard (two adult males and five adult females) over a five-year period (October 2001 to October 2005), totaling 1819 field days (Owen *et al.* 2010). We collected diurnal and nocturnal locations for all leopards between 05.30 h and 20.30 with intermittent continuous monitoring from 2 – 96 h at a time (Owen *et al.* 2010). Standard radio telemetry tracking methods were used (Mills 1996). A leopard database, maintained from 1999-2006, identified individuals by the spot pattern on their face and neck as well as facial features such as scars and ear tears, with each assigned a letter designating sex (F = female and M = male) and a unique number. Photographs were used to assist in the accurate construction of identikits. The sire and mother of cubs were determined during intensive following (Owen *et al.* 2010). Un-collared subadults were monitored by opportunistic sightings. We used the minimum count method with recognizable individuals, in conjunction with territorial mapping in the global information system (ArcGIS 9.3, Environmental Systems Research Institute, Redlands, California), tracks, and radio telemetry to determine population size (Kunkel *et al.* 2005, Owen *et al.* 2010).

When a leopard was located feeding on or near a carcass, the species, age class, and gender were noted using set ageing and sexing criteria (McBride 1984, Karanth & Sunquist 1992). Age was determined as birth to one year = fawn; 1 to 2 Years = Sub adult; > 2 = adult. Where a leopard (excluding lactating females) remained in the same location for two or more days, and visual observation was not possible, the area was searched for carcass remains once the leopard had moved off. We followed leopards to observe hunting behaviour and kills as they occurred (Balme *et al.* 2007). At each sighting, we recorded belly scores (Ginsberg *et al.* 1997) (one = very thin, to five = belly fully distended) to determine when the leopards were due to hunt, and to correct for missed feedings when estimating kill frequency and biomass removal. Kill rate was calculated using a spreadsheet of individual leopards daily belly scores and kills. Substantial belly score increases of at least one point on the scale, in the absence of a recorded kill, were an indication of a kill having taken place (Lehmann *et al.* 2008). Although small kills would be missed, it provided a more accurate indication of the actual number of kills made per annum. We assigned habitat of leopard kill locations in ARCGIS as per ungulate locations.

5.3.4 *Leopard diet selection*

Leopard diet selection was calculated using Jacobs' index, where p was the annual proportional abundance of that species in the total prey population, and r was the annual relative proportion that each species made up of the total leopard kills (Jacobs 1974).

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

The resulting value ranged from +1 to -1, indicating maximum preference (+1) and maximum avoidance (-1) (Jacobs 1974). If a species was killed more frequently than its relative abundance, then it was considered preferred. Significance of prey preference analyses and all subsequent tests was determined using χ^2 [chi-squared] at $P < 0.05$. Data were tested for the assumptions of normality and normalised when required (Kolmogorov–Smirnov and Lilliefors test).

5.3.5 *Habitat selection*

We derived habitat use from animal locations. Using Jacobs' index, ungulate habitat selection and leopard hunting habitat selection were calculated for each sampling habitat (Closed riverine, open riverine, closed woodland, open woodland and open scrub), and year (Y1 to Y5) (Jacobs 1974).

5.4 Results

Kill data from two male (173 kills recorded) and five female (286 kills recorded) leopard included 361 ungulate kills. Of the 24 species recorded, 12 were ungulate prey species. Seven species (n = 346 identified carcasses) constituted 99% of the leopards' ungulate diet (n = 361) (Table 5.1). Impala (*Aepyceros melampus*) was the most important species, comprising the greatest proportion of their diet (52%, n= 187), followed by warthog (*Phacochoerus aethiopicus*) (13%, n= 48), waterbuck (*Kobus ellipsiprymnus*) (9%, n= 31), bushbuck (*Tragelaphus scriptus*) (8%, n= 29) and common duiker (*Sylvicapra Grimmia*) (6%, n= 23) (Table 5.1). Impala were consumed significantly more than other species ($\chi^2 = 9.9$, d.f. = 1, P = 0.001). Ungulates in the reserve occurred in the ratio of 67% females to 33% males and 67% adult to 33% juveniles (0-2 yrs). Leopard killed significantly more females across species, with 73% of prey being females (n= 228) ($\chi^2 = 4.0$, d.f. = 1, P = 0.04). Leopard selection for juvenile prey was significantly greater than the ratio of juveniles in the population ($\chi^2 = 8.7$, d.f. = 1, P = 0.003), with juveniles making up 41% (n = 133) of kills categorised into an age class (n = 327). This skew was the result of a relatively large number of juveniles of some large species being killed, with 89% of waterbuck killed (n = 25) being juvenile, 94% wildebeest (*Connochaetes taurinus*) being juvenile (n =15), and 58% kudu (*Tragelaphus strepsiceros*) being juvenile (n =7) (Table 5.1). Ninety-six percent of kills that were accurately categorised in an age class fell within the 15 to 60 kg range (Table 5.1).

Based on the aerial census figures, the trend was for a sharp decline in leopards preferred prey duiker, bushbuck, warthog, waterbuck and impala numbers during 2003 and 2004, when leopard numbers were at their peak (Table 5.2). Although leopard made up 40% of the predator population, it should be noted that leopard predation was not the only factor affecting prey number decline. A drought year with < 247 mm of rain in 2003 (long-term mean rainfall = 482 mm) could have had an important effect on ungulate numbers (Table 5.2).

Over the study period, 34 ± 4.3 prey items / leopard / year (range 21– 62, n = 7 leopard) were recorded. Average daily biomass consumption was 4 ± 0.7 kg / adult / day (range 1.8 – 7.5, n = 7). Calculating consumption using belly scores, only approximately 34% of total kills made were located during the study. A more accurate annual prey consumption including missed prey indicated by changes in belly scores was estimated at 99 ± 3.6 prey items / leopard / year (range 84 – 116, n = 7), with estimated daily biomass consumption using belly scores of 11 ± 1.3 kg / adult / day (range 7 – 19.4, n = 7).

Jacobs' index scores for the 12 species killed by leopard highlighted five species selected more than expected: common duiker 0.86, bushbuck 0.57, warthog 0.33, waterbuck 0.17 and impala 0.08 (Table

5.1). Each ungulate showed a preference for specific habitat types (Fig. 5.1). Impala, kudu and bushbuck preferred closed and open riverine. Warthog and duiker selected open scrub with warthog also selecting open riverine. Wildebeest and waterbuck selected open woodland with waterbuck also selecting closed riverine (Fig. 5.1). In general, the principal prey species of leopard selected riverine habitats avoiding open and closed woodland (Fig. 5.1).

Leopard hunting habitat selection matched their preys', preferring to hunt in riverine habitats, with the exception of wildebeest which were hunted in open woodland and duiker and waterbuck which were also hunted in closed woodland (Fig. 5.1). Habitat classes were ranked across the seven principal ungulate species from most to least selected. Closed riverine was ranked the highest followed by open riverine and open scrub. Open riverine ranked top in leopard hunting habitats followed by closed riverine and open scrub.

Leopard generally killed their prey in the proportion that they occurred in the different habitats ($\chi^2 = 4.08$, d.f. = 4, $P = 0.4$). The percentage of prey killed in each habitat type varied, in declining order of carcasses found: closed woodland (42 %), open woodland (24 %), open scrub (14 %), closed riverine (10 %) and open riverine (10 %). Leopards killed their three preferred prey species and kudu, in the same proportion to that of the habitat they primarily occurred in, while impala ($\chi^2 = 10.71$, d.f. = 4, $P = 0.03$), waterbuck ($\chi^2 = 13.49$, d.f. = 4, $P = 0.009$) and wildebeest ($\chi^2 = 17.77$, d.f. = 4, $P = 0.001$) were killed in significantly different proportions. Significantly, fewer impala were killed in closed riverine and open scrub habitat than expected, and more than expected were killed in open woodlands; fewer waterbuck were killed in open woodlands and more killed in closed riverine; fewer wildebeest were killed in closed woodlands and more were killed in open riverine (Fig 5.2).

Leopard hunting habitat selection generally matched ungulate habitat selection. Risky habitats for each ungulate species were identified as the habitat type where leopards successfully killed a greater proportion relative to their availability, and where these prey were more easily captured (Fig. 5.3). Important habitat for leopard hunting each species were: bushbuck in open scrub, duiker in open woodland, waterbuck in closed riverine, warthog in closed riverine, impala in open woodland, wildebeest in open riverine, and kudu in open woodland. All ungulates avoided risky habitats except warthog and waterbuck who showed a slight preference for closed riverine.

Safe habitats for each species were those habitats where leopard hunted each species at lower than expected rate: bushbuck were safer in closed and open riverine, duiker in open scrub, waterbuck in open woodland, warthog in open woodland, impala in closed riverine, wildebeest in closed woodland and kudu in open scrub (Fig. 5.3). Ungulates generally selected safe habitats with the exception of warthog and kudu.

5.5 Discussion

Our results support the hypothesis that prey distribution reflects habitat riskiness, and that predator distributions match their prey's resources (Lima 2002). Ungulate species on Karongwe reduced their probability of being killed by avoiding risky habitats and distributing themselves in safer habitats (Lima 2002, Balme *et al.* 2007, Thaker *et al.* 2011). Risky habitats for cryptic ungulates like bushbuck and kudu were more open habitats, while risky habitats for species like waterbuck and wildebeest were thicker riverine habitats. Leopard hunted where prey were abundant and preferring to hunt in thick riverine habitat (Bailey 1993, Hayward *et al.* 2006). The spatial patterns of ungulates like waterbuck, warthog and kudu which selected risky habitat in spite of its riskiness may be driven by the distribution of resources (Thaker *et al.* 2011).

What predators choose to eat, and their foraging success, influences all aspects of their lives as well as those of their prey (Litvaitis *et al.* 1986). Leopards on Karongwe were feeding generalists, and the diversity of prey killed was relatively high ($n = 24$ species). Our results, however, also corroborate the hypothesis that in prey-rich habitats, predators should be selective in maximising available energy (Griffiths 1975). Analysis of their diet suggests feeding specialisation, with leopards selectively hunting vulnerable individuals who displayed minimal anti-predatory defences (Hayward *et al.* 2006, Balme *et al.* 2007). Selective feeding was most significant with regard to prey size (Hayward *et al.* 2006). Although (male) leopard were capable of killing large prey (80 kg), the majority of leopard prey fell within the predicted weight range, 15-60 kg, with a preference for lighter prey (Hayward *et al.* 2006). Impala were the principal prey species of leopard (52% of kills) in their preferred weight range and are an important part of leopard feeding ecology. They were, however, under-represented in leopard selection because prey that were solitary or in small groups were preferred (Hayward *et al.* 2006). Leopards also selectively hunted females and juveniles, which could reduce both the breeding segment of the population and the future stock of reproductive females, and may disrupt the age structure, especially in rarer species (Milner *et al.* 2011).

Prey richness in the reserve translated into a daily consumption rate double that of leopards studied in similar habitats elsewhere (Bothma & le Riche 1986, Bailey 1993, Stander *et al.* 1997). This may be a combination of easy catchability due to high ungulate numbers, and the inability of herds to escape predation.

The combination of heavy consumption, selection for vulnerability and the continued removal of rare preferred species resulted in a reduction of leopard's top seven preferred species during the period of high leopard density. Leopard, however, were not the only predators, and reductions in prey numbers could have been exacerbated by the increasing predator numbers as well as low rainfall. Very intense

generalised predation with hunting selection for vulnerability, will almost certainly limited low-density populations, and reduce species richness, and this could have far-reaching repercussions for wildlife conservation and management, especially in small, enclosed reserves (Fryxell *et al.* 1988, Stewart 2006).

Although a large group of generalist predators can have a detrimental effect on an enclosed reserve, the removal of apex predator could equally indirectly influence the persistence of species several trophic levels removed (trophic cascade), by altering the composition and abundance of both ungulates and other predators, leading to shifts in competitive interactions (Ripple & Beschta 2003). This may endanger the persistence of inferior prey competitors. An overpopulation of ungulate species such as impala and warthog, in the absence of predators, could severely impact the vegetation and change the composition of the herbaceous layer (Wentzel *et al.* 1991). It is also likely that there would be a reduction in available carrion, as well as an increase in mesopredators, which large predators constrain (Estes *et al.* 2001).

Large carnivores at the apex of an ecosystem food chain are sensitive indicators of habitat quality (Joseph *et al.* 2007). It is therefore beneficial to investigate their fine-scale foraging ecology as many are also keystone species and play an important role in maintaining the health of the ecosystem (Crooks & Soulé 1999). Enhancing our understanding of apex predators' ecological requirements enables us to plan for their future conservation in an increasingly fragmented environment, made up of small, enclosed reserves which limit the free movement of ungulates.

Predator conservation and management require more and better data than are currently available and in-depth investigations into habitat preference, across both predators and their prey, are clearly called for. We encourage researchers working with large carnivores to examine the factors affecting hunting habitat selection in a range of areas and conditions, especially where rare or threatened prey species are concerned.

Table 5.1. Leopard (n = 7 individuals) kills in order of utilisation frequency, identifying preferred prey species and age classes targeted during the study (2001 - 2005). The top seven species in the table made up 99% of the leopard diet.

Species	Number of individual leopard killing each species	Jacobs index (\pm SE)	Published Jacobs index	Species abundance (Mean \pm SE)	% of each species killed of total kills	Quantity killed	Herbivore ages killed by leopard		
							0-1 years old	1-2 years old	Adult (> 2 years old)
Impala	7	0.08 \pm 0.08	0.36 \pm 0.08	1571 \pm 175	52	187	28	28	118
Warthog	7	0.33 \pm 0.09	-0.20 \pm 0.13	184 \pm 26.3	13	48	8	5	29
Waterbuck	7	0.17 \pm 0.05	-0.39 \pm 0.17	212 \pm 16.9	9	31	22	3	3
Bushbuck	6	0.57 \pm 0.07	0.45 \pm 0.12	79 \pm 22.3	8	29	1	5	17
Common Duiker	4	0.86 \pm 0.03	0.42 \pm 0.11	17 \pm 4.3	6	23	2	1	14
Blue Wildebeest	4	-0.31 \pm 0.08	-0.77 \pm 0.06	264 \pm 16.7	5	17	13	2	1
Kudu	3	-0.19 \pm 0.14	-0.31 \pm 0.12	152 \pm 7.9	4	13	6	1	5
Nyala	2	-0.40 \pm 0.26	-0.37 \pm 0.23	21 \pm 2.6	1	4	0	1	3
Red hartebeest	1	-0.71 \pm 0.20	-0.65 \pm 0.11	16 \pm 6.1	0	1	0	0	1
Steenbuck	1	-0.23 \pm 0.32	-0.18 \pm 0.18	6 \pm 2.5	1	2	0	0	2
Giraffe	1	-0.72 \pm 0.11	-0.95 \pm 0.05	77 \pm 3.5	1	2	2	0	0
zebra	1	-0.61 \pm 0.12	-0.80 \pm 0.06	178 \pm 7.5	2	6	3	2	1
							26%	15%	59%

+Indicates significantly preferred, - indicates significantly avoided. Details of published Jacobs's index derived from Hayward *et al.* (2006). Blue wildebeest (*Connochaetes taurinus*), Kudu (*Tragelaphus strepsiceros*), Nyala (*Tragelaphus angasii*), red hartebeest (*Alcelaphus buselaphus*), Steenbuck (*Raphicerus campestris*), Giraffe (*Giraffa camelopardalis*), Zebra (*Equus burchelli*).

Other latin names can be located in the text.

Table 5.2. Summary of game count figures and leopard population numbers in Karongwe Game Reserve, South Africa

Species	2000	2001	2002	2003	2004	2005	Average \pm SE
Common duiker	11	16	18	7	0	0	17 \pm 4.3
Bushbuck	58	96	127	56	14	21	79 \pm 22.3
Warthog	244	261	266	119	113	138	184 \pm 26.3
Waterbuck	254	231	205	185	149	185	212 \pm 16.9
Impala	1953	2140	1782	1252	930	1124	1571 \pm 175
Kudu	183	166	144	140	154	118	152 \pm 7.9
Blue wildebeest	282	239	321*	298	219	203	264 \pm 16.7
Leopard population	13	16	24	25	19	12	16 \pm 2.6

*75 additional wildebeest were introduced into the reserve in 2002.

Leopard population includes young

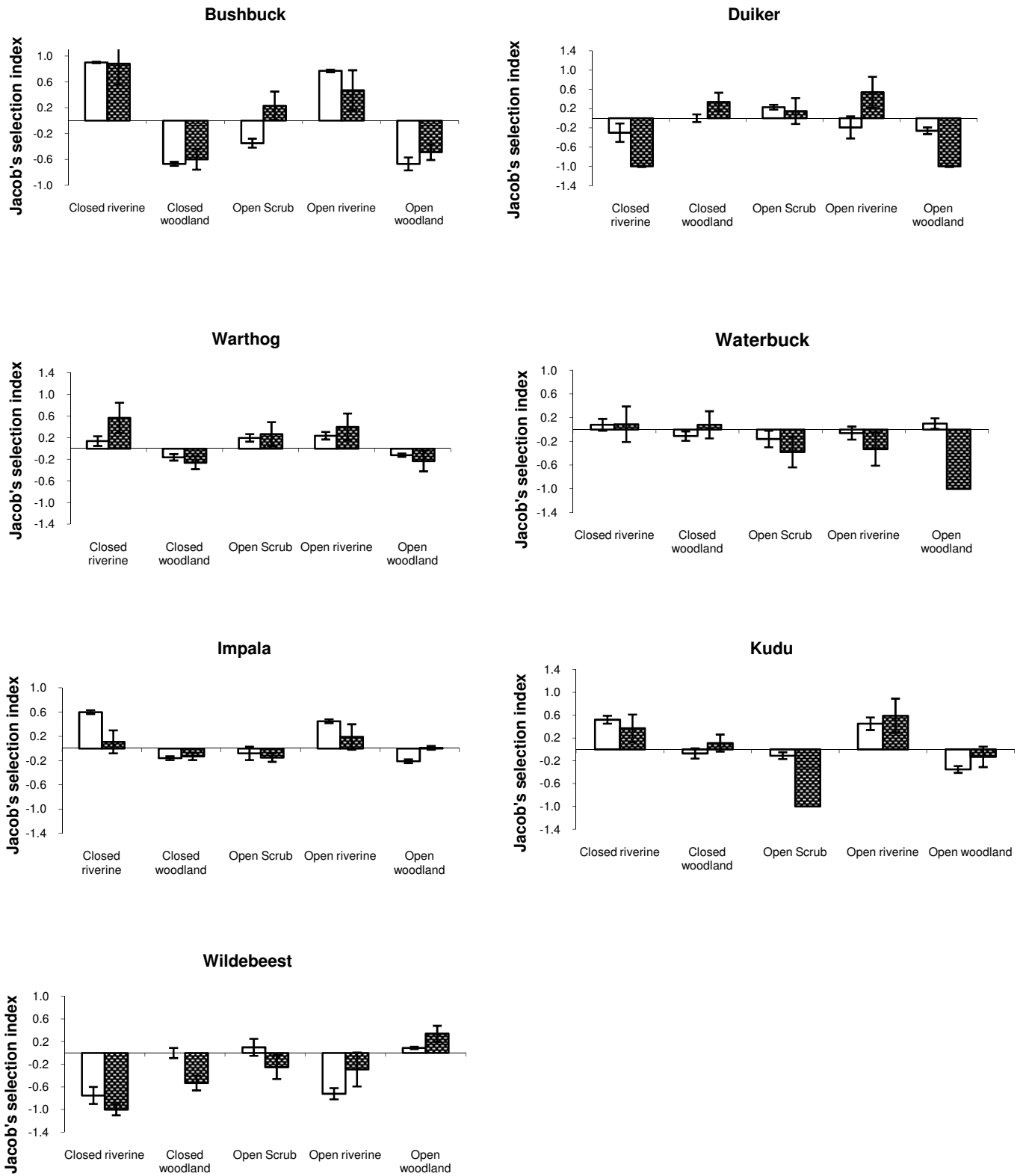


Figure 5.1. Ungulate habitat selection and leopard hunting habitat selection in the Karongwe Game Reserve, South Africa. +Indicates significantly preferred, -Indicates significantly avoided.

□ Ungulate habitat preference ▨ leopard hunting habitat preference. Mean ± SE.

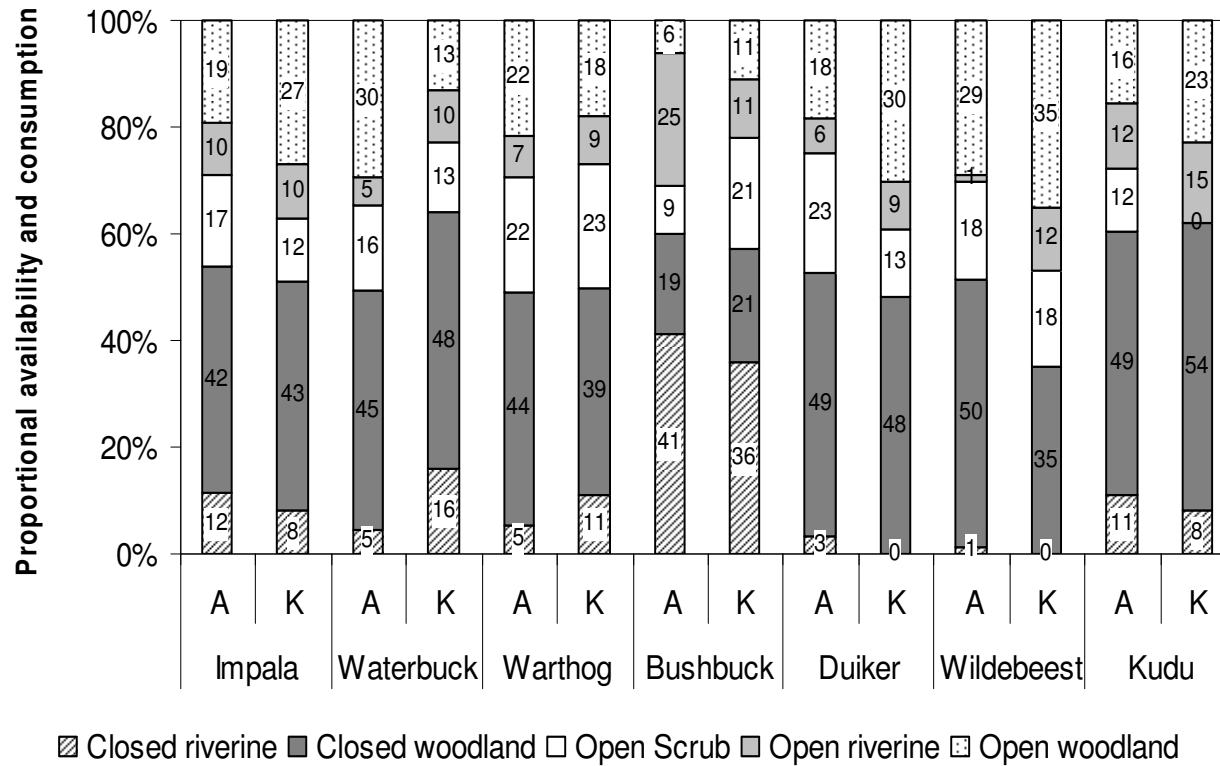


Figure 5.2. The proportional prey availability and actual consumption by leopard across different habitat types, indicating in which habitat each species was killed above availability. A = Available, K = killed and consumed. Numbers are sample size on which percentage was based.

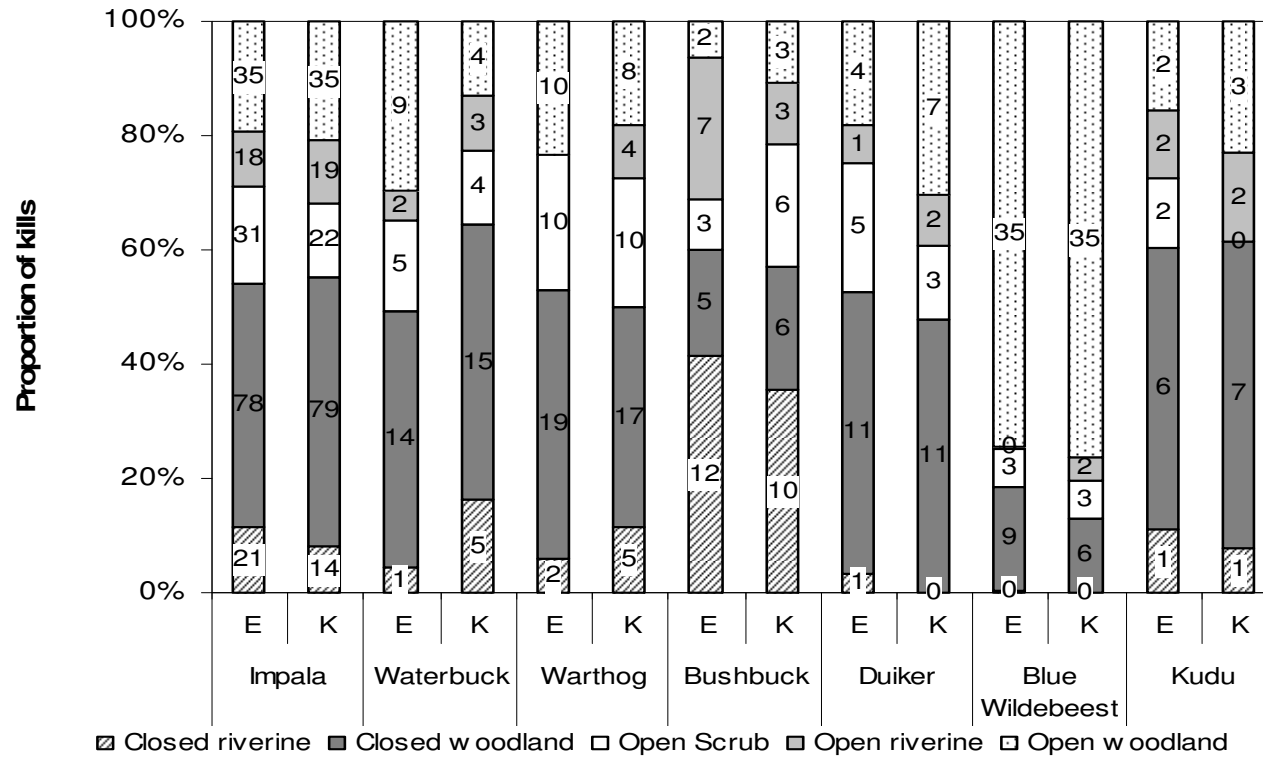


Figure 5.3. The effect of habitat type on predation of different species by leopard, showing the proportion of expected and actual prey consumed by leopard across different habitat types. It highlights which species were killed above what was expected in each habitat type, giving an indication of where each species is more vulnerable. E = Expected number killed, K = Actual number of kills in each habitat type. Numbers are sample size on which percentage was based.

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CHAPTER 6

COPULATORY PARAMETERS AND REPRODUCTIVE SUCCESS OF WILD LEOPARDS IN SOUTH AFRICA

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6.1 Abstract

Leopards (*Panthera pardus*) are a poorly understood, solitary felid, and additional study could provide novel insights into both evolution and conservation management. We studied the reproductive biology of seven adult female and two adult male leopards on Karongwe, South Africa, from 1999 to 2005. We intensively researched copulatory biology from 2001 – 2003, during which we observed 19 consortships and 4,855 copulations (1,809 copulations visually) during 2,449 h of following consort pairs. Leopards copulated on average 4 times per hour, with an average of 256 copulations per consortship. Conception rate was low, resulting, on average, after 2.3 consortships ($SE = 0.4$). All reproductive parameters except gestation length were shorter than those in published literature, which we suspect reflected a facultative response to superabundant resources. Although females produced the expected 1.6 cubs per year, lifetime reproductive rates on Karongwe Reserve were approximately half that reported elsewhere due to lower female survival resulting from intraspecific factors. These results offer encouragement for founding new populations of endangered felids in areas of high prey availability and resource abundance, provided factors affecting population regulation can be managed.

6.2 Introduction

Reproductive behaviour and mechanisms underlying reproductive success are particularly important because fitness is fundamentally a function of fecundity. The study of reproduction is therefore crucial to conserving species, populations, and indirectly to the vitality of entire ecosystems (Holt *et al.* 2003). Reproductive mechanisms are little understood in most species, with the exception of domestic livestock, a few other vertebrate species, and laboratory animals (Holt *et al.* 2003). Due to the secretive behaviour of large felids and the difficulty in obtaining visual observations, little is known of their basic reproductive parameters. Copulatory behaviour of leopards (*Panthera pardus*) has been the subject of little comprehensive research. Published accounts include a single mounting (Schaller 1972, Holt *et al.* 2003), a brief glimpse of a copulating pair (Hamilton 1976), and 13 copulations during one-half hour in the Serengeti (Laman & Knott 1997). Although reproductive parameters (oestrous cycle, gestation, lactational anovulation, and puberty) are better understood, published results are restricted to a handful of studies (Schaller 1972, Le Roux & Skinner 1989,

Bailey 1993). Several captive studies at zoos have been undertaken (Sadlier 1966, Eaton 1977, Schmidt *et al.* 1979, Shoemaker 1983), but none of these contain sufficient data on reproduction to provide conclusive insights into copulation and reproductive output.

It generally is accepted that nine subspecies of leopard exist (Wozencraft 2005). All are considered endangered or extinct with the exception of *Panthera pardus pardus*, which is widespread over nearly all of Africa south of the Sahara and over the greater part of southern Asia, including the Malayan peninsula and Java. Historically, population declines were due to hunting for the fur trade. Currently, hunting of the species continues, and populations are threatened by habitat loss and fragmentation due to land conversion for agriculture and urban development (Daly *et al.* 2005).

Comprehensive reproductive data of this subspecies (*P. p. pardus*) under changing environmental conditions can be used to enhance management and conservation programs designed to maximize genetic diversity and minimize inbreeding of critically endangered subspecies (Reed *et al.* 2002). These data would also be useful in developing models of population viability in South Africa and developing management plans (e.g., Balme 2009). Here, we provide a comprehensive description of the reproductive biology of leopard. Our specific objectives were to (1) understand the mating system of leopards, and (2) define the reproductive parameters of a leopard population.

6.3 Method

6.3.1 Study area

Field work was conducted on the 85-km² Karongwe Private Game Reserve, Limpopo Province, South Africa (24°13'S; 30°36'E). The reserve was formed in 1998, and a 2.4-m-high electrified game fence was erected around the reserve perimeter. Elevation in the reserve varies from 520 m above mean sea level in the west to 489 m above mean sea level in the east. Karongwe is located within the savannah biome (Rutherford & Westfall 2003) and lies within the Mixed Lowveld Bushveld (Low & Rebelo 1998). The study area was characterized by hot, rainy summers and warm dry winters, with an average annual precipitation of 487 mm. The main function of the reserve is ecotourism, with several charismatic wildlife species present. Carnivores that were introduced include the lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*), with 12 ungulate prey species available. The leopard was the only large carnivore species that was not introduced to the reserve because it was already present. We calculated the Karongwe ungulate mean biomass, according to Coe *et al.* (1976), as 4,064 kg/km² (*SE* = 938, range 3,703 – 4,532) for the survey years 1999 – 2005. Mean biomass across years was above the predicted mean for Karongwe (2,789 kg/km²) at which the ungulate biomass should be stocked and the predicted maximum (3,681

kg/km²) that should not be exceeded (Coe *et al.* 1976). Even the lowest ungulate biomass on Karongwe (2005: 3,703 kg/km²) was above this maximum stocking rate.

6.3.2 Capture methods

Our study, conducted from June 2001 to July 2003, was part of a larger study on leopard conducted over a 6-year period from September 1999 to August 2005. We used the minimum count method with recognizable individuals, in conjunction with territorial mapping in the Global Information System ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California), tracks, and radio telemetry to determine population size (Kunkel *et al.* 2005). This was calculated as the sum of all marked or recognizable individuals, plus those unmarked animals known to exist (Hamel *et al.* 2006). Through time we were able to acquire an estimate of the total population size using a combination of radio telemetry, natural markings, and tracks. Numbers of unmarked animals in the study were relatively easy to assess, as both male and female leopards are territorial (Mech 1986, Garshelis 1993).

Leopards were captured by free darting from a vehicle using a Dan-inject rifle JM Spl.CO₂ (Dan-Inject, ApS Sellerup Skovvej, 116 DK, 7080, Børkop, Denmark). A tiletamine-zolazepam combination at 4-6.5 kg/mg (Zoletil, Virbac) was used, and leopards were fitted with Telonics SB2 VHF transmitters (Telonics, Arizona) constructed by AWF (Africa Wildlife Tracking, Pretoria, South Africa) into radio collars weighing approximately 400 g.

During sedation subjects were sexed, reproductive characteristics noted (Mech *et al.* 1993), age estimated by examining body characteristics (Turnbull-Kemp 1967), dentition, and tooth wear (Stander 1997), and paws measured. Age also was based on observations; i.e., females with cubs, scent marking, and other territorial behaviours associated with adults or newly established subadults. Individuals that were not radiocollared were identified by spot patterns on the face and neck and facial features, such as scars and tears in the ears (Miththapala *et al.* 1989).

We distinguished four different age classes, including cubs 0-12 months, subadults 12-36 months, mature adults 3-10 years, and old adults >11 years of age (Stander 1997). For example, prior to having cubs, females had short pink nipples and thus were estimated at 30-36 months old (Turnbull-Kemp 1967). Although leopard were aged using recognized aging techniques (Turnbull-Kemp 1967, Stander 1997), additional information from territorial movements and known reproductive history also were used to obtain an accurate estimation of adult age. Estimated age might have been accurate within six months, but we could ensure the identification of the females' first litter with a high degree of certainty in four of seven females. To help age leopards, reproductive characteristics were noted. If

it was not possible for the attending veterinarian to assess accurately if females were pregnant during sedation, it was established through deduction from copulatory behaviour, pre- and post sedation and post sedation signs of localization (female leaving and returning to the same location).

Using callipers accurate to 1 mm, paws of sedated individuals were measured, and any unusual structures on the paw were recorded to help identify individuals from tracks. Length was measured from toe to pad across the longest part of the paw. Width was measured from toe to toe across the widest part of the paw, and a pad was measured from the top to the bottom. A database of tracks and locations was used to identify unknown individuals. Ecotourism guides, trackers, and researchers monitored roads daily for tracks. Researchers relocated any identified tracks and measured them in firm soil with a light covering of dust; anything softer caused track size to appear larger and was not measured. Only tracks that could be identified as front or back foot, and left or right, were measured. This allowed tracks (e.g., front, left track) of any two leopards to be compared for territorial information. Procedures used to handle subjects complied with guidelines established by the American Society of Mammalogists (Animal).

Using three vehicles and nine researchers, we attempted to locate each radiocollared leopard twice daily (0500-0900 h and 1600-2000 h) throughout the study period to obtain visual observations. Location was recorded to the nearest 20 m using a handheld Global Positioning System (Garmin, Olathe, Kansas). If a visual observation was not possible, we used the squelch on the telemetry receiver to estimate direction and distance, and a second reading was taken directly opposite of the estimated position of the animal to improve accuracy.

6.3.3 *Copulatory behaviour*

We used visual cues (head rubbing, excessive rolling) and vocalization (sawing call) as an indication of the onset of oestrus, which typically began several days prior to association with a male (Smith & McDougal 1991). We defined consortship as a male and female associating and copulating (Sadler 1966). When telemetry signals indicated that male and female leopards were together and visual observation was not possible, we used the postcopulatory roar as an indication that copulation had occurred (Hancock 2000). When one of the leopards was not collared the postcopulatory roar was used as an indication that copulation had begun, which was confirmed later through visual observation. Postcopulatory roars are distinguishable from other leopard vocalizations; males emit the roar just before dismounting the female after copulation (Hancock 2000). Postcopulatory roars are probably emitted during ejaculation, as they are not emitted during false copulations (i.e., male mounts female without penetration). We recorded the number of consortships until conception. Copulating leopards were interrupted by humans, other female leopards, and by lions. Human-

interrupted consortships, when a female was darted during copulation, were excluded when calculating the number of copulations to conception.

6.3.4 *Reproductive parameters*

Leopard were observed to be polyestrous (cycle regularly until conception), a reproductive characteristic also observed in the domestic cat (*Felis catus*) (Concannon *et al.* 1989) and lion (Packer & Pusey 1983). We measured interestrous intervals from the last day of copulation to the first day of the next copulation period. Interestrous intervals of 32.9 days have been recorded (Bailey 1993), and females were monitored more intensively for visual copulatory clues prior to the next copulation period. Gestation length was measured from the second-to-last day of mating to the day the female became localized (female leaves from, and returns to, the same place), suggesting denning behaviour (Herron 1986). We calculated interbirth intervals for those litters where >1 cub survived to disperse (i.e., 10 – 12 months) as the number of days between consecutive births. We estimated cub birth date as the day after the female became localized for a week, approximately 90 days after the last observed oestrus, and with no further copulations (Smith & McDougal 1991). We calculated seasonality of consortship, conception, and birth. Distribution of conceptions was compared to a random expectation of equal occurrence in each month of the year, using a Kolmogorov-Smirnov two-sample goodness of fit test (Sokal & Rohlf 1981).

6.3.5 *Reproductive success*

We estimated the reproductive rate of a female leopard as mean litter size/mean birth interval (Kerley *et al.* 2003), total lifetime productivity (total number of cubs produced in a lifetime—Sunquist 1981), and total number of young surviving their first year (total lifetime reproductive success—Clutton-Brock 1988). To estimate total lifetime productivity we assumed that female leopards are reproductively active for nine years from 3 – 12 years old.

6.3.6 *Intensive copulatory behaviour study*

From June 2001 to July 2003 we undertook an intensive study of copulatory behaviour during 19 consortships. From the onset of the copulatory period a vehicle with two observers remained with the consorting leopard 24 h/day, rotating in 6-h shifts until the leopard pair separated 2 – 4 days later. During visual observation we recorded number and initiator of copulations, copulation duration from purr and from the time of mounting to dismount, start and end times of the roar, whether the female rolled postcopulation, postmating aggression, unusual vocalizations such as snarls and calls and associated behaviour (Hancock 2000), false copulations, and distance moved after copulation. When visual contact was interrupted, the copulatory roar was used as a reliable indicator of copulatory frequency.

For all animals, we recorded leopard mortality as confirmed with recovery of a carcass, radiotracking device, remains of a leopard, or disappearance of cubs younger than eight months of age. Mortality was suspected when old leopards were no longer observed or when regularly viewed adult females that copulated previously with the resident male ceased to copulate and were no longer observed. All Statistical analyses were conducted using SPSS 15 (SPSS inc., Chicago, USA).

6.4 Results

Population size of leopards varied from 6 to 25 animals (including young) across the years of the study, with an average of 16 leopards per 85 km² ($SE = 2.6$). Population size increased from 2000 (13 individuals, 3 territorial females) to 2003 (25 individuals, 6 territorial females). During this time only one adult female was suspected to have died from natural causes, as she was no longer seen, and her subadult female offspring replaced her as the territorial female. From 2003 to 2006 the population declined to 6 individuals (2 territorial females). In 2003 one female died in a snare outside the reserve. Between 2004 and 2006 five adult females and two subadult females died. In 2004 two females died during same sex territorial clashes and one died from unknown causes. In 2005 one female died during same-sex territorial clashes, two females were killed by the new male after a territorial take over, and two subadult, recruited females and three cubs also were killed by the same male.

Ten leopards (three adult males, six adult females and one juvenile female) were immobilized; however, due to technical complications with radiocollars we report reproductive data on two collared adult males, five collared adult females, and two uncollared adult females. The territory of the breeding male (M1) encompassed the majority of the 85-km² area. Any additional subadult and adult males within the area were confined to small areas (< 7.5 km², C. Owen, pers. Obs.) and were in constant conflict with the breeding male until they either dispersed or were killed. Three successive breeding males occupied the reserve from 1999 to 2005. The breeding male (M0) present in 1999 was last seen in May 2001 just before the intensive reproductive study began. Three months later a resident subadult male (M1) became the breeding male at an estimated age of 3.5 years. M1 died in August 2004, and M4, a mature male estimated to be 5.5 years old, entered the reserve (October 2004) and became the breeding male. Neither M0 nor M4 were habituated, making reproductive data difficult to collect. Additional adult and subadult males also were monitored for reproductive activity.

6.4.1 Copulatory behaviour

Females regularly came into oestrus and during 13 consortships followed the male out of their own territory as he moved around the reserve, while nine times they remained in the females' territory for the duration of the consortship. When M1 was the breeding male two other adult males in his territory

(3 - 4 year olds) never were seen copulating within the reserve. On one occasion a female located another male outside M1's territory when M1 was not present. F3 copulated over a period of 86 h with M1 in F6's territory. F6 chased F3 away, and M1 and F6 proceeded to copulate for 26 h, after which F3 and M1 resumed copulation over a 3-h period. F6 and M1 then renewed copulation over an 11-h period until M1 made a kill and F6 searched for M3 (4 years old). Although the pair (F6 and M3) remained together for 24 h, no copulations took place despite continued attempts by the female. M3 had begun scent marking 4 months previously and was sexually mature. M3 was permitted to remain only in a small portion of M1's territory, and the two equally sized males were in constant conflict. Competition intensified, and the younger male was chased out of M1's territory and the reserve four months later.

6.4.2 *Intensive copulatory study*

During the intensive copulatory study we followed consorting pairs for 2,449 h. We observed 19 consortships, which included 4,855 copulations (1,809 copulations visually observed; Table 1). During consortship pairs walked and copulated, on average, over a period of 68 h ($SE = 4.6$, range 32 - 99, $n = 19$ consortships; 6.1). Females initiated 97% ($n = 1531$) of the 1585 observed copulations where initiator was visible and when the male initiated copulation, he approached a female and she presented herself in lordosis. False copulations ($n = 33$) were identified during 1.8 % of observed copulations (2.8 times/consortship, range = 0 - 6). In all cases males mounted females but did not penetrate or roar. Females immediately resumed wasping (the female moves back and forth in front of the male enticing him to mate) and the males remounted, completing penetration and copulation, followed by the mating roar and dismount.

Of 43 consortships, 16 % were interrupted by humans to collar individuals. Of the remaining 36 consortships, 31 % resulted in conception. Each conception occurred after a mean of 2.7 consortships ($SE = 0.4$, range 1 - 6; Tables 6.1 and 6.2). Natural interruptions of the consorting pairs occurred on 2 occasions by lions and on 3 occasions by other female leopards. No interruptions were caused by other male leopards.

6.4.3 *Reproductive parameters*

Mean interestrus period averaged 22.5 days ($SE = 1.6$, range 10 - 48, $n = 28$), and gestation averaged 95.5 days ($SE = 0.9$, range 89 - 98, $n = 10$) (Table 6.2). After successfully raising a litter a female leopard mated again when cubs, on average, were 10 months old ($SE = 0.5$, range 9 - 13, $n = 10$) (Table 6.2). Cubs attained independence as determined by detachment from the female at 11.6 months ($SE = 0.4$, range 11 - 13, $n = 7$; Table 6.2).

In three consecutive years of study 100% of females produced cubs and the mean population birth rate was 15.8 % per year, with a minimum of 19 cubs born over three years (excluding cubs that died before observation). In the third year two females lost litters and re-mated; however, it was not possible to calculate how soon it was after losing the cubs that the females mated, as the date cubs died was not known (Table 6.2).

Mean interbirth interval of leopards was 14 months ($SE = 0.6$, range 12 - 16, $n = 5$; Table 6.2), based on 15 litters of seven females from 2001 - 2005. Mean litter size was 1.7 cubs ($SE = 0.1$, range 1 - 2, median = 2, $n = 11$), and was determined by the investigators 63.7 days after parturition ($SE = 21.4$, range 12 - 139, $n = 6$; Table 6.2). Litters were not examined at birth, and therefore litter sizes likely were underestimated. Litter sex ratio of the cubs that were sexed was 3 males: 11 females (21% male: 79 % female) for 10 litters (Table 6.2). Direct observations indicated that litter mortalities were due to lions ($n = 1$), infanticide ($n = 4$), and other leopards ($n = 1$; Table 6.2). Adult sex ratios over the study period were 22.9 % males and 77.1 % females (1 males \pm 0.1: 5 females \pm 0.5, $n = 6 \pm 0.6$).

6.4.4 *Reproductive success*

Reproductive rate and success were calculated for the four females whose reproductive histories were known and whose ages could be calculated with an accuracy of within six months. An error of six months in age estimation is unlikely to have an effect on the accuracy of the reproductive calculations, as age was used as a measure of the onset of sexual maturity and longevity. Of the two subadult females (F1 and F2), F1 gave birth to her first litter (February 2002) at 38 months of age, and F2 gave birth to her first litter (January 2002) at 35 months of age. Of the two females that produced litters prior to this study (F3 and F4), F3 (five years old in October 2001) was still associating with two male cubs (11 months old). Her first litter (female cub) was born in 1999. F4 (four years old in February 2002) continued associating with a male and female cub (10 months of age), and this was assumed to be her first litter.

Mean reproductive rate was 1.6 cubs/female/year ($SE = 0.3$), with a mean of 0.8 cubs surviving to 12 months of age ($SE = 0.1$; Table 6.3). Assuming females were reproductively active for nine years from 3 - 12 years of age, predicted mean total lifetime productivity would be 14.5 cubs ($SE = 1.4$) and predicted mean total reproductive success would be 6.9 cubs ($SE = 0.9$). Although females were reproducing at an average 1.6 cubs/year, average productive life span was 6.6 years ($SE = 0.9$), which was shorter than the expected 12 years for leopards in the wild (Daly *et al.* 2005; Table 6.3). Of seven females monitored in this study, all died at ages < 10 years. The oldest female (F3), who lived to nine years, had produced six litters with a total lifetime production of eight cubs as opposed to a predicted 15 cubs, and had achieved reproductive success of 4 as opposed to a predicted 7 cubs (Table 6.3).

Mean reproductive success for all females monitored was 4 cubs / female ($SE = 0.81$, range 3 - 5, $n = 4$).

6.4.5 Seasonality

Although consortships occurred year round, 62% of consortships ($n = 47$) occurred from late spring to early autumn (October to March), with two peaks in November and January (Fig.1). A similar pattern occurred in consortships resulting in conception ($n = 15$), with 67% occurring between October and April with two conception peaks one in late spring/early summer and another in autumn (Fig. 6.1). Periods of conception differed from expected (Kolmogorov-Smirnov: $z = 1.63$, $n = 12$ months, $P = 0.01$), with at least one, and possibly two, peaks. These seven females gave birth in all months except May and December, ($n = 15$ litters), with births most frequent over June and July (33%) and January and February (27%; Fig. 6.1).

6.5 Discussion

Karongwe is a small enclosed reserve with artificially high numbers of ungulates that sustain predators and ensure a high number of sightings for ecotourism. Although the game fence was no barrier to leopards, ungulates were prevented from leaving the reserve, and this provided a constant, year-round food supply for predators that could affect their reproductive parameters and population sizes. Higher reproductive rate did not translate into higher lifetime reproductive success for female leopard on Karongwe Game Reserve. Although the prey rich environment enhanced reproductive measures, adult female survival was lower than expected, reducing the reproductive success of the population.

Our observations of leopard mating match previous descriptions (Laman & Knott 1997, Hancock 2000). However, reproductive parameters, with the exception of gestation length, were shorter than described previously, which we believe reflects removal of resource limitation (Rattray 1977, Laurenson *et al.* 1992). Reproductive parameters are affected by nutritional quantity and in food-abundant populations, reproductive output increases through increased pregnancy rate, rapid maturity, and/or higher survival (Sinclair 1985, Mduma *et al.* 1999). Gestation length of 95.5 days agrees with other studies (Sadlier 1966, Hemmer 1976, Eaton 1977, Skinner & Smithers 1990) and could be linked less to nutrition than other reproductive parameters.

Interestrous intervals in this study (22.5 days) were shorter than other leopard studies (32.9 days—Bailey 1993); 45.8 days for captive leopard—Eaton 1977; 25.3 days—Sadlier 1966) and, we believe, are close to the minimum for leopards. Similarly, interbirth intervals were shorter (14 months) than the published range of 17.1 -28.8 months (Schaller 1972, Le Roux & Skinner 1989,

Bailey 1993). Unlike female leopards in other studies (Schaller 1972, Muckenhirn & Eisenberg 1973, Bailey 1993), females gave birth annually over three consecutive years, possibly indicating they were well nourished. Lynx (*Lynx canadensis*) in areas of high hare (*Lepus americanus*) density were more likely to breed every year than those in areas where hares were scarce (Sunquist & Sunquist 2002). Leopard cubs on Karongwe attained independence at 11.6 months, shorter than published data (13 – 18 months— Bailey 1993; Le Roux & Skinner 1989, Skinner & Smithers 1990, Seidensticker & Lumpkin 1991). Enhanced resource availability can reduce age to sexual maturity (Sadler 1969). The cost of dispersal among asocial species is high (Packer 1986, Wrangham & Rubenstein 1986), and the majority of other large felid cubs disperse at around one to two years (Smith 1984, Mondolfi & Hoogesteijn 1986, Jackson & Ahlborn 1988). Timing depends on social circumstances and resource availability (Sunquist 1983). We believe improved resource availability reduced time to maturation, and thus, dispersal in leopard on Karongwe. However, because of small sample sizes, generalizations based on our findings should be made cautiously.

Leopards may be responding facultatively to a constant, year-round food supply by incorporating a second birth peak in mid winter. Lactation and feeding of young are the most energy-consuming activities related to reproduction (Sadler 1969, Bronson 1989, Clutton-Brock 1991), and females typically should not give birth in the winter dry season because of a lack of cover and limited food (Bailey 1993). Prey of leopards at Karongwe Reserve, however, move into more risky, thick, evergreen vegetation along the rivers in winter where leopard successfully killed a greater proportion relative to their availability, and where these prey were more easily captured. Winter births in June/July would ensure abundant food for lactating females, as prey congregated in the rivers where vegetation remained greener longer. Females were able to hunt easily to feed cubs weaned during the birth season of prey in November, and cubs would learn to hunt prey (six-month old cubs can catch their own prey—Turnbull-Kemp 1967). The study by Persson (2005) on wolverines (*Gulo gulo*) showed higher reproduction in females supplemented with additional food and suggests that reproduction can be limited by winter food availability.

Females living in prey rich environments are expected to grow and reproduce faster, resulting in higher population growth rate (Sibly & Hone 2002). This maximum productivity was evident with increasing population numbers until 2003, when intraspecific competition stabilized the population through effects on reproductive output and mortality rates. Seven territorial females died, and therefore female average life expectancy was shorter than expected, resulting in lower lifetime reproductive success. Higher reproductive rate therefore did not translate into higher lifetime reproductive success. Shorter life span was compensated for, to an extent, by female recruitment; however, males that obtained territories in 2005 killed subadult females and all previously sired cubs. Death of cubs through infanticidal killing lowered female reproductive success. These results were

mirrored in tigers (*Panthera tigris altaica*; Kerley *et al.* 2003), which suffered mainly from human-related mortalities. If the leopard population was subjected to added human-related mortality, population recovery could be affected negatively (Balme & Hunter 2004).

Territories expanded and retracted depending on the number of females; however, even at peak population size, the number of territorial females never exceeded six, which suggested a maximum number of territories available on the reserve (Lopez-Sepulcre & Kokko 2005). Average female territorial sizes of leopards on Karongwe (11.2 km², *SE* = 2.0, range 3.7 – 31.1 *n* = 17; C. Owen, pers. Obs.) were comparable to those of other *Acacia* woodland studies (11.3 km²—Bailey 1993; 14.4 km²—Hamilton 1976). As regions become dryer (188 km² – Stander *et al.* 1997) or more mountainous (487 km² – Norton & Lawson 1985), territory size increases.

Reproductive parameters affect population growth. Knowing the effects of various social and/or environmental factors on these parameters can help wildlife managers predict population responses to different conditions and enable them to manage effectively. With the exception of *P. p. pardus*, all subspecies of *P. pardus* are classified as endangered or extinct (Wozencraft 2005). Accurate reproductive data available from healthy populations of this subspecies provide valuable information for assisted reproductive technologies (i.e., artificial fertilization), and the effective management of endangered subspecies in captivity and in the wild.

In addition to providing the first comprehensive description of leopard reproductive biology, our results are especially pertinent to conservation management of large predators in prey-rich environments. Most reproductive parameters indicated a facultative response of faster reproduction when resources are abundant. These results offer encouragement for founding new populations of endangered felids in areas of high resource abundance. However, additional work is needed on the conservation implications of enhanced resource availability and whether resource availability is a primary determinant of adult female mortality or whether high mortality is a product of the leopard social system (Balme & Hunter 2004).

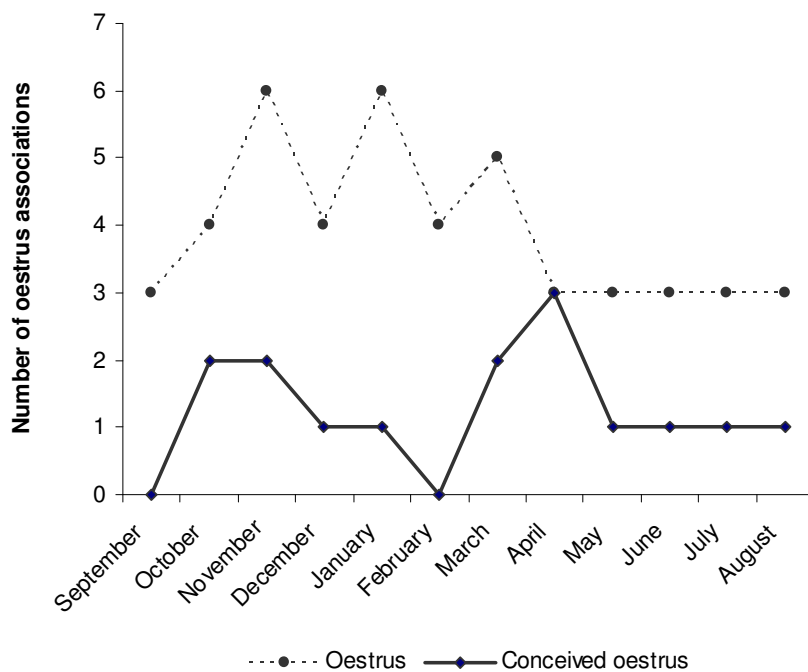


Figure 6.1. Seasonal variation in oestrus and incidence of conceptions among seven female leopards in consortships from 2001-2004. Conceived oestrus resulted in pregnancy, and birth occurred three months later. See text for statistical summary.

Table 6.1. Mean copulatory output of 7 adult female leopards from 19 consortships ($n = 4,855$ copulations) on Karongwe from June 2001 to July 2003

Female leopard	Length of	Length of	Inter-	Mean no. of copulations hour ⁻¹	Mean no. of copulations day ⁻¹	No. Copulations consortship ⁻¹	No. of consortships to conception	No. of hours consorting	% of times female rolled
	copulation from purr to dismount (s)	copulation from mount to dismount (s)	copulatory interval (min)						
F1	27.5	11.5	22.2	1.8	44	141	2.6	65.8	65.7
F2	36.5	9.0	8.8	5.9	142	278	3.5	61.5	76.5
F3	23.6	8.9	11.2	4.1	98	285	2.8	71.1	56.8
F4	26.7	9.0	7.8	4.3	104	234	3.0	53.7	40.7
F5	32.0	11.5	11.9	3.7	88	228	4.0	63.2	33.3
F6	29.0	9.5	11.3	3.3	79	303	1.0	92.2	47.1
F7	36.0	12.0	11.2	3.8	91	258	1.0	68.2	62.3
Mean ± SE	30 ± 1.8	10 ± 0.5	12 ± 1.8	3.8 ± 0.5	92 ± 11	247 ± 20.4	2.7 ± 0.4	68 ± 4.6	55 ± 5.7

Table 6.2. Reproductive output of individual female leopards on Karongwe from June 2001 to January 2005

Female leopard	Litter birth (year-month)	Gestation period (days)	No. of consortships to conception	Litter size	Outcome or cause of mortality in litters	Cubs' sex in each litter	Cub age when female remated (Months)	Cub age at independence (Months)	Interbirth intervals preceding this litter (months)
F1	02-Feb	96	5	2	D & R	2 ♀	10	11	-
	03-Apr	95	2	2	D & L	2 ♀	13	13	14
	#	-	1	-	-	-	13	-	14
F2	02-Jan	96	4	2	D & R	1 ♂ & 1 ♀	10	11	-
	03-Mar	97	2	1	D	1 ♀	10	11	14
	04-Jun	89	6	-	Died *	≠	-	-	-
	04-Oct	90	2	2	Inf*	≠	-	-	-
F3	02-Feb	98	2	2	D & Inf	1 ♂ & 1 ♀	9	11	-
	03-Jul	97	6	1	Li	1 ♀	-	-	16
	04-Jan	94	1	2	Died †	≠	-	-	-
	04-Sep	95	2	-	Inf †	≠	-	-	-
F4	02-Jun	-	3	2	D	1 ♂ & 1 ♀	11	13	-
	#	-	-	-	-	-	11	-	12
F5	02-Aug	-	4	-	-	-	-	-	-
F6	02-Jul	-	1	2	D	1 ♀	-	-	-
	03-Jul	-	1	-	-	-	9	-	-
F7	02-Nov	-	1	1	D	1 ♀	9	11	-
Mean		94.7	2.7	1.7			10.5	11.6	14
±SE	n = 15	±0.9	±0.4	±0.1		3 ♂ : 11 ♀	±0.5	±0.4	±0.6

- Data were not available as these individuals were not collared, collars were faulty, or the litter did not reach maturity and were not included in the calculations
- ≠ Cubs died before they could be sexed
- # Female died pregnant, litter data were not available
- L Killed by a leopard
- Inf Infanticidal killing
- Li Killed by a lion
- D Cubs reached the age of dispersal and independence from the female
- R Removed from Karongwe
- (*) Cubs died at one month old
- (✦) Cubs died at four months old

Table 6.3. Reproductive output of 4 of the 7 female leopards on Karongwe that could be aged accurately and with known reproductive history from June 2001 to January 2006.

Female leopard	Date immobilized	Estimated age at immobilisation	Date of death	Estimated	Lifetime	Reproductive success	Mean litter size	Mean birth interval (months)	Reproductive rate year ⁻¹
				age of females at death (years)	productivity (incl. cubs from previous litters)				
F1	01-Jun	2.5 years	04-Jul	5	4	3	2	14	1.7
F2	01-Aug	2.5 years	06-Jan	7	6	5	1.7	14	1.5
F3	01-Oct	5 years	05-Jan	9	8	4	1.7	16	1.3
F4	02-Feb	4 years	03-Aug	5.5	4	4	2	12	2
Mean ± SE				6.6 ± 0.90	5.5±1.9	4 ± 0.81	1.9 ± 0.1	14 ± 1	1.6 ± 0.3

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CHAPTER 7

TOP DOWN OR BOTTOM UP REGULATION OF A TOP PREDATOR (*PANTHERA PARDUS*) POPULATION

7.1 Abstract

Felids are vulnerable to local extinction, due mainly to low densities, large ranges and conflict with humans. Quantifying the effects of density-dependent “bottom-up”, and density-independent, “top-down”, factors and processes in demography and dispersal remains a major challenge in population ecology. Here we examined survival, mortality, and dispersal of a leopard (*Panthera pardus*) population in a prey-rich environment. We provided population estimates as well as density-dependent and independent influences on separate age groups within the population. The average leopard population ($0.18/\text{km}^2$) and adult ($0.07/\text{km}^2$) densities were in line with populations studied in similar habitats. The population responded positively to the “bottom up” effect of increasing prey density through subadult recruitment. Density-dependent intraspecific competition for space regulated the population close to carrying capacity through increased subadult mortality, and an increase in subadult dispersal the subsequent year. The population was further limited by top-down social behaviours during male territorial take-over (infanticide) and female territorial clashes. This study provided evidence of a complex interplay between density-dependent and density-independent factors affecting survival and dispersal of the different life stages of this predator in an environment not limited by food shortage, and in the absence of human persecution. To avoid over-estimation of conservation viability of leopard, or similar solitary territorial species, it is essential to measure the local carrying capacity for adult territories rather than simply population size or reproductive success, which may increase markedly during favourable years.

7.2 Introduction

Top-level mammal predators tend to be of conservation concern and face the problems of small population size, large home ranges, and human conflict (Woodroffe & Ginsberg 1998, Macdonald 2010). Understanding population dynamics and factors responsible for controlling top predators allows us to appreciate how these species interact with their environment, and enable effective population management (Kunkel *et al.* 2005). This information is regrettably lacking due to the difficulties of monitoring these species, which are often cryptic, and inhabit extensive areas of difficult terrain (Jackson 1996, Soisalo and Cavalcanti 2006).

A useful paradigm for examining population regulation is through top-down versus bottom-up views (Hunter & Price 1992, Power 1992, Pierce *et al.* 2012). Populations can be regulated by bottom-up

processes (e.g. resource limitation such as food, water and space) which are inherently density-dependent, providing an explicit negative feedback mechanism, which regulates the population (Sibly & Hone 2002, Navarrete & Manzur 2008). As the population increases, fewer resources are available and the growth rate declines through either an increase in mortality (intraspecific competition for food, starvation and disease) or a decrease in natality (Piatt & Van Pelt 1997, Mduma *et al.* 1999, Armitage 2012). The rate of increase of a population is negatively related to population density and most density-dependent change occurs at high population levels for large mammals (close to the carrying capacity) (Fowler & Smith 1981, Murdoch 1994, Turchin 1999, Hammill & Stenson 2011). The population is subsequently limited by the essential resource requirements of the species, in a bottom-up density dependent process (Hairston *et al.* 1960), possibly only after a delay (Sinclair *et al.* 2006).

The population could also be influenced by top-down processes e.g. abiotic events, density-independent social interaction (infanticide), natural enemies such as predators, parasites or human caused mortality (Kissui & Packer 2004, Schwarz *et al.* 2013). These are irregular, unpredictable, operate independently of density and are unable to regulate the population (Estes 1996, Kay 1998, Sinclair & Krebs 2002, Kissui & Packer 2004).

Whether trophic levels are structured from the top down or the bottom up is more than a theoretical debate because it influences how we manage the Earth's ecosystems, especially in reserves and other protected areas (Diamond 1992, Estes 1996, Khadka & Vacik 2012). To manage populations we need to understand what factors are affecting, and potentially limiting, population size. Although numerous inferences have been made about population regulation in carnivores, most studies have been hampered by difficulties in accurately estimating food availability, population carrying capacity, impacts of interspecific competition, and exposure to natural enemies (Kissui & Packer 2004).

This study aimed to elucidate factors influencing leopard (*Panthera pardus*) population size and demography in a protected, human-modified environment of artificially high prey density. Variation in prey biomass over time allowed us to describe the importance of bottom-up relative to top-down influences. I predicted that leopard population would be regulated by density dependent limitation for space through intraspecific competition as well as density independent social behaviours such as infanticide and territorial disputes. Our specific objectives were to (1) calculate population size, (2) identify the density-dependent and independent processes that may be responsible for stabilising the population and identify the causes of fluctuation and instability, (3) identify the bottom-up resource responsible for population limitation and (4) ascertain which age groups were most influenced by these stabilising or destabilising processes.

7.3 Method

7.3.1 Study area

Fieldwork was conducted on the 85-km² Karongwe Private Game Reserve (KGR), Limpopo Province, South Africa (24°139'S, 30°369'E). The reserve was formed in 1998, the main purpose being tourism. Karongwe is located within the savannah biome (Rutherford & Westfall 2003) and lies within the Mixed Lowveld Bushveld (Low & Rebelo 1998). The study area was characterized by hot, rainy summers and warm, dry winters, with an average annual precipitation of 487 mm (Table 7.1). Animals have access to waterholes and rivers across the reserve, and water is not limiting (Thaker *et al.* 2010).

A 2.4-m-high electrified game fence was erected around the reserve perimeter to contain carnivores that were reintroduced, including lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*), and 12 ungulate prey species (Thaker *et al.* 2010). Leopards were already present prior to establishment and fencing of the reserve. The fence was permeable to leopard and this study focussed on a core area of a much larger persistent leopard population. A minimum of two individuals of each predator species, reflecting the bulk of the adult populations, were radio collared and studied concurrently with the leopard study (Thaker *et al.* 2010).

7.3.2 Prey availability

We used prey availability to assess the impact nutrition had on population growth. A total count of ungulate species were censused annually in September by aerial counts undertaken in a Bell Jet Ranger helicopter. Using a GPS-aided computer, 300m wide strips were flown throughout the reserve. A data capture program "Capture", written by Mark Schormann, was used to plot the location of the animals, reducing the chance of replicate counting. We calculated the Karongwe ungulate mean biomass from annual aerial game counts according to Coe *et al.* (1976).

7.3.3 Population density

We studied the population ecology of eight radio-collared female, three radio-collared male, six un-collared female and two un-collared male leopard from 1999 to 2005. Leopard were captured by free darting from a vehicle and fitted with radio collars (Owen *et al.* 2010). Minimum age for collaring was 18 months and collars were fitted loosely to allow for growth. A leopard database, maintained from 1999-2006, identified individuals by the spot pattern on their face and neck as well as facial features such as scars and ear tears, with each assigned a letter designating sex (F = female and M = male) and a unique number. Photographs were used to assist in the accurate construction of identikits. The sire and mother of cubs were determined during intensive following (Owen *et al.* 2010). Un-

collared subadults were monitored by opportunistic sightings. We used the minimum count method with recognizable individuals, in conjunction with territorial mapping in the global information system (ArcGIS 9.3, Environmental Systems Research Institute, Redlands, California), tracks, and radio telemetry to determine population size (Kunkel *et al.* 2005, Owen *et al.* 2010). This method is widely used in radio telemetry-based research projects for species like black bear (*Ursus americanus*) (Garshelis 1993), grizzly bear (*Ursus arctos*) (McLellan 1989), wolf (*Canis lupus*) (Mech 1986) and mountain lion (*Felis concolor*) (Lindzey *et al.* 1992).

7.3.4 Potential leopard density

To validate adult population size we determined the potential adult leopard density for Karongwe using a model that predicts potential adult leopard density as a function of potential prey abundance (Hayward *et al.* 2007). Prey density (#.km⁻²) data were converted to biomass (kg.km⁻²) using 0.75 times the average female body mass in the population in order to account for subadults and young that are preyed upon (Hayward *et al.* 2007). The regression equations relate predator biomass to the biomass of prey falling within the predators' preferred prey weight range (Pw; 10 – 40 kg) as well as for significantly preferred prey species (Ps; bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), and impala (*Aepyceros melampus*)) (Hayward *et al.* 2006). The regression equations for potential leopard abundance = $(10^{(-2.248 + (0.405 * (\text{LOG } 10 (\text{prey biomass})))}) * (\text{area of reserve}))$. Prey biomass for each year was used in the equation to predict leopard densities the subsequent year, to allow for leopards to respond to changes in prey.

Using three vehicles and nine researchers, we attempted to locate and obtain visual observation of each radio-collared leopard twice daily (05:00-9:00 h and 16:00-20:00 h) throughout the study period. Location was recorded to the nearest 20 m using a handheld Global Positioning System (Garmin, Olathe, Kansas). If a visual observation from the extensive road network was not possible, we used triangulation and the squelch on the telemetry receiver to estimate direction and distance. A direction was taken from a point closest to the leopard. The second reading was taken from the closest point 180 degrees to the first point (opposite) the third point was taken at 90 degrees to the first or second point as close as possible thereby providing a smaller area in which to locate a GPS reading from the GIS map. Leopard frequented rivers and drainage lines, and where triangulation was not possible a second reading was taken directly opposite the estimated position of the leopard to improve accuracy.

For the purpose of this study, the study year was considered to start in September, which is the typical onset of spring and the first rains. Year one refers to September 1999 to August 2000, and subsequent years follow on from that to the end of the study in August 2005. Where a year is

stipulated, the second part of the study year is referred to, for example 2002 would refer to 2001 - 2002 study year.

7.3.5 Population regulation

Leopard mortality was categorised as confirmed or suspected. Mortality was confirmed with the recovery of a carcass, damaged radio-tracking device, remains of a leopard or the disappearance of cubs younger than eight months. Mortality was suspected when old leopards were no longer seen, or when regularly viewed adult females which had copulated previously with the resident male ceased to re-copulate and were no longer seen (Owen *et al.* 2010). Although they may have emigrated, they were considered deceased in terms of the population. Adult males and subadults of both sexes were always assumed to have emigrated rather than died, unless mortality was confirmed.

The causes of confirmed leopard mortality were established by direct observation, measuring bite marks if death was predator related, and from evidence and tracks around the site, and the other individuals with transmitters in the vicinity. Dead leopard were found within 24 h (48%) unless death occurred in the thick reeds of riverbeds, when sufficient time was allowed to elapse prior to walking-in, to ensure that the stationary leopard was not on a kill or injured. When determining the percentage of deaths in the population, we assumed that individuals reaching sexual maturity dispersed unless it was known that a new male on the reserve was presently harassing and killing sub adults, in which case we assessed each individual's disappearance to determine whether individuals had died or dispersed.

We calculated the percentage real mortality and annual percentage mortality. Real mortality is the proportion of total mortality that occurs in each life stage (cubs 0-12 months, subadults 13-36 months and adult) d_x/n_0 (d_x = the number dead in a category, n_0 = the total life stage size) (Bellows *et al.* 1992). This enabled us to identify the life stage with the highest mortality and, comparing each life stage over several years, we were able to observe which life stage experienced age specific density-dependent mortality (which age classes were regulated). Annual percentage mortality was also calculated, highlighting the annual losses in the population.

7.3.6 Cause of mortality

We categorised mortality into interspecific, intraspecific, human related and natural causes, to enable us to identify the primary cause of mortality and identify any density-dependent regulatory factors in the population.

7.3.7 Analyses

Using linear regression, we tested whether variation in prey biomass and population density influenced variance in mortality, density and dispersal in the leopard population life stages. We ascertained which life stages were most influenced by these processes, and which life stages were regulated by a density dependent negative feedback process. We additionally tested the relative influences of previous years' prey biomass and population density on mortality, density and dispersal because of the time required for predators to have offspring and subadults to mature. Changes in population in response to prey biomass and population density may not be immediately evident. Statistical analysis was performed using SPSS 15 (SPSS Inc., Chicago, Illinois). Means are presented with the standard error (\pm) subsequent to the mean. Normality of variables was tested using the Kolmogorov-Smirnov test and data that were not normal were transformed.

7.4 Results

With minimal management intervention (removal of two cubs) (Table 7.1) the leopard population changed markedly over the six-year study, owing to subadult maturation, emigration, immigration and mortalities (Fig. 7.1). Leopard population size varied from 6 to 25 animals (including young) across the years of study, with an average of 16 ± 2.6 leopard/ 85 km^2 ($0.18 \cdot \text{km}^{-2}$) (Table 7.2). This equated to 18.8 leopards/ 100 km^2 or one leopard/ 5.3 km^2 . There were 6 ± 0.6 adult leopard/ 85 km^2 ($0.07/ \text{km}^2$), 7 adult leopards/ 100 km^2 or one adult/ 14 km^2 . The average number of adult breeding females was 5 ± 0.4 (range 2 – 6) (Table 7.2). Adult male numbers ranged from 1 – 2. The breeding male's territory encompassed the majority of the 85 km^2 area. Any additional subadult and adult males within the area were confined to small areas ($< 16 \text{ km}^2$). There were three successive breeding males on the reserve. The breeding male present from 1999 was last seen in May 2001. Three months later a resident subadult male (M1) became the breeding male at an estimated 3.5 years of age. M1 died in August 2004 and M4, a mature male 5.5 years old (estimated) entered the reserve (October 2004) and became the breeding male (Fig. 7.1).

Karongwe Herbivore mean biomass, was $4\,064 \text{ kg/ km}^2$ ($SE = 938$, range 3,703 – 4,532) for the survey years 1999 – 2005. Mean biomass across years was above the Coe *et al.* (1976) predicted mean for Karongwe ($2\,789 \text{ kg/ km}^2$) at which the herbivore biomass should be stocked and was greater than the maximum recommended ($3\,681 \text{ kg/ km}^2$) for that area (Table 7.1). Predator to prey ratios were 1:53 (Thaker *et al.* 2011). Leopard numbers on Karongwe were in agreement with those predicted by the model predicting adult leopard numbers (Table 7.1).

There was a significant positive relationship between prey biomass and leopard population size ($r^2 = 0.57$, $n = 6$, $p = 0.049$). Subadult density recruitment responded positively to increasing prey biomass

($r^2 = 0.65$, $n = 6$, $p = 0.029$). There were no other significant correlations with prey biomass and any other life stage.

Leopard density only had a relationship with the subadult life stage in the population. Increasing population density resulted in increased subadult mortality ($r^2 = 0.66$, $n = 6$, $p = 0.049$). This weakened to a non-significant relationship when considering the previous year's population density ($r^2 = 0.034$, $n = 6$, $p = 0.768$). There were no significant relationships between population density and mortality in the other life stages (cub mortality: $r^2 = 0.053$, $n = 6$, $p = 0.660$; adult mortality: $r^2 = 0.147$, $n = 6$, $p = 0.453$). There were also no significant relationships between the previous year's population density and mortality in the other life stages (cub mortality: $r^2 = 0.137$, $n = 6$, $p = 0.540$; Subadult mortality: $r^2 = 0.034$, $n = 6$, $p = 0.768$; adult mortality: $r^2 = 0.403$, $n = 6$, $p = 0.250$).

Subadult dispersals were highly significantly influenced by previous year's leopard density ($r^2 = 0.911$, $n = 6$, $p = 0.003$), but not significantly with current year's density ($r^2 = 0.292$, $n = 6$, $p = 0.211$), ungulate density ($r^2 = 0.161$, $n = 6$, $p = 0.373$) or previous years ungulate densities ($r^2 = 0.263$, $n = 6$, $p = 0.298$). Six of the 25 recorded subadults were collared. Of these six subadults, four (three females and one male) were recruited into the population during low population density (Fig.7.1). In 2004, the year following the highest leopard population density the highest number (seven) of cubs dispersed (Fig. 7.1; Table 7.2).

In 2000, no leopard deaths were recorded (Table 7.2). This is likely an erroneous result as the project had recently begun, and daily monitoring activities were less thorough. Of the 21 suspected leopard deaths during the study, 14 were confirmed (Table 7.3). The primary cause of leopard related mortalities was not starvation, disease or human related. Leopard mortality was primarily the result of intraspecific encounters (eleven deaths, four of which were of radio-collared adults; 79 %) (Table 7.3, Fig. 7.1).

Excluding the first year, mean annual mortality was 4 ± 1.1 (range 2 – 7) (Table 7.2). Average percentage mortality was 19.3 %, of which adult female mortality accounted for 5.5 % and adult male mortality 1.8 % per annum (Table 7.2). The life stage that experienced the largest proportion of annual mortality were adults (male, 28.6 %; female, 19.4 %) and 0 – 12 month old cubs (24.2 %) (Table 7.2). Adults and cub mortalities were not statistically density-dependent and are therefore likely the result of density independent social behaviours during male territorial takeovers and female clashes.

Rainfall during 2000, the highest in 12 years (952 mm), resulted in peak in ungulate biomass the following year (Table 7.1). The leopard population responded to the environmental improvement

through an increase in subadult recruitment. This was reflected in an increase in leopard density from 1 leopard per 7 km² to 1 leopard per 3.4 km² in 2002. Not all these subadults secured territories. Only one extra territory was acquired and breeding adult females peaked during 2002 – 2003 (6 breeding females (Table 7.2)). The ungulate and predator populations stabilised through 2003 when leopard reached their resource imposed limitation (space). The high leopard population was regulated through subadult mortalities lowering the leopard population in 2004 and further regulated in 2004 by subadult dispersal (Table 7.1; Table 7.2). Low rainfall in 2003 resulted in lower ungulate densities in 2004. In 2005, the leopard population was severely reduced because of a significantly lowered ungulate population resulting in reduced subadult recruitment, in combination with the top-down influences of a male territorial takeover on all life stages of the population. The result was an all-time population low of three adults and three cubs (Fig. 7.1).

7.5 Discussion

Conservation and management decisions of populations depend critically on what factors drive population growth (Sinclair & Krebs 2002). No critical tests of the roles of density-dependent and independent factors play in regulating populations of leopards have been obtained, primarily because of the difficulty in gathering data simultaneously on large carnivores and their prey (Fryxell *et al.* 1999). This data set provided a unique opportunity to evaluate the importance of density-dependent and independent regulation on the different life stages of a leopard population in a prey-rich reserve in the absence of human persecution. The conclusions drawn are not based on experimental tests and should be used with caution.

Three processes could have influenced this leopard population. The first and primary process was the bottom-up regulation of carrying capacity through food supply, which sets the upper limit of trophic-level growth (Bertram 1975, Stander *et al.* 1997, Sinclair & Krebs 2002). An increase in primary producers (plants) through increased rainfall provided more food for primary consumers (ungulates). Ungulates showed a numerical response to increased food and increased numbers. Secondary consumers (leopards) also showed a numerical response to increased availability of prey through subadult recruitment. These cycles vary dependent on environmental conditions, and have a year delay because of the time required for ungulates to have offspring (Trostel *et al.* 1987, Parker *et al.* 2009). Mortality was not significantly affected by prey biomass. Density-dependent limitation of prey numbers on leopard was not evident; we found no leopards emaciated or diseased. If food shortage were the mechanism controlling the population around carrying capacity, then increased infant mortality through abandonment (Packer & Pusey 1984, Kelly *et al.* 1998), starvation in subadults (Packer & Pusey 1995, Inman *et al.* 2012) and lowered reproductive output (Krebs 2010) would be strongly apparent.

The second, may be a density-dependent regulatory process, limitation of territorial space (intraspecific competition), which would stabilise the population prior to food becoming limiting. This was seen by the high percentage of subadult mortalities during years of high population density. When population numbers were low these subadults would be recruited into the population. The assumption is that space or more specifically territories is the limiting factor. When resource imposed limitations were reached, a steady density was maintained through social behaviour (intraspecific competition, i.e. territoriality, dispersal, subadult mortalities) (Begon *et al.* 1996, Sinclair & Krebs 2002). Territorial behaviour could be the mechanism that limits the number of adult leopards that are able to coexist in this particular habitat, have access to food supply, and engage in reproductive activities.

Territory size is related to available resources and this could put a limit on the adult population size (Hayward *et al.* 2009). The leopard population was also regulated close to carrying capacity and stabilised through increased subadult mortalities and dispersal. During years of high population density subadult mortality was high, as a result of infanticidal killing of subadults unrelated to the breeding male. The year following high population number saw high numbers of dispersing subadults related to the current breeding male. These density-dependent regulatory processes altered the relationship between carrying capacity and population size enabling the population to return to its mean level relative to available resources after a disturbance, and thus regulated the local population size (Solomon 1949, Holling 1965, Krebs 2002, Sibly & Hone 2002).

The third population limiting factor on Karongwe could be density independent top-down social behaviours. These included male territorial takeover, infanticide and female territorial disputes, but could equally include non-infectious disease, stochastic disturbance and human related mortalities at other times (Le Roux & Skinner 1989, Bailey 1993, Meserve *et al.* 1999, Balme & Hunter 2004). These density-independent processes were uninfluenced by population density, did not determine or regulate population densities, but did have an important influence on, and determined the level of realised growth and structure in the population (Solomon 1949, Rockwood 2006).

Natural removal of breeding males resulted in higher mortality rates and in an environment where these density-independent mortalities are large and variable, they could override density-dependent mortalities so that the population fluctuates markedly (Sinclair 1998, Balme *et al.* 2012). This has been shown in populations where human-related removals further destabilise a leopard population having a devastating impact on the population and impeding population recovering (Balme & Hunter 2004, Whitman *et al.* 2004). There were three different breeding males in six years, and leopards may

be similar to lions in that breeding males may only have a 3-4 year tenure, thereby preventing inbreeding (Packer & Pusey 1982).

We suggest that bottom-up forces determined the maximum productivity and range of possibilities in this ecosystem. The stabilising influence on leopard carrying capacity was density-dependent social limitations (territorial space, dispersal and subadult mortalities), which limited the eventual size of the adult population. Top-down forces governed details of realized growth and resultant structure (Gutierrez *et al.* 1994, Sinclair & Krebs 2002). The rate of leopard population growth is dependent on both the density of prey as well as on the density of conspecifics (Fryxell *et al.* 1999). Interactions between these controls produce the variety of complex, nonlinear effects on population growth (Sinclair & Krebs 2002). Rigorous testing of these findings can only come from direct experimentation; however it is encouraging that our results are consistent with the documented patterns of prey dependence and density dependence (Fryxell *et al.* 1999).

Ungulate densities on Karongwe were high and the leopard population was reproducing at a high rate (Owen *et al.* 2010), yet this abundant and diverse resource base did not translate into increased leopard numbers. The average density was comparable with studies undertaken in similar habitats (Hamilton 1981, Norton & Henley 1987, Jenny 1996, Mizutani & Jewell 1998). Studies in areas of lower prey abundance (10–60 kg) showed lower leopard densities, e.g., Serengeti (3.5 adults/ 100 km² – Schaller (1972)); (4.7 adults/ 100 km² – Cavallo (1993)); and two forest habitats (4 adults/ 100 km² – Rabinowitz (1989); 3.4 adults/ 100 km² Eisenberg & Lockhart (1972)). In low rainfall areas (Kalahari – Bothma & le Riche (1984) and farming areas – Grimbeek (1992)), leopard densities were even lower (1.4 adults/ 100 km²).

Bailey's (1993) study, in similar habitat showed unusually high leopard densities (10-17 adults/ 100km²) probably due to high impala numbers. This verifies the Hayward *et al.* (2007) model, which suggests leopard numbers are related to their preferred prey within the preferred weight range. Bailey (1993) also showed that sixty four percent of leopard deaths were the result of starvation in the early dry season, when small leopard territories prevented hunting of widely scattered impala.

The high of 25 individuals on KGR in 2003 were similar to those densities reflected by Bailey (1993), and almost certainly reflect the upper limit of carrying capacity. It seems unlikely that leopard populations in South Africa can attain densities as high as 1 per km² (Myers 1976). Predator to prey ratios (1:53) were intermediate to the Serengeti (1:82) and the Kruger (1:27) and we believe that the decisions driving this leopard population are relevant to other African savannas (Thaker *et al.* 2010).

Although our study suffers from similar limitations to other leopard studies of small population size, large home ranges, cryptic nature, difficult terrain and a lack of experimentation and correlative assumptions our results are still pertinent to the conservation and management of leopard and other solitary territorial species. Understanding population dynamics and factors responsible for controlling top predators allows us to appreciate how these species interact with their environment, and enable effective population management. Unless it is known which factors drive and limit population growth of top-level predators, additional pressure such as hunting, culling and persecution, which alter the internal characteristics of a population, may drive the population into a reproductive dead-end (Grimbeek 1992, Balme & Hunter 2004). Absolute numbers of leopards in South Africa are difficult to determine owing to their secretive habits, together with the nature of the habitat in which they live (Norton 1990, Gros *et al.* 1996). We believe the carrying capacity on Karongwe is close to the maximum, and planning should focus on the envisaged spatial-social structure of the population (i.e. number of territories of adults that the local environment can support), which could be the ultimate limitation on future population size. Reintroduction plans should be formulated around this premise, and post-reintroduction monitoring (Kleiman 1989) should be designed to assess this component, rather than overall population size or productivity, which can fluctuate widely.

Table 7.1. Rainfall, herbivore biomass, ungulate biomass and predators on KGR from 2000-2005. Total herbivore biomass includes ungulates, elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibious*) and white rhinoceros (*Ceratotherium simum*).

	2000	2001	2002	2003	2004	2005
Annual Rainfall (mm)	952	507	478	247	547	523
Ungulate biomass (15-40kg) (kg/km ²)	3622	3843	3659	3667	3278	2564
Total herbivore biomass (kg/km ²)	3949	4505	4532	4320	3945	3703
Leopard numbers	13	16	24	25 (2)*	19	12
Adult leopard numbers	6	6	7	8	6	5
Estimate of adult leopard population following (Hayward <i>et al.</i> 2007)	7	7	7	7	6	5
Total large predators ²	22	35	50	64	59	46

* () figure indicates annual removals

² Includes lion, spotted hyena, cheetah, African wild-dog.

Table 7.2. The leopard population size, sexes, ages and mortalities of the KGR leopard population from 2000 – 2006.

A. Leopard population information

	2000	2001*	2002	2003	2004	2005*	2006	Total over the study period (%) #	Average ± SE
Population size	13	16	24	25	19	12	6	109	16 ± 2.6
Males	5	8	11	7	3	1	1	35 (32.1)	5 ± 1.4
Females	8	8	13	16	12	8	4	65 (59.6)	10 ± 1.5
Adult males	1	1	1	2	1	1	1	7 (6.4)	1 ± 0.1
Adult females	5	5	6	6	5	4	2	31 (28.4)	5 ± 0.5
Adults	6	6	7	8	6	5	3	38 (34.9)	6 ± 0.6
12-36 months	5	6	7	11	7	2	0	38 (34.9)	5 ± 1.4
0-12 months	2	4	10	6	6	5	3	33 (30.3)	5 ± 1.0

B. Annual mortality within each life stage of the leopard population (% mortality)

	2000	2001*	2002	2003	2004	2005*	Total mortality	Average ± SE
Total mortality	0	2 (12.5)	2 (8.3)	4 (16)	7 (36.8)	6 (50)	21 (19.3)	4 ± 1.1
Adult males	0	1 (6.3)	0	0	1 (5.3)	0	2 (1.8)	0.4 ± 0.2
Adult females	0	1 (6.3)	0	1 (4)	3 (15.8)	1 (8.3)	6 (5.5)	1 ± 0.4
12-36 months	0	0	2 (8.3)	1 (4)	0	2 (16.7)	5 (4.6)	1 ± 0.4
0-12 months	0	0	0	2 (8)	3 (15.8)	3 (25)	8 (7.3)	2 ± 0.6

C. Annual percentage real mortality within each life stage of the leopard population

	2001*	2002	2003	2004	2005*	Average % real mortality within each life stage
Males	12.5	18.2	0.0	33.3	0.0	11.4
Females	12.5	0.0	6.3	25.0	37.5	12.3
Adult males	100.0	0.0	0.0	100.0	0.0	28.6
Adult females	20.0	0.0	16.7	60.0	25.0	19.4
Adults	33.3	0.0	12.5	66.7	20.0	21.1
12-36 months	0.0	28.6	9.1	0.0	100.0	13.2
0-12 months	0.0	0.0	33.3	50.0	60.0	24.2

* New male take over, # totals exclude 2006, which only highlight the number of leopard remaining at the end of 2005 and were not used in calculations

Table 7.3. Number of leopard killed and the causes of leopard mortality on Karongwe from 2000 – 2006

Cause of mortality	Confirmed	Suspected	Total
Intraspecific:			
Same sex clashes	2	-	2
Male female clashes	2	-	2
Male kills subadult	2	1	3
Infanticide	4	-	4
Subadult kills next litter	1	-	1
	52%	5%	57%
Interspecific:			
Lion	1	-	1
	4.8%	-	4.8%
Human related			
Snare	1	-	1
Vehicle	1	-	1
	9.5%	-	9.5%
Natural causes			
Old age	-	2	2
	-	9.5%	9.5%
Unknown	-	4	4
Total	14	7	21

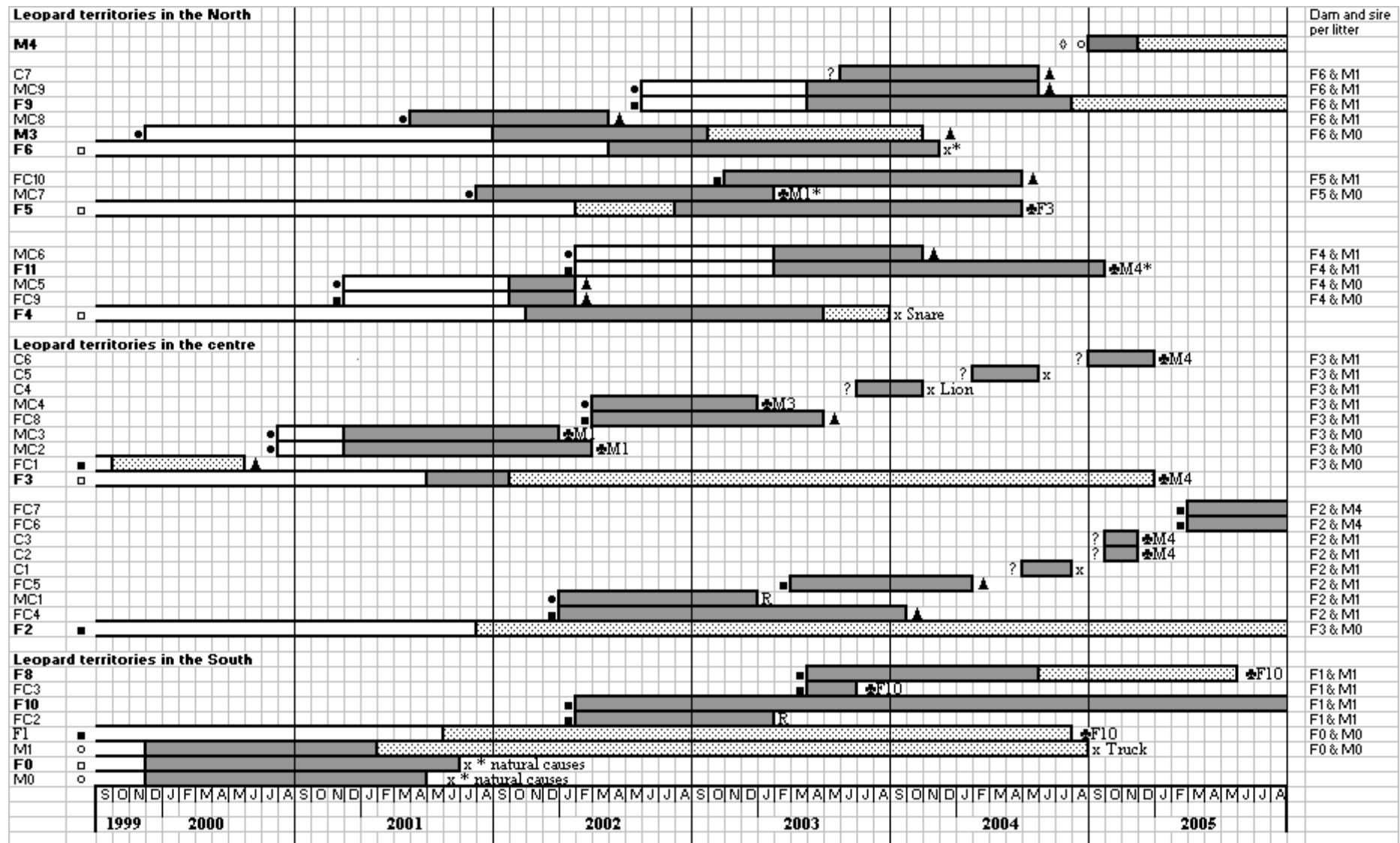


Figure 7.1. Reproductive output and population demographics of the leopard population on the KGR over six years (1999 – 2005). Points on the left-hand side indicate the date at which the individual entered the system while those on the right-hand side are when the individual died, dispersed or was translocated. Numbers to the left of each symbol are the studbook numbers. Cubs born are shown above their mother, while the dam and sire for each litter are given on the right-hand side of the figure. Location within the reserve of adult females is also indicated on the left.

□ = adult female, ○ = adult male, ■ = female cub, ● = male cub, ? = Sex unknown. X = died,

♣ = killed by another leopard number indicates which leopard,* = what probably happened, ▲ = dispersed, R = removed, ◇ = immigrant adult.

7.6 References

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CHAPTER 8

SPACE USE REGULATION OF A SOLITARY FELID IN A PREY RICH RESERVE

8.1 Abstract

Space use and territorial behaviour of individuals can influence species' population structure and dynamics. Key resources that are fundamental for survival and reproductive success of a species are critical in determining space use, and ultimately govern population density. We explored the relationship between space use and the key resources of seven female and two male radio-tagged leopards (*Panthera pardus*) in a prey- rich reserve in South Africa. The breeding male's territory included the majority of the reserve ($78.8 \pm 0.5 \text{ km}^2$) and overlapped with the home ranges of all the females. The territory of the non-breeding adult male was smaller ($15 \pm 4.7 \text{ km}^2$) than the average female territory ($21.8 \pm 3.1 \text{ km}^2$; range $9.3 - 51.5 \text{ km}^2$). In this reserve, where prey was not limiting, habitat was the major driver of the leopard territorial system. Leopard habitat selection within home ranges, and range size, was determined by their foraging decisions matching the resources of their preferred prey, and by riparian areas, and these were the key limiting resource, regulating population density in this reserve. Female leopard were highly territorial, with relatively low overlap between females. Territoriality (exclusive use) was governed by ungulate biomass, increasing during years of high ungulate density. Our results contribute to the understanding of space use, key resources and territoriality that influence population structure and dynamics in prey rich areas. These baseline data used alone or in conjunction with historical data provide valuable information to agencies involved in habitat protection and restoration, for not only this species but other threatened species as well.

8.2 Introduction

How species distribute themselves within the landscape and their spatial organisation in core areas, home ranges and territories provides us with an understanding of species' population density, social organization, key resource requirements, and the limiting factors that restrict populations (Fretwell & Lucas 1969, DuVal 2002). A home range is usually defined as the area in which an animal confines its daily activities of gathering food, mating and caring for young (Burt 1943). This excludes exploratory 'forays' and therefore this is not the entire area traversed during its lifetime (Mizutani and Jewell 1998).

Home range size, spatial utilisation and the degree of territorial overlap vary widely within species, because they are strongly influenced by key resource requirements. These resources include prey

quality and quantity (Powell *et al.* 1997), body mass (Litvaitis *et al.* 1986), prey distribution and abundance, population density (Dahle & Swenson 2003), cover for hunting (Lucherini *et al.* 1995) water, denning sites, habitat requirement (Sandell 1989), and possible mates (Marker & Dickman 2005) among others that are fundamental for survival and reproductive success.

Home range size is a primary ecological parameter which determines the spatial scale at which natural processes operate, and is crucial to our understanding of species' distribution, and population estimates (Wiens 1989). Such appreciation of scale is also essential for many aspects of management and conservation planning, as understanding how much space individuals need facilitates an estimation of potential carrying capacities (Smallwood 2001, Herfindal *et al.* 2005).

The leopard is described as a solitary felid, only coming together to mate and where females have dependent cubs (Sunquist & Sunquist 2002). Their spatial organisation shows little overlap between neighbouring males. One male's range overlaps the range of between four to six females and superimposed on that are transient subadult and old adult leopards (Bailey 1993). The spacing patterns of female leopard like most felids are determined by food supply and habitat, while males ensure access to a number of females in the absence of neighbouring male interference (Bothma *et al.* 1997, Mizutani and Jewell 1998, McManus 2009, Grant 2012).

Large carnivores generally cover great distances to meet their resource needs (Gibson & Koenig 2012) and, although their home range is traversed during the course of daily activities, the boundaries are seldom defended against conspecifics (Gibson & Koenig 2012), and often the home ranges of several individuals overlap (Moorcroft & Lewis 2006, Macdonald *et al.* 2010).

The socio-spatial organisations of leopard are determined by territoriality, where the defended area (territory) is usually a smaller area within the home range where a fixed area of limiting resources are defended to the exclusion of conspecifics by territorial defence, thereby ensuring access to these resources all year round (Adams 2001). A territory is a spatially stable and exclusive area which is defended against rivals and territoriality is one of the most important behavioural traits affecting spatial organisation of wildlife population (Mizutani and Jewell 1998).

In territorial species, space use, overlap and ranging patterns are used to identify social systems, and provide indirect information and insight about social interactions (Shier & Randall 2004). In nocturnal predators, direct territorial interactions are difficult to observe, and territoriality is confirmed by the exclusive use of an area (less than 25% overlap between same sex conspecifics) (Poole 1995, Ferreras *et al.* 1997, Azevedo & Murray 2007), often with the highest concentration of kills centred in the core area (Poole 1995).

We investigated the home range size and intraspecific spatial overlap of leopard (*Panthera pardus*) in a protected reserve with artificially high prey density. By examining territoriality, we aimed to understand how this social factor can regulate population density in the absence of forage limitations and human disturbance (Maher & Lott 2000). Resource availability may regulate populations (Bailey 1993), but in small enclosed reserves where ungulate numbers are abundant, carnivore numbers may be regulated at a level below that expected from available resources, through territorial competition and density dependent social behaviours (Hairston *et al.* 1960, Trinkel *et al.* 2010, Chapter 7). Such small, enclosed, reserves make up 16.8% of the total land in South Africa, and undertaking sound ecological research in these areas will provide valuable data for evidence-based conservation and management decisions (Cousins *et al.* 2008).

I hypothesise that prey density would be instrumental in determining home range size and that leopards would have heavier prey use in the core of their ranges. I also expect territories to be smaller with less overlap when population density is high. This study aimed to elucidate key factors limiting the population size of leopard in the absence of prey constraints. Our specific objectives were to (i) determine home range and territory size, (ii) identify key resources that determine range and territory size, (iii) identify key factors responsible for increasing territory overlap, and (iv) understand how territory size and overlap influence population size and potentially population regulation.

8.3 Methods

8.3.1 Study area

Fieldwork was conducted on the 85 km² Karongwe Private Game Reserve (KGR), Limpopo Province, South Africa (24°139'S, 30°369'E). The reserve was formed in 1998 and is located within the savanna biome (Rutherford & Westfall 2003) comprising of Mixed Lowveld Bushveld (Low & Rebelo 1998). The study area was characterized by hot, rainy summers (November – April) and warm, dry winters (May – October), with an average annual precipitation of 487 mm. Animals have access to waterholes and rivers across the reserve, and water is not limiting (Thaker *et al.* 2010). The main function of the reserve is ecotourism, and leopards are protected within the reserve.

8.3.2 Herbivore population assessment

A total count of herbivore species were censused annually in September by aerial counts, and mean herbivore biomass was calculated according to Coe *et al.* (1976). Wet season (October – March) herbivore presence and distribution was determined using road strip census procedures (Chapter 2). Herbivore utilisation distributions were georeferenced, and intersected with the habitat map using ARCGIS 9, thereby assigning a land cover type to each herbivore location. We produced annual utilization distributions (UD) for each ungulate species. The UD layer was converted into a point

layer and overlaid on the habitat map using Arc GIS 9.3, producing a UD-weighted estimate of use for each ungulate species in each habitat.

8.3.3 *Habitat*

We used a habitat map of Karongwe with the following physiognomic classes (Thaker *et al.* 2010, 2011): Closed riverine (1.6% of total area), consisting of gallery forests along rivers; Open riverine (15.8%), consisting of open canopy forest with thick understory along rivers and drainage lines; Closed woodland (54.4%), consisting mainly of *Combretum* and *Mopane* woodlands with closed tree canopies; Open woodland (24.1%), consisting mainly of *Acacia* with separated tree canopies; and Open scrub (4.1%), consisting of old agricultural lands now reverting to open scrub habitat.

8.3.4 *Home range data collection*

The study, conducted from September 2001 to August 2005, was part of a larger study on leopard conducted over a 6-year period from September 1999 to August 2005. We monitored seven female and two male leopards, captured by free darting from a vehicle, and fitted with radio collars (Owen *et al.* 2010). We collected diurnal and nocturnal locations for all collared leopard between 05:30 h and 20:30 h with additional intermittent continuous monitoring of 2 – 96 h duration (Owen *et al.* 2010). To determine population size we used the minimum count method with recognizable individuals (Kunkel *et al.* 2005), in conjunction with territorial mapping in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California), tracks, and radiotelemetry.

All home range data were taken from resident collared leopards. Although the small size of the reserve restricted the sample size, individuals were followed intensively which provided detailed information on social interactions, hunting and movement behaviours. For spatial analyses, we only used one morning and one evening location per 24 h period for each leopard to avoid autocorrelation. Home ranges were calculated using the Animal Movement Extension (Version 2.04) in ARCGIS 9.3 (Hooge *et al.* 1999). The fixed kernel estimator, with contours of 95% (active use) and 50% (core use) probability of use, was used to estimate home and core range areas respectively, based on more than 30 locations per estimate (Seaman *et al.* 1999). We used Least Squares Cross Validation (LSCV) to determine the appropriate smoothing parameter for the kernel estimates (Seaman *et al.* 1999).

Using these techniques, we produced annual utilization distributions for each individual leopard, using only 95% of the UD to decrease likely bias from the UD tails (Anderson 1982, Millspaugh *et al.* 2006). The UD layer was converted into a point layer and overlaid on the habitat map using Arc GIS 9.3, producing a UD-weighted estimate of use for each habitat type for individual leopards. Leopards

show individual variation in behaviour and home range habitat selection, and data were therefore not pooled.

8.3.5 *Prey preference*

The preferred prey of leopards was calculated and a comparison was drawn between habitat use of leopard and that of their preferred prey. Diet selection was calculated using Jacobs' index, where p was the proportional abundance of that species in the total prey population, and r was the relative proportion that each species made up of the total leopard kills (Jacobs 1974):

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

The resulting values ranged from +1 (maximum preference) to -1 (maximum avoidance) (Jacobs 1974). We calculated annual prey selection within the home range of each female. If a species was killed more frequently than expected from its relative abundance within that leopard's territory, then it was considered preferred.

Similarly, we derived habitat use from animal locations. Using Jacobs' index, both ungulate habitat selection and leopard hunting habitat selection were calculated for each habitat (Closed riverine, open riverine, closed woodland, open woodland and open scrub), and study year (Y1 to Y5) (Jacobs 1974).

8.3.6 *Space use overlap*

To assess overlap of space use between leopards, and to understand limitations on territoriality and spatial use, we calculated the volume of intersection (VI) (Seidel 1992, Millspaugh *et al.* 2004). The VI quantified the degree of overlap in shape and location of two individual leopards' UD's as:

$$VI = \iint f^A(x, y), f^B(x, y) dx dy$$

where f^A is the estimated UD for leopard A and f^B is the UD for leopard B . We identified leopard B as the closest individual of the same sex. VI scores range from 0 – 1, where VI scores approaching 1 indicate a high degree of overlap between UD's. Percentage overlap was calculated on home range rasters using the VI Index in ArcGIS. Where two or more leopard overlapped, an average percentage overlap was taken for each leopard to assess average changes each year. To understand the factors that influence territoriality (i.e. lead to a decrease in overlap), percentage overlap was correlated with key

resources (prey biomass, habitat type, river length), and with population density, age and season (wet and dry).

To understand if home range plays an important role in determining leopard population dynamics as limited by food, we calculated the number of kills in the core area (50% range), and compared this to the number of kills in the remaining home range. To understand the factors responsible for territory sizes we ran separate regression analyses to quantify significant effects of each variable on territory size (power was too low for GLM approaches). All data were tested for the assumptions of normality (Kolmogorov– Smirnov and Lilliefors test) and normalised when required. We conducted all statistical tests using SPSS Version 19 (SPSS inc. 233 S, Wacker Drive, 11th floor, Chicago, IL).

8.4 Results

Leopard population size on the reserve varied from 6 to 25 animals (including young) across the years of study, with an annual mean of 16 ± 2.6 leopard/ 85 km^2 ($= 0.18 \text{ km}^{-2}$) (Table 8.1). There were between four and six breeding territorial females at any one time (Table 8.1). On three separate occurrences, territories were taken over by daughters after the mother died (F8 replaced F1, F11 replaced F4 and F9 replaced F6 (Table 8.1)). In 2002 and 2003, we collared five of the six adult breeding females, but due to one collar failure we were able to obtain space use data on only four females. In 2004 and 2005, all territorial females were collared.

The home range sizes of females ranged from $9.3 - 51.5 \text{ km}^2$ (mean $21.8 \pm 3.1 \text{ km}^2$, $n = 17$). The breeding male's home range was considerably larger and covered the majority of the reserve, mean size $78.8 \pm 0.5 \text{ km}^2$ (range $77.9 - 79.4$, $n = 3$ years) which encompasses the entire reserve and all the territorial females' home ranges. The non-breeding adult male held a much smaller home range (mean $15 \pm 4.7 \text{ km}^2$ range $10.13 - 24.61 \text{ km}^2$, $n = 3$ years) (Table 8.1). The average core comprised about 29 % of females' home range $6.4 \pm 1.2 \text{ km}^2$ (range $1.3 - 16.7 \text{ km}^2$, $n = 17$). The non-breeding male's mean core was $5 \pm 1.6 \text{ km}^2$, about 33% of his home range, while the breeding male's core was $35 \pm 4.3 \text{ km}^2$, about 45% of his home range (Table 8.1).

Average ungulate biomass was $4,064 \text{ kg/km}^2$ ($SE = 938$, range $3,703 - 4,532$) for the survey years 1999 – 2005. Mean biomass across years was above the predicted mean for Karongwe ($2,789 \text{ kg/km}^2$) at which the ungulate biomass should be stocked, and above the predicted maximum ($3,681 \text{ kg/km}^2$) that should not be exceeded (Coe *et al.* 1976). Even the lowest ungulate biomass on Karongwe (2005: $3,703 \text{ kg/km}^2$) was above this maximum predicted stocking rate (Table 8.1).

The preferred prey of leopard were duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus scriptus*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus africanus*), and impala (*Aepyceros melampus*), with annual principal prey indicated in Table 8.3.

All leopard principal prey selected either closed or open riverine if not both as a preferred habitat type and actively avoided closed woodlands (exception duiker and wildebeest selected open scrub and open woodland respectively) (Table 8.3).

All female leopard home ranges contained the three most abundant habitats, closed woodland, open scrub and open woodland in the greatest proportions (Table 8.4). The utilisation distribution of female leopard indicated that they generally used the habitat of their preferred prey and the habitat in which they selected to hunt their preferred prey in, in the greatest proportion (Table 8.4). With few exceptions, female leopard utilisation distribution showed closed riverine and open riverine (riparian), used in greater proportion to their availability (Table 8.4).

Significantly important aspects determining the size of female leopards' home range were river length ($r = 0.81$, $SE \pm 0.32$, $P < 0.001$, $n = 17$), closed woodland ($r = 0.97$, $SE \pm 3.1$, $P < 0.001$, $n = 17$), the area of their preferred prey's habitat ($r = 0.80$, $SE \pm 5.7$, $P < 0.002$, $n = 17$), and area of riparian habitat ($r = 0.56$, $SE \pm 11$, $P = 0.02$, $n = 17$) in particular open riverine ($r = 0.70$, $SE \pm 9.5$, $P = 0.002$, $n = 17$) within their home range. Home range size was not significantly correlated with closed riverine on its own ($r = 0.07$, $SE \pm 4.9$, $P = 0.78$, $n = 17$), but was correlated with the area of preferred prey's habitat, suggesting that leopard primarily used closed riverine for hunting. Territory size reflected their prey's habitat resource.

Length of river within a home range did not increase significantly with leopard age ($r = 0.42$, $SE \pm 5.6$, $P = 0.09$, $n = 17$). Three young females inherited their mother's home range, thereby reducing the statistical power of the results. Length of river did not correlate to the area of riparian habitat. Length of river was highly significantly correlated with area of closed woodland ($r = 0.68$, $SE \pm 4.5$, $P < 0.001$, $n = 17$) and open woodland ($r = 0.54$, $SE \pm 5.2$, $P = 0.03$, $n = 17$). This suggests that river length was selected by leopard for the adjacent closed and open woodland used for hunting.

Although there were seasonal changes in individual home range size, there were no overall patterns of seasonal expansion or contraction of their home range, or of their core. Average home range size during both wet and dry season was 21.3 km^2 (core size 6.19 ; core range $1.23 - 17.09 \text{ km}^2$).

Overlap of home ranges of adjacent leopards was low, with a mean VI score of 0.11 ± 0.01 , median 0.11 ($n = 27$, range $0.01 - 0.3$), suggesting that same-sex resident individuals established exclusive areas (Table 8.2). Percentage territorial overlap of female home ranges increased significantly with population size ($r = 0.70$, $SE \pm 0.03$, $P = 0.002$, $n = 17$) and with the number of territorial females in the population ($r = 0.70$, $SE \pm 0.03$, $P = 0.001$, $n = 17$). Although overlap increased during years of high population density, home range size did not change. Both wet and dry season overlap were the

same 0.07 ± 0.02 . An increase in prey biomass, resulted in increased territoriality (less overlap) ($r = -0.69$, $SE \pm 0.03$, $P = 0.02$, $n = 17$).

The density of kills in each leopard home range was not equally distributed (Table 8.5). Leopard made on average 5 ± 1.1 kills.km⁻² in the core, and only 1.2 ± 0.2 kills.km⁻² in the remainder of the home range. There was no significant seasonal variation in kill distribution, either inside or outside the core area (Table 8.5).

8.5 Discussion

The most important finding from this study was that, in a prey-rich environment, prey abundance did not translate into smaller leopard territories and thence increased population size (Swanepoel 2008). Leopard territorial habitat selection and size were determined by their foraging decisions, matching the resources of their preferred prey, and riparian areas. Closed woodland was the most abundant and important prime hunting habitat as well as riparian habitat, used for hunting, also provided shade, and its three dimensional structure likely permitted shared use of riverine habitat with lion (Chapter 5). In addition, riparian areas are important for connectivity between habitats, especially for animals such as leopard, needing to travel large distances over the fragmented landscape (LaRue & Nielsen 2008). Both riparian and its associated closed and open woodlands habitat were limiting key resources, resulting in average female territorial sizes being larger than that reported for other Acacia woodland studies (11.3 km² - Bailey 1993; 14.4 km² - Hamilton 1976). This highlights that, even in prey dense areas, the availability of quality habitat defined by other characteristics determined territorial size, and set the upper population limit (Lima 2002, Chapter 5). This contradicts the reasoning that increased prey numbers would result in increased leopard numbers and therefore an increase in leopard hunting quota can be made (Swanepoel 2008)

As with other studies we observed limited intrasexual home range overlap, with leopard using both defence and exclusive use of area to determine territorial spacing within their home range (Maher & Lott 1995, Mizutani & Jewell 1997, Swanepoel 2008, Grant 2012, Chapter 7). There was evidence of territorial influence on prey selection patterns, corroborated by heavier prey use in the core of their ranges (Mech 1977, Pierce *et al.* 2000, Azevedo & Murray 2007, Chapter 5). In contrast, there was a high degree of intersexual overlap, suggesting that female distribution influences male spacing patterns (Sandell 1989, Odden & Wegge 2005, Swanepoel 2008, Macdonald *et al.* 2010, Grant 2012). This was expected for a solitary predator in a mesic area of abundant evenly distributed forage (Poole 1995, Mizutani & Jewell 1997). Some studies have revealed considerable intrasexual homerange overlap. This is likely in areas of heavy persecution as a result of range expansion by immigrants and subadults following the removal of a breeding male (Marker & Dickman 2005).

Annual increases in ungulate density did not translate into smaller home ranges as has previously been proposed (Smith & Shugart 1987) in birds. The home range of leopard remained the same size as prey density changed. However, the degree of territorial overlap decreased with increasing prey density, and leopard became more territorial (spent more time within their defended area rather than across their entire range), locating sufficient forage in a smaller area.

During periods of increasing prey density, adult encounters with sub adults and floaters were lower, allowing these transitory individuals to persist in the gaps between territories, and resulting in a population increase (Mech 1977, Pierce *et al.* 2000, Chapter 7). At the upper population limit, the number of territorial females never exceeded six, suggesting this to be the maximum number of available territories on the reserve. With decreasing ungulate density, territoriality decreased, with females expanding use outside of exclusively defended areas, and across their entire range, resulting in increased density dependent intraspecific encounters and increased mortality associated with conflict, and, thereby, population decline (Chapter 7). A study undertaken by Marker and Dickman (2005) also found a higher percentage overlap in food scarce areas. Both wet and dry season overlap were the same, therefore home ranges were large enough to accommodate seasonal shortages in this super abundant reserve (Simcharoen *et al.* 2008).

As with other large carnivores, territoriality plays an important role in determining leopard population dynamics, by limiting the number of adult leopards that are able to coexist in a particular habitat, have access to resources, and participate in reproductive activities (Azevedo & Murray 2007, Owen *et al.* 2010, Wehtje & Gompper 2011). The number of territories available to females was set by spatial limitations, and the size of each territory was determined by, among other things, available key resources and population density (Clutton-Brock & Harvey 1978, Litvaitis *et al.* 1986, Dahle & Swenson 2003, Azevedo & Murray 2007).

The effective management of wildlife populations depends largely on understanding the relationship animals have with their environment, how they are organised in space, and factors affecting spatial arrangement (Ben-Shahar & Skinner 1988, Manly *et al.* 1993, Kernohan *et al.* 2001, Moore *et al.* 2013). A reduced prey base, conflict with livestock farmers, an increased fragmentation, and habitat loss have drastically reduced leopard populations (Nowell & Jackson 1996). In South Africa, this has resulted in isolated populations which continue to be harvested with little chance of population recovery (Balme & Hunter 2004). Characterising species habitat selection, and important resources that dictate population persistence in a stable environment, can guide and streamline conservation efforts. Determining the effects of habitat loss, degradation and fragmentation on species' risk of extinction can be critical when planning habitat restoration (Myers 1976, MacMahon 1997, Simcharoen *et al.* 2008). To develop long-term conservation plans for large carnivores, it is not enough to maintain large numbers of prey; riparian habitat and appropriate hunting habitats are

important for leopard to flourish (Hopcraft *et al.* 2010). Top carnivore populations can fluctuate markedly (Chapter 7), and we demonstrate here the importance of not simply knowing population numbers, but rather understanding the effective population size (in this case the territorial females).

Table 8.1. Annual home range size (km²) of the seven female leopard (F1 to F11), M1 (the breeding male) and M3 (a non-breeding male) for the core range (50%) and the overall range (95%).

Year	Population size (including young)	No of territorial females	F1 50%	F1 95%	F2 50%	F2 95%	F3 50%	F3 95%	F4 50%	F4 95%	F8 50%	F8 95%	F9 50%	F9 95%	F11 50%	F11 95%	M1 50%	M1 95%	M3 50%	M3 95%
2002	24	6	2.4	10.9	7.6	27.1	9.2	37.0	2.4	10.5	-	-	-	-	-	-	35.07	79.05	4.37	10.13
2003	25	6	1.3	9.3	10.6	31.5	3.5	18.0	10.8	30.6	-	-	-	-	-	-	27.91	77.91	2.66	10.67
2004	19	5	3.0	14.0	16.4	42.1	3.9	14.3	-	-	-	-	2.7	10.7	3.2	13.1	42.66	79.42	8.11	24.61
2005	12	4	-	-	16.7	51.5	2.0	11.1	-	-	4.5	14.6	8.1	24.6	-	-	-	-	-	-
Mean			2.2	11.4	12.8	38	4.7	20.1	6.6	20.6			5.4	17.6			35.2	78.8	5.0	15.1
±SE			±0.5	±1.4	±2.2	±5.5	±1.6	±5.8	±4.2	±10	4.5	14.6	±2.7	±7	3.2	13.1	±4.3	±0.5	±1.6	±4.7

Table 8.2. Annual territorial, overlap and habitat information for leopards and their preferred prey from 2002 – 2005 on the Karongwe Game Reserve.

Leopard ID	Year	Average VI index % overlap	Annual Preferred prey	Preferred hunting habitat	Preferred prey habitat	Abundance of preferred prey	Prey biomass (kg)	Abundance of principal prey	Leopards population size (including young)	Length of river in territory (km)	Area of Closed woodland in each HR (km ²)	Area of preferred prey habitat (km ²)
F1	2002	12%	Duiker	OR	OS	18	3659	2398	24	7.2	5.9	5.9
F1	2003	4%	Impala	OR	CR	1252	3667	1619	25	4.8	4.9	4.9
F1	2004	6%	Duiker	OR	OS	15	3278	1206	19	8.6	7.4	7.4
F2	2002	19%	Duiker	OR	OS	18	3659	2398	24	8.5	17.3	17.3
F2	2003	11%	Duiker	OR	OS	7	3667	1619	25	12.9	19.5	19.5
F2	2004	11%	Duiker	OR	OS	15	3278	1206	19	21.5	24.8	24.8
F2	2005	13%	Duiker	OR	OS	16	2564	1468	12	21.3	29.2	29.2
F3	2002	14%	Warthog	OR	CR	266	3659	2398	24	18.7	20.5	20.5
F3	2003	17%	Warthog	OR	CR	119	3667	1619	25	15.6	9.4	9.4
F3	2004	15%	Bushbuck	CR	CR	14	3278	1206	19	12.9	5.7	1.1
F3	2005	18%	Bushbuck	CR	CR	21	2564	1468	12	12.4	4.6	0.9
F4	2002	10%	Bushbuck	CR	CR	127	3659	2398	24	5.4	5.2	0.6
F4	2003	12%	Bushbuck	CR	CR	56	3667	1619	25	22	13.5	2.1
F9	2004	1%	Bushbuck	CR	CR	14	3278	1206	19	8.4	4.3	1.0
F9	2005	14%	Bushbuck	CR	CR	21	2564	1468	12	18.7	10.6	2.0
F11	2004	9%	Bushbuck	CR	CR	14	3278	1206	19	6.1	10.6	0.5
F8	2005	10%	Impala	OR	CR	1124	2564	1468	12	9.5	6.5	6.5

CR- Closed riverine, OS-Open scrub, OR- Open river

VI index- the percentage territorial overlap between adjacent leopards

Annual preferred prey and hunting habitats - individual leopards' preferred prey and habitats calculated using Jacobs index

Preferred prey habitats are the preferred habitat of each leopard's preferred prey calculated using Jacobs index

Prey biomass - the calculated biomass of all prey on the reserve

Principal prey - the eight most frequently consumed prey

Table 8.3. Habitat selection by principal prey of leopard on Karongwe Game Reserve using the Jacobs index of preference.

Habitat	Impala	Waterbuck	Warthog	Bushbuck	Duiker	Wildebeest	Kudu	Rank
Closed riverine	0.60	0.08	0.14	0.90	-0.30	-0.75	0.52	1
Closed woodland	-0.16	-0.11	-0.16	-0.67	0.00	0.00	-0.07	4
Open Scrub	-0.08	-0.16	0.20	-0.35	0.23	0.10	-0.11	3
Open riverine	0.45	-0.06	0.24	0.77	-0.19	-0.72	0.45	2
Open woodland	-0.21	0.10	-0.12	-0.67	-0.26	0.09	-0.35	5

Values range from +1 (maximum preference) to -1 (maximum avoidance)

Rank indicates the habitat type with the highest preference rating across all principal prey

Table 8.4. Comparing the proportion of habitat in each leopard territory with their UD, relative frequency of occurrence on Karongwe.

	F1 territory habitat proportions	F1 UD	F2 territory habitat proportions	F2 UD	F3 territory habitat proportions	F3 UD	F4 territory habitat proportions	F4 UD	F8 territory habitat proportions	F8 UD	F9 territory habitat proportions	F9 UD
2001-2002												
Closed riverine	1.6	2.5	0.2	0.4	2.3	1.4	5.5	8.6	-	-	-	-
Closed woodland	54.0	50.3	64.0	63.2	55.3	58.5	49.4	48.1	-	-	-	-
Open scrub	24.5	24.4	11.0	13.3	10.8	10.6	12.4	12.0	-	-	-	-
Open riverine	7.3	11.5	0.9	1.5	2.3	1.6	6.7	8.8	-	-	-	-
Open woodland	12.2	10.7	23.6	21.4	28.2	27.2	24.7	20.4	-	-	-	-
2002-2003												
Closed riverine	1.8	3.3	0.3	0.3	3.5	6.7	7.0	8.2	-	-	-	-
Closed woodland	53.0	44.9	62.0	64.1	52.6	44.5	44.0	43.2	-	-	-	-
Open scrub	24.1	26.0	10.6	12.7	10.6	13.7	11.6	10.2	-	-	-	-
Open riverine	8.5	15.1	0.5	0.7	3.5	7.9	6.6	7.1	-	-	-	-
Open woodland	12.1	10.0	26.3	22.1	28.3	24.9	28.2	28.1	-	-	-	-
2003-2004												
Closed riverine	1.3	2.3	1.1	0.2	7.7	10.2	-	-	-	-	9.7	12.2
Closed woodland	52.5	48.3	58.8	62.0	40.3	39.2	-	-	-	-	40.7	41.3
Open scrub	25.9	26.9	10.4	10.9	11.2	11.6	-	-	-	-	11.4	12.0
Open riverine	6.0	10.8	1.7	0.4	7.3	11.0	-	-	-	-	6.8	7.7
Open woodland	14.1	11.1	27.4	26.0	31.0	24.7	-	-	-	-	27.5	21.1
2004-2005												
Closed riverine	-	-	2.2	4.3	8.1	10.1	-	-	1.3	1.9	8.4	10.8
Closed woodland	-	-	56.7	50.9	41.6	40.2	-	-	45.0	43.3	43.1	41.5
Open scrub	-	-	11.3	10.7	11.6	12.7	-	-	27.1	28.2	12.3	11.1
Open riverine	-	-	3.3	4.4	8.1	13.0	-	-	5.4	7.2	7.9	8.1
Open woodland	-	-	25.8	28.1	28.4	21.4	-	-	21.0	19.1	25.3	24.2

Table 8.5. Leopard kill distribution, number of kills and density of kills inside their core (50% area of territory), density of kills in the remaining portion outside the core, and seasonally, on Karongwe Game Reserve from 2002–2005.

Female leopard ID	Year	Core area (50% of territory) (km ²)	Annual number of kills made in the core	Number of kills made per km ² in the core area	Number of kills made in the core during the wet season	Number of kills made in the core during the dry season	Number of kills made per km ² in core area during the wet season	Number of kills made per km ² in core area during the dry season	Area of the territory outside the 50% core (km ²)	Annual number of kills made outside the 50% core	Number of kills made per km ² outside the 50% core	Number of kills made outside the core area during the wet season	Number of kills made per km ² outside the core area during the wet season	Number of kills made outside the core area during the dry season	Number of kills made per km ² outside the core area during the dry season
F1	2002	2.4	9	3.8	3	6	1.3	2.5	8.5	11	1.3	3	0.4	8	0.9
F2	2002	7.6	17	2.2	3	14	0.4	1.8	19.5	10	0.5	2	0.1	8	0.4
F1	2003	1.3	22	16.9	9	13	6.9	10.0	8	7	0.9	3	0.4	4	0.5
F2	2003	10.6	74	7.0	42	32	4.0	3.0	20.9	60	2.9	28	1.3	32	1.5
F3	2003	3.5	16	4.6	12	4	3.4	1.1	14.5	7	0.5	5	0.3	2	0.1
F4	2003	10.8	14	1.3	0	14	0.0	1.3	19.8	16	0.8	0	0.0	16	0.8
F1	2004	3	11	3.7	8	3	2.7	1.0	11	14	1.3	12	1.1	2	0.2
F2	2004	16.4	32	2.0	13	19	0.8	1.2	25.7	22	0.9	7	0.3	15	0.6
F3	2004	3.9	32	8.2	13	19	3.3	4.9	10.4	27	2.6	17	1.6	10	1.0
F2	2005	16.7	32	1.9	18	14	1.1	0.8	34.8	27	0.8	9	0.3	18	0.5
F3	2005	2	6	3.0	1	5	0.5	2.5	9.1	6	0.7	4	0.4	2	0.2
F8	2005	4.5	29	6.4	19	1	4.2	0.2	10.1	6	0.6	6	0.6	0	0.0
F9	2005	8.1	41	5.1	17	24	2.1	3.0	16.5	27	1.6	19	1.2	8	0.5
Sum		91	335	66	158	168	31	33	209	240	15	115	8	125	7
Mean		7	26	5	12	13	2.4	2.6	16	19	1.2	8.8	0.6	9.6	0.6
±SE		±1.5	±5	±1.1	±3.1	±2.5	±0.6	±0.7	±2.2	±4	±0.2	±2.2	±0.1	±2.5	±0.1

8.6 References

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CHAPTER 9

SUMMARY AND CONCLUSION

In this concluding chapter I focus on in-situ conservation, highlighting the central points of the study which contribute to our understanding of leopard (*Panthera pardus*) ecological processes on the Karongwe Game Reserve. I offer baseline knowledge on what constitutes normal or adaptive behaviour for comparison with other reserves, including after ecological perturbations have occurred. I discuss the relevance of the results in relation to leopard conservation, which can be applicable more broadly for felid conservation in general. I highlight gaps in current knowledge and provide recommendations for further research.

9.1 Carnivores

Large carnivore populations living in our modern human-dominated, fragmented landscape continue to decline outside large government reserves, because of conflict (Woodroffe & Ginsberg 1998, Singh & Bagchi 2013), habitat loss, fragmentation (Wilcove *et al.* 1986, Dutta *et al.* 2012) and degradation (Rojas *et al.* 2011). Habitat fragmentation and landscape modification are considered to be severe threats to global biodiversity (Sala *et al.* 2000, Tschamtker *et al.* 2010), and are key drivers of global species loss (Fischer & Lindenmayer 2007), while human conflict compounds these already dire circumstances (Swanepoel 2008).

Keystone carnivores at the apex of the food chain play an important role in maintaining the health of the ecosystem, and act as sensitive indicators of habitat quality that can be used to determine the health of the environment (Joseph *et al.* 2007). They perform the several crucial roles of regulating ungulates (Hopcraft *et al.* 2010), provisioning for scavengers (Wilmers *et al.* 2003) and mesopredators regulation (Crooks & Soulé 1999, Johnson & Vanderwal 2009). Further, the disappearance of apex predators from an environment can result in trophic cascades (Pace *et al.* 1999, Terborgh & Estes 2010).

9.2 Small enclosed reserves

Over the past few decades we have seen a change in land use from commercial farming to an increasing number of small, enclosed wildlife reserves, whose primary objective is to utilise natural resources to generate an income from ecotourism (Barnes 2001, Bond *et al.* 2004, Reyers 2004). These natural habitat areas have huge conservation potential, providing good quality resources to support threatened-species reintroduction programs (Cousins *et al.* 2008).

Large reserves are favoured to meet conservation goals for species with large home ranges, are more resistant to disturbance, and have increased habitat diversity and landscape heterogeneity, thereby reducing the risk of species extinction (Schwartz & van Mantgem 1995, Schwartz 1999, Cardillo 2003). However, in a human dominated landscape there are often no alternatives to small reserves due to a high degree of habitat loss and fragmentation (Tschamntke *et al.* 2002). Also, reserve size alone does not accurately predict population size or diversity. Large, disturbance-prone sites may have lower diversity than smaller, higher quality sites (Schwartz 1999) which have the potential for exponential growth rate (Mitchell & Hebblewhite 2012). One method of identifying high biodiversity areas is to model the habitats of top predators, because these sites are often biodiversity hotspots (Schmitz 2003, Sergio *et al.* 2005). Focusing on the protection of high biodiversity sites is believed to be the most effective way of conserving biodiversity globally (Myers 1976, Gavashelishvili & Lukarevskiy 2008). Although much of the practical implementation of ecological restoration is focused on the species, it is the habitat which is often most important (Miquelle *et al.* 1999), as this study shows.

9.2.1 Predator re-introduction

To restore natural ecosystems and increase their appeal to tourists, complex suites of predators (e.g. cheetah (*Acinonyx jubatus*) - Hayward *et al.* 2007a, lion, (*Panthera leo*), - Hunter *et al.* 2007 and wild dog, (*Lycaon pictus*) - Gusset *et al.* 2006) and mega herbivores (e.g. elephant (*Loxodonta Africana*), - Slotow *et al.* 2005) were reintroduced into these reserves. Leopards are usually naturally occurring, but have been reintroduced where populations are low (Hayward *et al.* 2007a). Where they are naturally occurring, tourism observation potential is low because of years of persecution. In addition, as a result of the reserves' small size and enclosed nature, natural processes may be unable to function in these reserves, leading to a host of complications which need to be intensively managed to maintain a balanced biodiverse ecosystem in a financially sustainable way (Grubbich 2001, Riley *et al.* 2002, Patterson & Khosa 2005).

9.3 Challenges of managing small enclosed reserves

To ensure successful reintroduction programs, a post release management plan of clearly defined aims, in conjunction with ecological monitoring, and adaptive management practices are essential (Haney & Power 1996, Pyne *et al.* 2010). In the absence of ecological monitoring, conservation managers rely on limited experience-based information, developed from traditional land management practices (Pullin *et al.* 2004).

Ecological monitoring provides information which enables managers to adapt and improve strategies for integrated sustainable resource and land use, with concomitant biodiversity conservation (Kremen

et al. 1994). Ecological monitoring should assess the impact of predators on prey populations in small, enclosed areas and the potential for loss of genetic diversity (Hayward *et al.* 2007a). It should also monitor the impact on woody vegetation, for example, of mega herbivores like elephant (*Loxodonta africana*), especially where their movements are confined at moderate to high population densities (Guldmond & Van Aarde 2008). Through long-term monitoring, evidence-based conservation holds promise for predicting which management actions are likely to be most effective in achieving conservation goals (Pullin & Knight 2003).

Where ecological monitoring is not available, and in the absence of historical baseline data, relatively undisturbed sites with similar ecological features to disturbed sites can be used as reference sites (Economou 2002). Baseline sites represent the expected status of biological communities in the absence of stress from human activities and are able to provide a control in which we can measure human disturbance (Moehrenschrager & Somers 2004), justify recovery and restoration programs for endangered species (Alagona *et al.* 2012), and recreate conditions that allow for ecological processes to follow a similar evolutionary path (Van Andel & Aronson 2006).

Small reserves with restored populations need to be managed to maintain a balanced bio-diverse ecosystem, through the regulation of population growth (Kettles & Slotow 2009), genetic integrity (Trinkel *et al.* 2008) and structure, and balancing predator-prey relationships (Van Dyk & Slotow 2003), in a financially sustainable way (Grubbich 2001, Riley *et al.* 2002). Small reserve management is compounded by strict fencing standards, substantially higher reproduction rates (Druce *et al.* 2004) and pressure from tourist expectations of seeing the charismatic species (Swarbrooke 1999).

9.4 Ecological monitoring and management

9.4.1 Predator prey balance

Predator-prey competitive interactions are among the major forces that shape food webs and ecological communities (Loladze *et al.* 2004). What carnivores select to eat determines their fitness (Pyke 1984), population density (Boyce 1989), reproductive success (Owen *et al.* 2010) and territoriality pattern. However, disproportionate selection pressures by predators can have an alarming impact on both prey biomass, and the system as a whole (Johnson 1980, Thaker *et al.* 2011).

9.4.2 Balancing leopards and their prey

Portrayed as a super generalist, leopard should be able to stabilise a system (Lidicker 2000). However my results highlight that leopard are more likely to destabilise small enclosed systems because, in order to maximise energy gain, they become selective consumers (Hayward *et al.* 2006, Balme *et al.*

2007). Leopards' more preferred prey were not selected according to abundance. Leopards selectively preyed on specific species, and females and juveniles, which appeared closely tied to vulnerability (Stein & Magnuson 1976, Shultz & Finlayson 2010). Selection pressure by leopard may be able to affect micro distribution and behaviour in ungulates while the impact on breeding ungulate females might be severe enough to cause extinction in small populations (Stein & Magnuson 1976, Shultz & Finlayson 2010).

I showed how leopard continue to hunt preferred species even when they became rare (Balme *et al.* 2007) and, combined with their high consumption rate, this is likely to have serious consequences on species richness in small enclosed reserves (Chapter 5). Predator-prey interaction needs to be monitored carefully (Druce *et al.* 2004). Preferred prey populations need to be in sufficient numbers to prevent inbreeding, maintain a balance of sex ratios to ensure successful breeding, and sustain predator populations (Slotow & Hunter 2010).

The widespread use of buffer species, like impala (*Aepyceros melampus*) and warthog (*Phacochoerus africanus*), which are both common and cheap, has the aim of reducing predation of more expensive and rare species (Cousins *et al.* 2008). There is evidence that the use of buffer species is ineffective (Lehmann *et al.* 2008) and I show that leopard continue to select preferred prey even where abundant buffer species are readily available. Managers armed with this information can ensure that there are buffer species and a sufficient preferred prey base to sustain the leopard population, and ensure the long term survival of both predators and their less abundant prey.

Leopard habitat selection and territorial size were governed by their foraging decisions. Leopard hunted where prey were most abundant, in their preferred prey's selected habitat and riparian areas (Balme 2009). Closed woodland was the most abundant and important prime hunting habitat while riparian habitat, used for hunting was both important for other key resources and connectivity between habitats (LaRue & Nielsen 2008) (Chapter 8).

Characterising leopard habitat selection, and the important resources in these protected environments (source populations) that relate to population persistence, can be used to guide conservation efforts in combating the effects that habitat loss, degradation, and fragmentation have on species risk of extinction, and for planning habitat restoration (Myers 1976, MacMahon 1997, Simcharoen *et al.* 2008).

If the leopard is to be preserved in South Africa, a network of potential habitats that are within the species dispersal limits need to be protected (Oppel *et al.* 2004, Stamps *et al.* 2005). These source

habitats could produce surplus reproduction, which could in turn disperse to sink habitats where density is lower.

9.4.3 Population ecology

Monitoring population birth, growth, reproduction and death identifies the factors that influence the success and distribution of populations (Montalvo *et al.* 1997). Restoration usually establishes a relatively small founding population and fences restrict movement, compounding genetic disturbance and overpopulation (Montalvo *et al.* 1997, Hayward *et al.* 2009).

9.4.4 Inbreeding

Inbreeding depression and loss of genetic variability (Trinkel *et al.* 2010), as a result of closely related individuals mating and producing offspring with reduced fitness, increase the population's risk of extinction (Lande *et al.* 1999, Trinkel *et al.* 2011). Inbreeding has been reported in lion (Packer *et al.* 1991, Trinkel *et al.* 2008), grey wolf (*Canis lupis*) (Laikre & Ryman 1991) and the Florida panther (*Puma concolor coryi*) (Pimm *et al.* 2006). Inbreeding depression in leopard is seen in critically endangered sub populations of leopard like the Amur leopard (*Panthera pardus orientalis*) with numbers as low as 25-40 (Perez *et al.* 2006) and the Far Eastern leopard (*Panthera pardus orientalis*) (Uphyrkina *et al.* 2002). Isolation and inbreeding results in congenital and reproductive abnormalities and has deleterious consequences on all aspects of survival (Trinkel *et al.* 2010). Although the leopard population of South Africa is not at risk of extinction, small fragmented and isolated populations could, as a result of stochastic events such as prey deprivation, human depredation, and disease, see numbers dropping so low, that they are driven to extinction (Uphyrkina *et al.* 2002, Daly *et al.* 2005). Conservation efforts should endeavour to save the integrity of small isolated populations; however, as a rescue strategy, genetic augmentation/restoration should be carefully considered (Uphyrkina *et al.* 2002, Trinkel *et al.* 2008).

9.4.5 Overpopulation

Small founding populations (Reading & Clark 1996) on prey rich, fenced reserves, and in the absence of threatening processes, have resulted in exponential reproductive rates in top predators and mega herbivores (Maddock *et al.* 1996, Vartan 2001, Hayward *et al.* 2007b, Kettles & Slotow 2009). A lack of post introduction monitoring or management intervention further compounds the problem if numbers are allowed to exceed the reserve's sustainable carrying capacity and impact negatively on ungulates and the environment (Slotow *et al.* 2005, Kettles & Slotow 2009).

Popular thought is that enhanced nutritional quantity translates into higher predator numbers (Swanepoel 2008). Low density founder populations in favourable environments have led to

unusually rapid population growth (exponential), as a result of high reproductive output and high recruitment (Kettles & Slotow 2009). Rapid population growth rate in small reserves is compounded by the lack of environmental stressors like infanticide, disease, intraspecific conflict and starvation which limit population growth (Foose & Ballou 1988, Kettles & Slotow 2009, Druce *et al.* 2011, Edwards & Edwards 2011).

Unless numbers of top predators such as lion (Jolley 2006, Kettles & Slotow 2009) and mega fauna such as elephants (Biggs *et al.* 2008, Kerley *et al.* 2008) are controlled, they have the potential to change the habitat and prey community composition (Peel & Montagu 1999, Vartan 2001, Kettles & Slotow 2009). High predator numbers impact negatively on the breeding potential of weaker predators as well as the underlying prey species (e.g. Power 2002, Slotow & Hunter 2010). High numbers of elephant with population eruptions have the potential to have significant environmental consequences (Biggs *et al.* 2008, Kerley *et al.* 2008, Druce *et al.* 2011).

Enhanced nutritional quantity on Karongwe did augment leopard reproductive parameters and reproductive output through increased pregnancy rate and sub adult maturity (Sinclair 1985, Mduma *et al.* 1999) (Chapter 6). This increased reproductive output however did not translate into increased population density. Leopard population density on Karongwe was in line with populations studied in similar habitats (Chapter 6), and my study shows that leopard populations in small reserves are self regulating because leopard moved across fences and therefore more natural processes affecting the population were able to take place, and minimum management intervention for population size or inbreeding was required.

Prey density was important and set the upper limit of the population carrying capacity (Bertram 1975, Stander *et al.* 1997, Sinclair & Krebs 2002). However, density-dependent intraspecific competition for space regulated the population close to carrying capacity, before food became limiting thereby controlling population numbers naturally (Kettles & Slotow 2009, Edwards & Edwards 2011) (Chapter 7).

Territoriality played a fundamental role in determining leopard population dynamics, limiting the number of adult leopard that were able to coexist, have access to resources, and participate in reproductive activities (Owen *et al.* 2010, Wehtje & Gompper 2011). Leopard territorial size was determined by available resources, and availability of space placed a limit on the adult population size (Hayward *et al.* 2009) (Chapter 8). Any territory that became available was filled by subadults, or floaters in the population (Jacquot & Solomon 2004).

Annual increases in ungulate density did not translate into smaller territories and more breeding adults. Leopard territories remained the same size; however, the degree of territorial overlap decreased with increasing prey density and leopard became more territorial by locating sufficient forage in a smaller core area (Chapter 8). During these periods, subadult recruitment (Chapter 7) and adult encounters with sub adults and floaters were lower, resulting in a population increase (Chapter 8, Mech 1977, Pierce *et al.* 2000). At the upper population limit, the number of territorial females never exceeded six, suggesting this to be the maximum number of available female territories on the reserve (Chapter 8).

With decreasing ungulate numbers, density-dependent regulatory processes were amplified (Chapter 7). Territorial overlap increased resulting in increased density-dependent intraspecific encounters (Chapter 8), with an increase in subadult mortalities and dispersals (Chapter 7). This highlights that, even in prey dense areas, the availability of quality habitat determined territorial size and set the upper population limit (Lima 2002, Chapter 8) suggesting that landscape composition is vital to predator prey dynamics, and that prey density alone may not be enough for successful carnivore conservation (Balme 2009).

The leopard population was further limited by top-down density-independent social behaviours during male territorial take-over (infanticide) and female territorial clashes (Chapter 7). Natural removal of breeding males resulted in higher mortality rates in all sectors of the population, and in an environment where these density-independent mortalities are large and variable, they could override density-dependent mortalities so that the population fluctuates markedly (Sinclair 1998, Balme *et al.* 2012). This has been shown in populations where anthropogenic removals further destabilise a leopard population, having a devastating impact on the population and impeding population recovery (Balme & Hunter 2004, Whitman *et al.* 2004). My results highlight that the number of territories available to females, and the dynamics between predators and their prey, are a function of not only the relative abundance of prey, but also population size, key resources and landscape attributes (Clutton-Brock & Harvey 1978, Litvaitis *et al.* 1986, Dahle & Swenson 2003).

I have demonstrated that the intraspecific social system, even in a solitary species, plays a significant role in population control. Density dependent measures, which rely on the species' own density to reduce the population, and density independent social influences which have effects on the population in the absence of density, were responsible for maintaining leopard population dynamics (Sinclair & Pech 1996). In social species (e.g. lion), density dependent influences also play a significant role in population control, by regulating reproductive output (Kissui & Packer 2004). During low densities, lionesses' age at first litter was significantly younger, and litters were larger, than when the population was close to carrying capacity (Trinkel *et al.* 2010). This may explain why

small populations reintroduced into nutrient rich environments, in the absence of density dependent constraints, breed so quickly.

Understanding population densities is important to be able to sustainably manage predator populations and set sustainable harvesting quotas (Balme *et al.* 2010a). A major benefit of exponentially breeding populations, especially in endangered species, is that these managed populations can serve as reservoirs of genetic material that can be harvested before density dependent factors take effect (Foose & Ballou 1988). A metapopulation management scheme, where surplus individuals from these exponentially breeding populations are introduced into remnant populations or unoccupied areas, to boost not only numbers but improve genetic variation, would be especially beneficial for populations which are too far from other dispersing populations (Akcakaya *et al.* 2007). Leopards, as one of the most sought-after big game trophy species in South Africa, are commercially important and emphasis on this value could foster farmer tolerance, especially in areas where leopard are heavily persecuted (Turnbull-Kemp 1967, Swanepoel 2008). Currently leopards are harvested all over South Africa; however, to maximise off-take without further jeopardising population survival or depleting the genetic variation, hunting should be confined to the non breeding portions of viable, exponentially breeding populations (Balme *et al.* 2010a).

Problems with exponential breeding populations arise, however, when there is no more space, and supply is greater than demand (Jolley 2006, Grobler *et al.* 2007). As the boom in wildlife reserves in South Africa slows, available land for wildlife has become saturated. Exponential breeding of predators and mega herbivores that were once rare have increased. Reserves are no longer able to move animals and are looking at alternatives to control populations, like contraception, hunting and culling (Orford *et al.* 1988, Delsink 2006, Kettles & Slotow 2009).

9.4.6 *Habituation*

In order to achieve regular and prolonged visual observations the appropriate habituation is necessary. The habituation of wildlife was first pioneered by zoologists such as Dian Fossey, for the purpose of research (Harcourt *et al.* 1980). In Chapter 4, I highlight a method for fast and successful habituation of leopards, minimizing capture and following stress that does not impact negatively on the animal or the reserve's objectives of having safe wildlife interactions. Free darting, collaring, and habituation were intensive, costly processes. However, the payback in terms of behavioural and ecological data, invaluable to management, made it viable. Radio tracking is a widely used tool for efficiently locating and studying free ranging animals, which although it has transformed field studies, is seldom exploited to its full potential in behavioural studies of species like the secretive

leopard (Balme & Hunter 2004, Balme *et al.* 2010b). A combination of radio tracking and habituation enabled continuous following, and recording of valuable behavioural ecological data.

Tourism reserves receiving an income from animal viewing are tolerant of predators, placing a substantial value on them, especially those which are easily viewed (Shackley 1996). Viewing large animals, such as lion, leopard and elephant, on a daily basis may result in over-habituation, particularly if there is, for example, only one pride of lion (Cousins *et al.* 2008). Animals that become over-habituated and a danger to humans may need to be destroyed (Schaller & Crawshaw 1980, Sunquist 1983, Jackson 1996), and managers need to develop strategies that enhance tourism potential without putting long term ecological sustainability at risk (Cousins *et al.* 2008).

Although it is relatively easy to manage easily-observable reintroduced predators like lion and cheetah which are constrained by fences, the management of the naturally occurring leopard is fraught with complications because they easily leave the reserve, incurring the risks that they can be killed or cause damage to livestock (Swanepoel 2008). Leopard will often live in close proximity to humans and, as such, habituation of leopard in areas where they could be persecuted, or constitute a danger to humans outside the safety of the reserve, should not be considered. However, in a survey on game ranches where predators were persecuted, farmers reported that habituation would increase the value of leopard, reducing their likelihood of being killed (Swanepoel 2008).

Habituation itself is neither good nor bad. Rather, the negative or positive value of habituation to both people and wildlife depends upon context and perception (Knight 2009). The need to capture and habituate wild animals to facilitate research can be justified, provided the benefits do not exceed ethical, ecological, social and economic costs (Swanepoel 2008). When considering an immobilisation and habituation programme, wildlife researchers need to assess each situation carefully to ensure the conservation and protection of the target species, and evaluate human safety, especially in a species not constrained by fences (Gill 2002).

9.5 Methods for managing reserves

Managing large mammals restricted by fences is challenging, and managers can use translocation, culling/hunting (Festa-Bianchet 2003) or contraception to maintain a balance between large mammals and their environment, control over population and maintain genetic integrity (Orford *et al.* 1988, Biggs *et al.* 2008, Kettles & Slotow 2009, Druce *et al.* 2011, Delsink & Kirkpatrick 2012).

9.5.1 *Managing inbreeding and overpopulation*

Translocation can be used to establish new populations (Hayward *et al.* 2007a), supplement existing populations (van Heezik *et al.* 2009) and for population reduction (Kettles & Slotow 2009). Suitable conservation areas, which have re-introduced predators, should adopt a metapopulation management program, where periodic translocations among other suitable reserves mimic natural dispersal and maintain gene flow (Gusset *et al.* 2006). Translocation, although difficult due to recent legal changes and expense, is an effective management strategy (Trinkel *et al.* 2008). Negatives of translocation include increased stress and mortality of relocated animals, negative impacts on resident animals at release sites, increased conflicts with human interests, and the spread of diseases (Teixeira *et al.* 2007, Chipman *et al.* 2008). The primary predator population regulation measure used in small reserves is the capture and removal of subadults (usually two years old) from the population, with older individuals occasionally being hunted (Vartan 2001, Kettles & Slotow 2009, Slotow & Hunter 2010). Although not a common practice in leopard due to their strong homing instincts (Riley *et al.* 2002), unsuitability for soft release (Hunter 1998), and occasional escape to cause problems in adjacent pastoral areas (Hayward *et al.* 2007a), juvenile leopards can also be translocated to assist in the repopulation of low density areas (Hunter 1998, Moehrenschrager & Somers 2004). The leopard population is self-regulating and the removal of sub adults is not necessary for population control (Hayward *et al.* 2007a). However, translocating sub adults from well-populated areas, where they would be under pressure as a result of natural density dependent processes (Chapter 7, Trinkel *et al.* 2010), can benefit inbred and low density populations, although population disease status and genetic compatibility should be carefully considered (Trinkel *et al.* 2011).

Culling or hunting is used on wildlife reserves for population control and balancing male and female ratios. This however raises serious ethical issues when directed at endangered and charismatic species, setting dangerous precedents when our intention should be to protect living creatures and their habitat (Slotow *et al.* 2008, Kettles & Slotow 2009). Culling or hunting at times may be the only option, but is likely to bring negative publicity upon tourism orientated reserves, and affect them financially (Kettles & Slotow 2009).

Contraception might provide an alternative to culling, and provide a long term solution for limiting numbers on game reserves (Orford *et al.* 1988, Delsink & Kirkpatrick 2012). What makes this solution attractive is that it is both practical and humane, and has been very successful in controlling both lion and elephant populations (Orford *et al.* 1988, Delsink 2006). Furthermore it seems to cause less disruption of biological processes, is reversible, and prevents genetic loss - especially useful in endangered species (Orford *et al.* 1988). Annual decisions can then be made to allow certain females to breed, for the well-being of the animals, as well as for tourism (Orford *et al.* 1988, Delsink &

Kirkpatrick 2012). To prevent males inbreeding with their offspring, different bloodlines can be swapped between reserves (e.g. Druce *et al.* 2004, Kettles & Slotow 2009), while older males may be hunted (e.g. Festa-Bianchet 2003, Kettles & Slotow 2009, Balme *et al.* 2010a).

I show that leopard require minimal management intervention and are self regulating and are therefore an easy to manage top predator which perform the same regulatory task as other top predators. Where management is not possible, larger tracts of land would lessen the intensity of management requirements and allow more natural processes to occur.

9.6 Managing a free roaming predator

9.6.1 Problems facing leopard

The leopard is a top predator and the most adaptable, and widespread, wild representative of the family Felidae. They live in and around human dominated agricultural landscapes, playing a crucial role in maintaining the health and well-functioning of the ecosystem (Nowell & Jackson 1996). They have a wide habitat tolerance, thrive and adapt to a variety of environmental conditions and are an abundant predator in many areas. There is a widely held perception that they are resilient in the face of anthropogenic threats and therefore these ‘super-generalists’ need little dedicated conservation action (Townsend *et al.* 2003, Balme 2009, Thapa 2011). Yet this one of South Africa’s highly sought-after ‘Big Five’ continue to decline and are at serious risk of local population extinction due to fragmentation, habitat loss (Holling 1992), human activity like hunting (Redford 1992) and persecution (Swanepoel 2008), with the likelihood of extensive local extinctions (Balme & Hunter 2004).

As a free roaming predator leopard move between protected and human dominated environments where they come into conflict with humans (Swanepoel 2008). Commercial farmers use indiscriminate methods of destruction like trapping and poison (Avenant & du Plessis 2008). Game farms of high commercial value that specialize in antelope breeding, contain leopards’ natural prey and should be able to sustain leopard. Unfortunately these reserves derive their income from game sales and hunting, and these reserves directly compete with and often exclude predators by trapping and hunting (Swanepoel 2008).

The removal of a few individual leopards from an area does not deplete or eliminate the population at the removal site (Balme *et al.* 2010a). I show how individual removals resulted in vacant territories, which were immediately colonised by younger sub-adults or other immigrants (Bailey 1993). However, continued selective shooting of large adult males may distort the sex ratio, causing genetic depletion (Ginsberg & Milner-Gulland 1994), and increase infanticide preventing population recovery

(Balme & Hunter 2004). Single removals in small isolated populations, with few offspring and floaters, may result in vacant territories, a declining effective breeding population, and increased extinct risk. Single focused removals (Kettles & Slotow 2009) are preferable to indiscriminate trapping and poisoning, which do not target specific individuals or even a particular species.

Conservation areas are not immune to the threats that originate outside their boundaries and are vulnerable to legal and illegal hunting in the areas surrounding them (Balme 2009). Leopard are not constrained by fences (Balme *et al.* 2007) and anthropogenic mortality causes an edge effect within protected areas through increased infanticide and lowered reproductive outputs, reducing the effectiveness of large carnivore conservation in protected areas (Woodroffe & Ginsberg 1998, Balme *et al.* 2010b).

Fragmented metapopulation of leopards around the north and northeast of South Africa are safe from extinction, even in the face of intense persecution, because they draw from large source populations (Kruger National Park, Kgalagadi Transfrontier Park and surrounding countries) for continual turnover through immigration (Hubbell 1997, Daly *et al.* 2005). In the rest of the country the network of small patches of leopard have no persistent metacommunity and inadequate dispersal, combined with additional persecution and sport hunting, lead not only to local, but regional extinction (Hubbell 1997, Daly *et al.* 2005).

9.6.2 *How to protect leopard*

In order to promote successful persistence of leopard it is crucial to restore and protect habitat (including prey) while simultaneously reducing human removals (Ferrerias *et al.* 1997). Enlarging suitable areas and maintaining buffers around sensitive areas (Fischer *et al.* 2006), will increase carrying capacity. Providing areas of suitable habitat within dispersal distance (Morrison 2002), and creating conservation corridors between these fragmented habitats, will increase genetic flow (Mech & Hallett 2002). Conservation efforts must be based on viewing fragmentation as a range of conditions that occur in a landscape mosaic, and management should focus on the mosaics rather than focusing solely on reserves. It will take the simultaneous protection efforts of private landowners, conservationists and managers, through incentive driven conservation (Swanepoel 2008), traditional low-tech husbandry (Ogada *et al.* 2003), and education, to minimise ecosystem-specific threatening processes (Hubbell 1997, Daly *et al.* 2005) and ensure the future protection of leopards in South Africa (Cousins *et al.* 2008).

9.7 Limitations of the study and gaps in current knowledge

Some of the methods used in this study were unique, as no previous work has studied the process of habituation, copulatory behaviour and reproductive parameters of leopard in such detail in the wild. The major limitations of the study were that an area of 8500 ha could support a limited number of leopards, and, therefore, the number of females that could be collared and studied at any one time was relatively small. Small sample size precluded the study of natural population processes such as gene flow (there was only one breeding male at a time) and dispersal, which would have provided more depth to the study. There were also problems with subjects leaving the reserve, losing a darted female, collars not working and the death of many focal animals from a range of causes during the study. Not all the leopards were collared at one time, and so only a maximum of seven leopards were studied simultaneously, which made statistical analysis difficult. The lack of comparable data from open systems made contextualising the results of the study very difficult. Although I attempted to gather data both incidentally and systematically, using direct and indirect methods of study, difficult logistics, loss of subjects and small sample size hampered efforts. Although this made the study very difficult, the results obtained exceeded our expectations. I acknowledge that the study is purely correlative which does not mean causation and that the conclusions drawn are not able to be substantiated without experimentation. Many of the conclusions drawn are as a result of correlative observation and not experimentation and should be used with caution.

The constraints of my study system highlighted for me some of the missed opportunities to further advance understanding: for example, studying a larger population to better understand the influences of additional males (Balme 2009), and to understand the reproductive and population implications on disruptions and growth from additional male takeovers (Balme *et al.* 2012). It would also have been nice to study the population for longer to witness additional periods of high population density and to see if the responses were consistent.

I would have liked to study the degree to which landscape structure facilitates movement among different required habitat types (Palomares *et al.* 2001), and to understand the trade-off between dispersal rate and competitive ability in a fragmented habitat (Palomares *et al.* 2001). In lynx (*Lynx pardinus*) dispersing individuals used lower quality habitat to avoid resident individuals. I would have liked to understand the relationship between dispersing individuals' survival, habitat fragmentation and threatening processes on leopard survival (Palomares *et al.* 2001). Further in-depth investigation into habitat preference, in both predators and their prey, is also called for, because understanding the coevolution of habitat-selection strategies in strongly interacting species is essential to predicting species distribution (Meynard & Quinn 2007) and interpreting spatial and temporal dynamics (Morris 2003). Understanding predator numbers, and what the ecological, and ultimately economic, influence of their presence is, are critical, particularly on small reserves.

9.8 Conclusion

Predator conservationists and managers require more and better data than are currently available. In order to enhance the role of wildlife ranching within conservation, *in situ* conservation research is imperative to help manage and minimise economic loss within these systems (Slocombe 1993, Cousins *et al.* 2008). The study highlighted that it is possible to safely habituate leopards for research purposes, and provides a framework through which to undertake habituation without impacting negatively on leopard or the reserve's objectives. Having habituated leopard allowed me to collect a wealth of behavioural and ecological data, some aspects of which had never been studied before in the wild. I highlighted how nutrition increases breeding potential, and I emphasised the importance of removing excess numbers prior to density dependent regulatory processes, if source populations are to be most effectively used to enhance deficient populations. I highlighted that it is not necessary to manage leopard populations as intensively as other predator species that are confined by fences. Prey numbers set the upper population limitations, while availability of space maintained numbers around carrying capacity through density dependent regulation. My results indicated that leopard populations may be naturally self-regulating, and regular gene flow (presumed from new males coming into my population) ensured that inbreeding is of limited concern for conservationists where populations are not severely threatened by anthropogenic disturbance.

To develop long-term conservation plans for leopard, it is not enough to maintain large numbers of prey. The conservation of appropriate hunting habitats and riparian habitat are important, as well as a complex integration of ecological, economic and social factors in the planning of effective conservation strategies (Swanepoel 2008, Hopcraft *et al.* 2010). Advancing our understanding of apex predators' ecological requirements enables us to plan for their future conservation in an increasingly fragmented environment made up of small-enclosed reserves impermeable to ungulate movements. Since other members of the cat family are subject to similar persecution as the leopard, the results of this study provides a baseline dataset valuable for the conservation of the wider carnivore population.

This highlights the necessity of understanding species behavioural ecology in relation to their environment when developing conservation initiatives (Slocombe 1993, Cousins *et al.* 2008). Managers can emphasize long-term economic and ecological health by implementing sound management practices that maintain their resource base indefinitely and justify a marketing claim of being truly sustainable land use (Cousins *et al.* 2008). My data therefore provides a baseline dataset of ecological information for management decisions relevant to the species, and for comparison with future research and conservation initiatives. This baseline dataset can be used as a guideline of current regional conditions and knowledge of species specific requirements on which to make

informed decisions (Morrison 2002, Martins & Martins 2006, Hayward *et al.* 2007a). Even though the ecological parameters may vary among populations of leopards in response to different climates, habitats, prey densities, and other environmental parameters, these data may be the only information available to managers for making evidence-based decisions. I hope that my study is applied for such a foundation, to promote conservation of leopard and threatened large carnivores more broadly.

9.9 References

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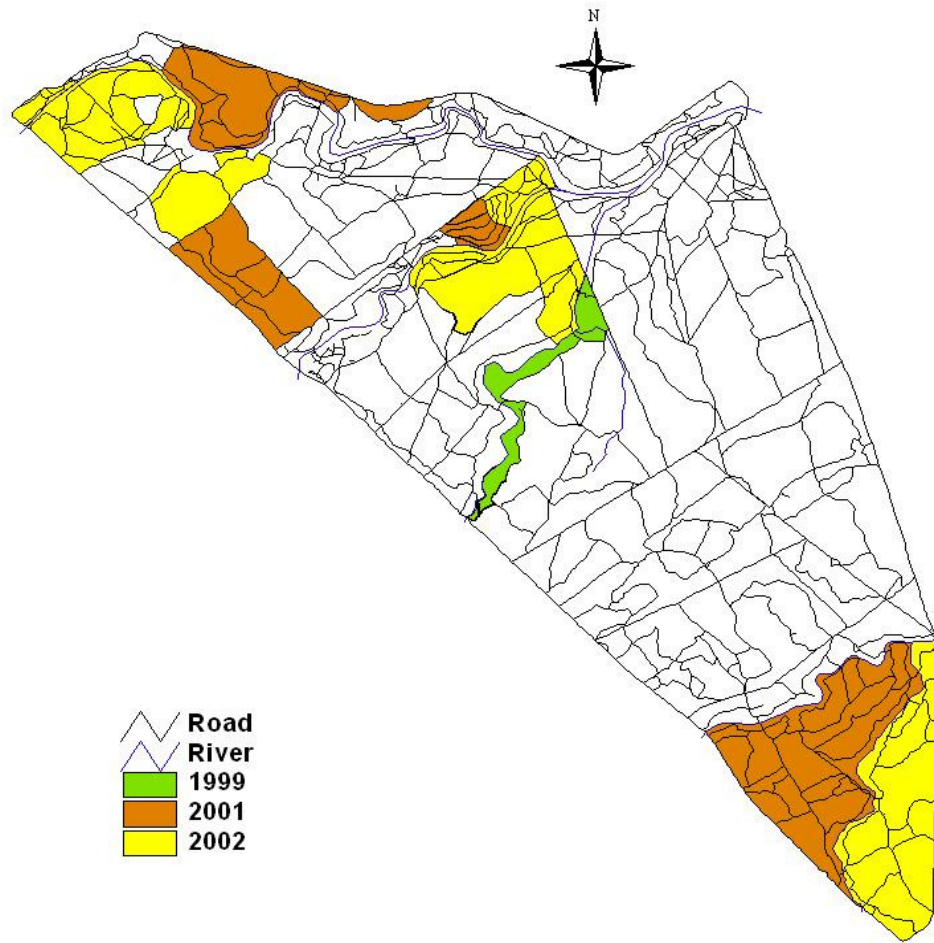
LIST OF APPENDICES

Appendix A1: Rainfall figures collected on the Karongwe Game Reserve between 1995- 2005

Yearly rainfall figures

Month	95/96	96/97	97/98	98/99	99/00	00/01	01/02	02/03	03/04	04/05
July	0	0	0	2	0	1	0	0	0	3
August	0	0	0	0	0	0	0	0	0	4
September	0	8	22	3	0	0	1	16	12	2
October	20	85	29	42	61	16.5	36.5	10	6	23
November	101	100	43	110	72	126	168.5	8	36	154
December	62	100	22	142	79	92	62	50	46.5	62
January	126	51	37	105	158	7	7	65	68	98
February	285	128	3	35	258	201	142	45	202	112
March	73	73	0	125	230	25	5.5	25	92.5	18.5
April	36	10	14	30	72	26	36	18	78	39
May	128	25	0	2	5	12	3	5	1	7
June	15	0	0	2	17	0	16	5	5	0
Total	846	580	170	598	952	506.5	477.5	247	547	522.5

Appendix A2: Areas of controlled patch mosaic burning on the Karongwe Game Reserve



Appendix A3: Individual immobilisations undertaken between October 1999 and August 2003**Cage capture****F0 (Sheena)**

The trap was set on the afternoon of the 23rd October 1999 in the Mafunyane River, 100m west of Tambotie loop crossing, (24.21324 °S, 30.59470 °E), in a shady area where a young female leopard and tracks of an older leopard were seen regularly. On the third night, the 26th October 1999, when the impala smelt strongly, a subadult female entered the cage. No other predators entered the trap during the time the cage was open. She was discovered at 07h20 and left alone in the trap until 08h15. The darting team arrived with sedative, medication and the collar and Mr Owen was the only one who approached the cage to dart. Every time the dart gun was placed near the small holes in the cage she would swing around aggressively and try to bite it. I approached the opposite side of the cage to distract her and she was finally darted at 10h27 and was asleep at 10h30. The collar was fitted at 10h32 and by 10h46, measurements were taken and drug administration completed.

Recovery

F0 was left in the shade to recover and monitored from a nearby tree.

Post- handling habituation

Two days later meat was left near her three times: each time she approached it to within 5m and then ran off. The second time, on the 29th October, I approached within 20m of her and dropped off fresh meat. She spent two hours watching it before she finally approached the meat and dragged it off. This was the second of three visual observations obtained of her and on the 3rd March 2000 her signal disappeared and it is assumed she left the reserve.

Immobilisations from a vehicle

M1 (Roelani)

Darted on the 12th February 2001 at 19h15, just north of Roelani's gate on the eastern fence, (30.64595 °E, 24.28183 °S)

Habituation prior to darting

At 17 h30 nearly every day M1 could be located on the eastern fence, south of the Karongwe River. Having grown up on the fence with cars driving past daily and not stopping, this male was already relatively relaxed with vehicles, and habituation to get within darting distance was quick. M1 was followed at least four times a week for 2-3 hours a night for a month, before he could be approached

close enough to dart softly. He was followed at a distance that did not cause him to turn and look at the vehicle or leave the road. If he looked nervous or left the road the vehicle following him would pull back and stop. If he resumed his natural behaviour or returned to the road the vehicle would continue to follow but a little further away. If M1 became stationary or stopped to mark his territory, the vehicle would approach slowly trying to get within 15-20m from him, watching for signs of irritation. At the slightest sign the engine was switched off and the vehicle would come to a halt. Slowly he became relaxed in the presence of a vehicle travelling 30m behind him and approaching to within darting distance (15-20m) whenever he stopped.

Darting procedure

Using a game drive vehicle with a tracker seat, the reserve manager, Mr. Owen performed the darting. The vehicle was driven in the usual manner and every time M1 turned side on to mark a bush the vehicle approached to within 15-20m and stopped switched off and allowed the male to continue. This was performed a number of times over the period of an hour until at 19h15 a safe shot could be taken and he was darted just north of Roelani's gate on the south eastern fence. He was darted softly in the rump. He jumped, ran 15m and then pulled the dart out with his mouth, lay down for about 30 seconds and chewed the dart. Then he carried on in the direction he was going as if nothing had happened. The vehicle remained where it was until M1 was out of sight and then the engine was started and we followed at a distance maintaining visual contact. At 19h22 the drug started to take effect, the vehicle was switched off and no talking or noise was permitted. At 19h25, M1 started to go down and the vehicle approached slowly. Mr Owen was the only one to approach M1 on foot and ensure he was asleep and well and at 19h30, M1 was sufficiently asleep to load onto the vehicle and was driven to the veterinarian hospital to be implanted.

Recovery

The operation went well and M1 was allowed to recover overnight near the site where he was darted, in a sturdy wooden recovery crate (1m wide x 1.2m high x 2m long) with a layer of dry grass inside. The following morning at 05h30, M1 was released by pulling on a rope slung over a tree branch attached to the sliding door. He exited with speed but only ran 10m, stopped looked at the vehicle and walked off slowly. Once out of sight the vehicle left and the loading of the crate was left until M1 was no longer in the area. This was to prevent his associating humans and vehicles with what happened to him.

Postoperative care

That evening, (13th February 2001) M1 was located and visual observation obtained. He had moved a kilometre, and half an impala was dropped off for him to prevent his moving excessively, or having to

catch something after the operation. He was located every evening to ensure he was well and that the stitches were holding, and he was fed every three days for nine days.

Post-darting habituation

The night after the darting he was followed for an hour before he could be seen, and he was habituated for 11 hours and 45 min over seven days.

F1 (Tashinga)

F1 was darted on the 14th June 2001 while mating with M1 in the Matumi River in Mundulea (30.63859°E, 24.28359°S).

Darting procedure

No pre-darting habituation was carried out. M1 and the very shy female were followed for two hours using the telemetry. The female remained with him but always kept out of view. Mr Owen finally managed to position the vehicle between M1 and F1 and she sat down and watched uncertain of what to do. She turned her head away and was darted in the neck at 18h26. The telemetry dart hit hard and she ran 100m in a circle, came back towards the male and ended up 40m from the vehicle, where her eyes could be seen by spotlight. It was not necessary to use the telemetry to track the female and the vehicle was not started until she was fully sedated which took just eight minutes. F1 was loaded in the vehicle and driven a kilometre away and at 19h05 (half an hour) all medication, measurements and collar fitting were complete. The male was curious and went looking for her and called. M1 and other potentially dangerous predators were continuously checked for, using the telemetry throughout the procedure.

Recovery

F1 was placed in the recovery crate on the highway near the Gravelotte dam. The following morning the door was raised in the same manner as with the male

Post- darting habituation

Habituation was carried out as in general habituation but often no visual contact was possible as F1 was in the river. The vehicle would go as close as possible to the signal and if no visual contact was possible and the signal didn't move, the engine was switched off and the vehicle would stay with her for at least 15 min to get her used to it, and to try and see her in the thick vegetation. Habituation was easier when she was copulating with the male as she was lured out of the river and could be followed.

F2 (Yanina)

F2 was darted on the 13th August 2001 at 17h50 on the first road south of Rhino Walk in Mundulea (30.62363°E, 24.25655°S) while mating with M1.

Darting procedure

No pre-darting habituation was carried out. We started following the pair at 16h20. The male walked in the road and the female walked parallel to him in the bush, making it impossible to get a clear shot of her. Visual contact was maintained and the vehicle followed at a comfortable distance. The female slowly became more relaxed with the vehicle as the male obviously showed no concern towards it. At 17h50, F2 was darted in the rump after the post-copulatory roll, lying a few meters away from M1. F2 did not move far and, at 17h53, M1 smelt her and then moved off in a southerly direction and his signal was lost. At 18h00 F2 was fully sedated, loaded on to the vehicle and driven to the ridge 200 meters north. All medication, measurements and collar fitting were completed while she was still on the vehicle and at 18h18 she was offloaded and kept covered with blankets until she started to show signs of being more alert.

Recovery

During recovery a vehicle was parked far enough away so that visual contact was still maintained. Once the female was seen to be waking up and lifting her head, the vehicle left to prevent any association with people and vehicles and the darting. The vehicle then drove around the area checking for lions (*Panthera leo*) and M1. None were present and F2 was left to wake up in peace. At 19h37 M1 was located one kilometre away near the Mundulea boma, still moving away south. The next day M1 was mating with F1 (Tashinga) west of Rocky Crossing.

Post- darting habituation

Habituation was carried out as in general habituation.

F3 (Shongile)

F3 was darted on 22nd October 2001 at 23h15 just north east of Beestcamp (30.60037 °E, 24.23928 °S).

Darting procedure

At 18h18 the female was located copulating with M1 at Daskop (30.60193 °E, 24. 23354 °S). They had killed and almost finished an adult female impala and were mating frequently. It was impossible to get close enough to dart the female as she lay safely among the rocks. At 21h10 the kill was finished and a brown hyaena (*Crocuta crocuta*) moved into the area. M1 started moving south and visual contact with him was lost at which point the female followed. We followed them through the

bush but the female stayed out of darting range. They were moving into thicker vegetation and there was concern that they would be lost. At 23h15 a chance was taken and the female was darted from 40m just north east of Beestcamp. The male's signal was followed and they were found sitting together at 23h25. The female was lying down and the male started moving close and sniffing her. The recovery vehicle drove right up to her and the male was reluctant to leave her, circling the vehicle in the spotlight. At 23h30 the female was fully sedated and loaded and driven 1km and offloaded. The male continued to call looking for the female and someone was made responsible for tracking his movements with the spotlight, telemetry and audio. The collar was fitted and all measurements and drug administration completed

Recovery

At 00h00, the female was loaded and driven to the ridge south east of Croc Dam (30.58598 °E, 24.22787 °S) where she was allowed to recover under a thicket. A vehicle remained with her, checking for lions (*Panthera leo*) and M1, who was moving north. The vehicle left twice to look for M1, and returned to check on her. She experience vehicular activity during recovery

Post darting habituation

The following day (24th October) at 09h00 she was located and had moved south one kilometre and by 14h42 she was mating again with M1, and was followed for 18 hours continuously.

M2 (Croc Dam male)

M2 was darted at 19h15 on the 19th December 2001 at Croc Dam (30.58535 °E, 24.22818°S)

Darting procedure

M2 was located by game drives at the dam at 18h30. The darting crew arrived at 19h00 to find him relatively relaxed but lying behind low, thick bushes. At 19h15 he was darted in the chest when he turned his head away. He ran in a southerly direction behind some boulders. Another vehicle had visual contact for a few more minutes and then visual contact was lost. At 19h25, when he should have been fully sedated, the search began. It was dark and everyone looked randomly in the area he was last seen, but even with ten people looking with torches he could not be found. It was suggested that we start looking in ever-increasing circles, and he was finally located 55 min after darting, at 20h20. by which time he was starting to lift his head. A top-up dose was administered so that the collar could be fitted, medication administered and measurements taken. At 20h45 he was left with one vehicle watching him.

Recovery

During recovery, a vehicle was parked far enough away so that visual contact was still maintained. Once he started lifting his head the vehicle left to prevent his associating people and vehicles with what had happened to him. The vehicle then checked the area for lions (*Panthera leo*) and M1. None were present and M2 was left to wake up in peace.

The following day

The collar was located 300m from where he was left to wake up. There were no bite or scratch marks, which suggests it was removed fairly easily.

F4 (Amanzi) first darting

F4 was darted at 19h40 on the 15th January 2002 at Aloe Junction (30.58217 °E, 24.20768 °S).

Darting procedure

At 17h13, F4 was heard copulating with M1 in the Kuvyenami River. They moved east and, at 18h46, visual contact was obtained for the first time at Second River Crossing, as they continued east. Although the female was very relaxed there were no opportunities to dart until 19h40, when she was darted softly in the rump. Visual contact was retained for only a minute and then she entered a drainage line. The male continued in an easterly direction, calling, and at 19h50, when she should have been fully sedated, eight people started looking for her.

F4 (Amanzi) second darting a month later

F4 was darted at 20h10 on the 9th February 2002 in the spruit north east of the Mafunyane main gate (30.56476 °E, 24.22930 °S).

Darting procedure

M1 and F4 were located at 18h02, east of the Lehmann's (30.56534 °E, 24.21577 °S) copulating and mobile in a westerly direction in the river. At 19h00 they moved out of the river in a south westerly direction and the darting team started to follow. At 20h10, F4 was darted softly in the rump and she moved away 80m. Visual observation was retained: at 20h16 she was starting to go down and she was fully sedated at 20h20. M1 continued south and, by the time the female's collar had been fitted, his signal could no longer be picked up. The collar was fitted, medication administered and measurements taken.

Recovery

During recovery a vehicle was parked far enough away so that visual contact was still maintained. Once she started lifting her head the vehicle left to prevent her associating people and vehicles with

what had happened. The vehicle then checked the area for the lions (*Panthera leo*) and M1. None were present and F4 was left to wake up in peace.

The following day

She had moved one kilometre and, when she hadn't moved on the second day, the area was walked to check on her, but all that was found was the collar.

F4 (Amanzi) 3rd darting 15 months later

F4 was darted on the 22nd May 2003 at 17h48, 600m north of the junction of Guarry Loop and Madash Road (30.61287 °E, 24.24441 °S)

Darting procedure

The darting team did not want to interrupt the mating of Amanzi and Roelani, and waited until the fourth (often the last) day of mating. The team went in at 17h00 to assess the situation but there was no visual observation of F4. M1 started moving south and she followed. She appeared only once and then visual contact was lost of the pair. M1's signal was followed for 30mins and it became evident that F4 was no longer with him. The team returned to where she was last seen and drove through the bush from the original point in the direction M1 had travelled. The team regained visual observation of her, however, she was moving fast through the bush away from M1, heading towards her territory. She was followed for 30mins during which time visual was lost and regained several times. As she started heading into very thick vegetation she stopped for a brief second, and was darted in her rump from 30m. She ran into the drainage line and the team drove up and down the road shining, but couldn't locate her. They returned to where she was darted and found the dart, which had discharged, then spent 20 min looking for her in the drainage line. It was then decided to walk from where she has been darted in a straight line in the direction she had been moving and she was found 130m further on, fully asleep. She was loaded and taken to where she would be implanted and measured and have drugs administered.

Recovery

The operation went well and she was left in her territory near Ingwe Bush Dinner where she remained until the following morning. No post-operative feeding was done as her implant was very weak, and she continued to move east, then north and on the second evening she relocated her subadult cub and continued north before going missing for five days. After that she was only located sporadically because the implant was not very strong.

F5 (Qumbile)

F5 was darted at 21h03 on the 22nd February 2002 north east of the Mafunyane main gate spruit, 300m from the fence (30.56363 °E, 24.22615 °S)

Pre-darting Habituation

Initially she would lie still in the grass until she was certain she had been seen, whereupon she rushed out at the vehicle in a short dash. Then she would stand, ears back and tail flicking, for a few moments before turning and trotting off to find a bush in which to hide. It became apparent that we were dealing with a leopard that was not nervous with vehicles so much as she disliked having them around. After having rushed the vehicle, she would stand looking at it with irritation, before trying to lose it. Pre-darting habituation was carried out as in habituation while mating for 26h30 (?), during which time she relaxed enough to dart.

Darting procedure

At 19h15 on the 22nd February 2002 the darting team arrived and followed the pair in a southerly direction. F5 was very difficult to get close to and a shot was not possible for two hours. At 20h30 the pair entered a drainage line where they became stationary and began to relax. It was extremely difficult driving up the spruit and the vehicle got stuck three times. M1 stayed near F5 and kept her relaxed as the vehicle manoeuvred into position. At 21h03 when she approached M1 to copulate she was darted softly in the rump and she ran 20m into bush then came back to M1. She started moving in the direction they were originally travelling before darting, trying to encourage M1 to follow her. At 21h08 she lay down and M1 moved towards her to investigate her strange behaviour. The darting team waited until 21h13 when she was fully sedated and M1 had to be chased away from her. She was loaded onto the vehicle and driven one kilometre away where drugs were administered and measurements taken. Her neck was too large for a collar so she was driven to the veterinary surgery to be implanted.

Recovery

The operation went very well and as she was already starting to wake up she was allowed to recover in the transport crate with the door open (1.4m x 1.2m x 1.6m). All vehicles and people left her alone and checked the area for lions (*Panthera leo*) and other leopards.

Postoperative care

On the second night visual contact was obtained in the same area she was dropped off. An impala was left for her, to prevent her moving too far or having to hunt. She stayed on the impala for two days then disappeared. Her implant signal had only a 300m pick up and after she was located copulating

with M1 a month later, her signal was located only once more on the reserve. Using a helicopter she was located outside of the reserve and I believe she left the reserve to the north.

M1 (Roelani) 2nd darting

M1 was darted at 16h47 on the 11th July 2002 north of the Mafunyane spruit 1km east of R36 fenceline (24.23725 °S, 30.58267 °E)

Darting procedure

M1 was followed using the telemetry and was found lying relaxed along the R36 fenceline. The darting team got within 15m of him with the vehicle and at 16h47 he was darted softly in the rump. He jumped up and moved 2m away and then lay down again. The vehicle remained switched off the whole time and at 16h55 he was asleep, loaded and moved for surgery. He was weighed for the first time, in a net using a block and tackle and meat scales.

Recovery

It was a very cold night and even though he was covered in three blankets M1's temperature dropped to 35°C while on the operating table. When the stomach is open a lot of heat is lost and once the temperature drops it can become life threatening as the animal goes into hypothermia. While still on the operating table, hot water bottles were packed around his body (making sure not to put it in direct contact with the skin) in an attempt to raise his temperature. Once the operation was complete he was driven around in a vehicle with the heater on and warmed up slowly until his temperature stabilised and he was beginning to wake up. He was offloaded on a ridge where it was warmer, still covered with blankets, and allowed to wake up.

Postoperative care

The following day M1 had moved 300m and the front of a male impala was left for him. No other meat was left for him

M3 (Muhle)

M3 was darted on the 9th October 2002 at 20h00, east of Barend's gate (30.54369 °E, 24.17749 °S) on the fenceline.

Habituation prior to darting

M3 was followed for approximately two months as described by general habituation until relaxed enough to dart. Over a two-week period the darting team tried to dart M3 on four different occasions and each attempt was for about three hours.

Darting procedure

On the night he was darted, M3 was located on the fence between CJ's gate and Barend's gate at 17.00h and was followed for three hours. He was moving east, 200m parallel with the fence, into the block, and was finally darted in the shoulder from about 30m. He jumped, ran for 30m and then stopped. He continued to slink off slowly in the direction he was originally going and moved about 100m before the sedative started to take effect (eight minutes). He was followed slowly with the vehicle and visual contact was retained. After 10 min he was sufficiently sedated to load and be moved to be implanted. An implant was chosen because he was a young male with good tourism potential, and his neck was very thick and therefore a collar was not an option.

Recovery

The operation went very well and he was offloaded below Impala Dam as he was starting to wake up. After 15 min the vehicle left to check the area for hyenas, (*Crocuta crocuta*) lions (*Panthera leo*) and other male leopards.

Postoperative care

The following day he was located a kilometre further south in the Edeni spruit. On the 11th he had moved back north into his territory and was given half an impala, which was eaten. It was unsure if he had eaten it or if hyenas (*Crocuta crocuta*) had taken it, so two days later the other half of the impala was offloaded for him and wedged into a fork in the tree 2m high, which was also consumed.

A new batch of darts was purchased**M4 (F2's male cub) 1st and 2nd attempt failed**

27th November 2002 at 04h47 in Monate 300m east of Mundulea boma 100m north of Yanina's road (30.62411 °E, 24.23925 °S). Then Monate Big Dam (30.63070 °E, 24.23849 °S).

Darting procedure

The darting team started following F2 and her cubs at 04h30, and at 04h47 the young male was darted in the rump. The dart did not inject and it was suspected that the dart was not pressurised properly, so a second dart was loaded and pressurised. The young male was a little more wary and only at 06h00 was another shot possible. The young male was darted again in the rump at Monate Big Dam. Unfortunately the same happened and the dart failed to inject. The darting was terminated to prevent excessive stress on the youngster.

F1 (Tashinga) 2nd darting failed

28th November 2002 at 19h30, 500m west of Wilderness Camp (24.27153 °S, 30.62444 °E)

Darting procedure

F1 and one female cub were followed in a northerly direction out of the river. F1 was to be immobilised first and her collar changed and, at 19h45, F1 was darted from 15m in the rump. She jumped and ran in the direction they had been travelling. When the dart was retrieved and checked, it had not discharged, the same as the previous day.

F13 (F1's female cub) 1st darting failed

28th November 2002 at 20h45, 500m west of Wilderness Camp and 200m north, (24.62439 °S 30.62439 °E).

Darting procedure

At 19h50 a new dart was taken, loaded and pressurised and, using the telemetry, F1 was followed for an hour but it was not possible to obtain visual contact with her again. At 20h45 the cub was darted in the rump from 10m:, she jumped and visual contact was retained as she moved off 30m and sat down. The vehicle was kept between her and mother and after 10 min there was still no affect. The dart was retrieved and again the dart hadn't discharged. The darting was abandoned.

The recently purchased batch of darts was taken back to the agent and a new batch obtained.**F13 (F1's female cub) 2nd Darting successful**

4th December 2002 at 19h15, just south of the Karongwe River 100m west of Spectra Crossing (30.62003 °E, 24.27336 °S), F13 was darted and removed from the reserve.

Darting procedure

F1's two female 11-month-old cubs were watched and followed for 30 min. One was darted at 19h15 from 20m in the rump and although she ran 50m visual contact was retained all the time, and the vehicle kept her away from the river. The drugs started to take effect after just four minutes. The young cub was loaded into a crate and driven away where measurements and drug administration were carried out. She was allowed to wake up in the crate during transport to a new reserve. The mother was unaware of what was going on as she was occupied with three hyenas (*Crocuta crocuta*), who were trying to steal her kill.

M4 (F2's male cub) 3rd darting successful

5th December 2002 at 23h48, 450m north east of Mundulea boma and 150m east of Boma Road (30.62097 °E, 24.24037 °S) M4 was removed from the reserve

Darting procedure

F2 was followed from 17h00 for nearly seven hours in the hope that she would link up with her cubs. She finally made a kill (impala adult female) and went to fetch her cubs, and brought them in. At least an hour was spent trying to dart the female cub but she was too shy, and finally the team darted the male cub in the rump at 23h48. He ran 15m and then slowly continued to move away. He stopped, but after six minutes, as the drug started taking effect, his sister tackled him and made him run further. F2 became anxious and followed the cubs. Using the telemetry we followed her, and the cub was located, loaded and driven away. F2 was close by but there was no visual observation of her. M4 was measured and drugs were administered before he was loaded in a crate to be transported. F2 and her remaining cub went back to the kill and the following morning had moved several kilometres north.

F1 (Tashinga) 3rd darting successful

20th December 2002 at 20h44 North West of central Sickle Bush Road (30.61612 °E, 24.26489 °S). To be re-collared.

Darting procedure

F1 was found mating with M1 in the Karongwe River. They began to move north at 19:54 and the darting team began following them in a northerly direction. At 20h44 M1 finally lay in the open and F1 approached him. She was darted in the shoulder while they were busy mating so she would assume it was the male hurting her and not associate the darting with humans. After mating she jumped up and moved off 10 m and lay down. The drug started taking effect after six minutes but the leopards continued moving north. The vehicle remained switched off and after 10 min, when the drug would have taken full effect, F1 was located 100m away. M1 had moved with her and had to be chased off but he refused to leave her and F1 had to be loaded quickly, with the male just a few meters way. She was driven 1km away where measurements and the collaring could be undertaken safely.

Recovery

F1 was placed under a thick bush and the vehicle was parked 500m away. Observers were left to keep an eye on her and check for lions (*Panthera leo*), hyenas (*Crocuta crocuta*) and M1. Once she started to come round the observers left quietly and walked to the vehicle and drove off.

F2 (Yanina) 2nd darting

27th December 2002 at 22h00 200m north of Rhino Gate 70m east of R36, (30.58497 °E, 24.24871 °S). Collar change.

Darting procedure

At 20h30 the darting team arrived. F2 was located in a drainage line and the team waited until she came out at 20.45. She moved north and was followed through the block for about a kilometre. It was assumed that she was avoiding the darting team: however, when she turned and started zig-zagging back south through the block it became apparent that she was hunting. The team withdrew and followed on the road and waited 30 min, until the signal became stationary. They drove in and found her on a fresh young wildebeest kill. It took a further 20 min to manoeuvre into position. As the bush was very thick, Mr Owen had to alight from the vehicle to get a clear shot through the branches. She was darted at 22h00 in the rump and ran off. The vehicle was switched off and she was monitored with her existing signal. After five minutes Mr. Owen started looking for the dart, which he did not locate, and after eight minutes drove the vehicle in and found her 50m away already in a deep sleep. She was collared, measured and had drugs administered.

Recovery

She was moved 200m from the kill under a thick bush and covered with branches and grass. A vehicle stayed with her for two hours until she started to come around, then the area was scanned for other predators that may be interested in her kill. The following morning she was found feeding on the same kill.

F3 (Shongile) 2nd darting

9th May 2003 at 20h13, 350 m south on Snake Eagle Road from Mafunyane spruit (30.59876 °E, 24.22196 °S). Collar change.

Darting procedure

The darting team started following F3 through the bush at 18h00. Although she didn't move far, she moved continuously, trying to flush out a herd of impala. She finally settled down on a termite mound, and at 20h13 she was darted in the rump from 25 m. She ran down the other side of the mound, the vehicle drove up to the mound and the engine was switched off. Mr. Owen located the discharged dart on the mound and after 10 min the search began. F3 was located 40m away from the termite mound in the direction she had originally been travelling. Her collar was changed, drugs were administered and measurements taken.

Recovery

She was left to recover under a bush covered with grass and branches in the area where she had been darted. A vehicle waited with her for 40 min until she was lifting her head, then moved further away and stayed for another 30 min, and finally pulled out. The following morning she had moved 50m down into the spruit.

M1 (Roelani) 3rd darting

13th August 2003 at 16h15, in the Karongwe River 400m east of the fenceline outside the reserve (30.65327 °E, 24.25937 °S). Brought back in.

Darting procedure

The darting was undertaken on horseback because there were no roads and the vegetation was very thick. The backup rider held all the equipment, and M1 was quite relaxed because he had been viewed before by riders on horse safaris. The horse riders guided him into the open, with an escape route down-river. It took 15 min to get a good shot and he was darted from above, softly in the rump from about 10m. He roared and ran away about 50m, and vervet monkeys alarmed as he moved down the river, which made it easy to follow without the telemetry. He moved 100m in total. The team was brought in to move him to the vehicle and he was driven back to Karongwe.

Recovery

He was driven to the research station and as we arrived he started to wake up, and had to be pulled off quickly into the shade and left to wake up fully.

Appendix A-4: Measurements taken during the initial immobilisations of female leopards

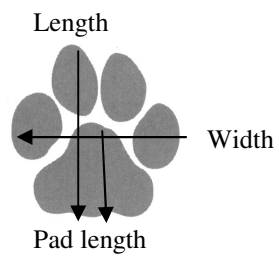
Female leopards measurements								
ID number	F0	F1	F2	F3	F4	F5	F13	
Age darted (years)	1	2.5	2.5	5	4	5	10 (mths)	
Date darted	Oct-99	Aug-01	Aug-01	Oct-01	Feb-02	Feb-02	Dec-02	
Weight estimated (Kg)	30	35	38	55	42	46	25	
Previous cubs	N	N	N	Y	Y	Y	N	
Measurements (cm)								
Body Length	100	120	105	125	132	132	112	
Tail length	70	73	73	78	77	78.5	80	
Total length	170	193	178	203	209	210.5	192	
Shoulder height	48	63	63	74	64	70	50	
Chest	55	69	65.5	74	66.5	72.2	56	
Neck	34	46.5	44.5	20	49	46	35	
Canine left	1.4	2.9	2.9	3.2	3	3.1	1.4	
Canine right	1.4	2.7	2.9	3.2	2.9	3.1	1.4	
Spoor size (cm)								
Front Length	right	-	7.3	8.5	9	7.5	7.9	8.0
Width	-	-	5.3	6.5	7	6.5	7	6.0
Pad	-	-	3.9	4.5	4.5	4.2	4.5	4.0
Front Length	left	-	7.6	7.3	8	7.6	8	8.5
Width	-	-	6.8	6.2	7.2	6.5	6.9	6.2
Pad	-	-	3.9	4	4.3	4.5	4.7	3.7
Back Length	right	-	7.6	7.6	9.2	7.5	8	-
Width	-	-	5.0	5.8	6.3	5.7	5.8	-
Pad	-	-	3.6	3.5	4.6	4	4.3	-
Back Length	left	-	7.3	7.3	7.6	7.7	8.3	-
Width	-	-	5.6	5.4	6.2	5.9	6.1	-
Pad	-	-	3.5	3.6	3.6	4.1	4.4	-

Appendix A-5: Measurements taken during the initial immobilisations of male leopards

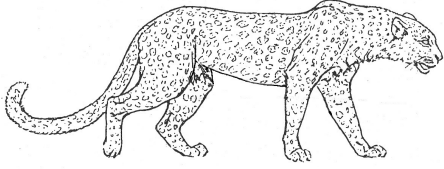
Male leopards measurements					
ID number		M1	M2	M3	M4
Age darted (years)		5	4	3	11 months
Date darted		Jul-02	Dec-01	Oct-02	Dec-02
Weight estimated (Kg)		* 74.5	80	* 71	32
Measurements (cm)					
Body Length		140	152	157	122
Tail length		89	89	92	74
Total length		229	241	249	196
Shoulder height		84	80	80	70
Chest		86	85	86	62.5
Neck		60	58	62	42.5
Canine left		4	3.5	4	1.5
Canine right		4	3.5	4	1.5
Spoor size (cm)					
Front	right				
Length		9	9.4	10	7.5
Width		8.5	6.3	8.5	7.0
Pad		5.5	4.6	6.2	4.5
Front left	Length	10	9.5	10	8.0
Width		9	7.6	8.5	7.2
Pad		5.2	4.7	5.8	4.7
Back right	Length	9.2	7.5	8.5	-
Width		7.1	6.9	7	-
Pad		5	4.2	5	-
Back left	Length	10	8	9	-
Width		7.2	7.2	6.9	-
Pad		5.1	4.6	5.2	-

* indicates actual weight of leopard

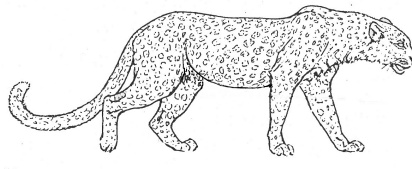
Appendix A-6: How to measure leopard paws and tracks



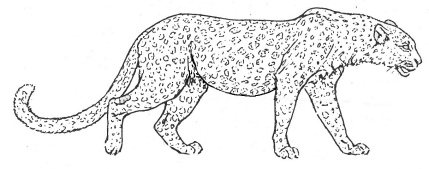
Appendix A-7: Belly scores are rated between 1 – 5. One being the thinnest and 5 being the fullest



Belly score 1



Belly score 3



Belly score 5