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Aspects of the feeding ecology and behaviour of female leopards (*Panthera pardus*) in the Waterberg Mountains, South Africa

by

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ABSTRACT

Leopards (*Panthera pardus*) have the widest distribution of any of the large cats in Africa and are found in habitats including savannas, deserts, forests and, mountains. Although well studied in savanna habitats, their feeding ecology and behaviour are still poorly understood elsewhere, especially in mountainous regions. Scat analysis and direct observations have been the most commonly used techniques to study leopard diet. However, leopards in mountainous areas hide their kills in dense vegetation or rocky overhangs and finding scats are difficult. All of these factors have contributed to the dearth of information on leopard diet and behaviour in these areas.

This study investigated the general feeding ecology and behaviour of three female leopards in the Waterberg Mountains of South Africa. Leopards were fitted with global positioning system (GPS) collars and leopard feeding sites were identified and navigated to in the field using GPS cluster analysis. Over a five month period I investigated 200 potential leopard feeding sites and located 96 leopard feeding/kill sites. Prey remains were collected and analysed to determine gender, age, and subsequently mass of prey species. Together these data were used to estimate prey biomass intake of the leopards. The most frequently consumed prey species were impala (*Aepyceros melampus*), baboon (*Papio ursinus*), and klipspringer (*Oreotragus oreotragus*). Kudu (*Tragelaphus strepsiceros*) made the biggest contribution to the leopards' biomass intake, followed by impala and baboon. This study recorded the highest levels of predation on baboons to date, which may have significant effects on the population structure of these baboon populations. The management implications of seasonal predation on plains species in a mountainous reserve are discussed.

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CHAPTER 1:

GENERAL INTRODUCTION

CHAPTER 1:

GENERAL INTRODUCTION

Introduction

Leopards (*Panthera pardus*) have the widest distribution of any of the large cats in Africa and are found in a wide range of habitats including savannas, deserts, and mountains. While well studied in savanna habitats, their feeding ecology and behaviour are poorly understood elsewhere, especially in mountainous regions (e.g. Martins *et al*. 2011, Jenny & Zuberbüler 2005). There are several possible reasons for the dearth of studies on mountain populations, but this can most likely be attributed to the difficulty in studying leopards in those areas. Thus, ecological information on their diet and behaviour in these habitats is still limited (but see Martins *et al.* 2011). Further, the most commonly used techniques to determine leopard diet—scat analysis and direct observation (Bothma & Le Riche 1984, 1994; Bailey 1993; Ott *et al*. 2007)—are difficult in mountainous regions because these leopards hide their kills under dense vegetation or rocky overhangs (Martins *et al*. 2011) and finding scats is unlikely.

Leopards have diverse diets and prey records collected by Bailey (2005) from around the African continent totalled more than 90 different species. However, leopards prefer to prey on medium sized ungulates that occur in small herds and present minimal risk of injury during capture (Hayward *et al*. 2006). Further, there is some evidence that leopards might be more specialised than previously thought, especially in the selection of hunting habitat, which is often limited to thick vegetation (Balme *et al.* 2006). In mountainous and forested areas, leopards typically feed on smaller animals, mainly because larger ungulates are less abundant (Bothma & Le

Riche 1984; Norton *et al*. 1986). For example, impala were the most preyed upon species by leopards in the Waterberg Mountains (Grimbeek 1991), and mountain reedbuck (*Redunca fulvorufula*) and bushbuck (*Tragelaphus scriptus*) made the biggest contributions to leopards' diets in the Baviaanskloof region (Ott *et al*. 2007). Likewise, rock hyraxes (*Procavia capensis*) formed the majority of the diet in the Western Cape Mountains (Norton *et al*. 1986), and contributed significantly to leopards' diets in the Cederberg Mountains (Martins *et al*. 2011) and the Soutpansberg Mountains (Chase-Grey 2011).

Throughout the literature it is clear that leopards do not favour baboons (*Papio ursinus*) as prey, but they are the primary predators of baboons across Africa (Cowlishaw 1994). Even though baboons may be abundant in an area, their extreme aggressiveness and ability to escape into smaller branches of trees or high cliffs may limit leopard predation (Bailey 2005). Male baboons are particularly aggressive towards leopards and retaliation often leads to death of the leopard (Cowlishaw 1994). Savanna primates like baboons, are preyed on so rarely that they are often left off prey lists by researchers of terrestrial carnivores such as leopards (Isbell 1994).

In addition to the lack of knowledge on leopard diet in mountainous areas, no previous studies have investigated the effects of prey biomass calculations on predator carrying capacity estimates. Although the carrying capacity of several large carnivores have been predicted and tested for small reserves based on the abundance of their preferred prey (Hayward *et al*. 2007), other important factors such as prey availability, mass, and range have never been considered.

General Study Design

In this study, three female leopards on Welgevonden Private Game Reserve in the Waterberg Mountains of South Africa were fit with global positioning system (GPS) collars. Potential leopard feeding/kill sites were identified using GPS location clusters obtained from GPS collars. Potential leopard feeding sites were physically navigated to and searched for prey remains.

Study Objectives

I attempted to answer the following questions regarding leopard feeding ecology and behaviour:

Leopard diet and biomass intake

- What is the prey selection of female leopards on the study site?
- What is the contribution in biomass of each prey species?
- Are there differences between the actual determined biomass intake of the study leopards and the biomass calculated using the unit mass?

Leopard hunting behaviour

- Do the study leopards use certain measured variables differently when hunting dangerous species such as baboons?
- Do leopards learn specialised hunting skills from their parents?
- Are the study leopards mostly nocturnal?
- Are the study leopards a threat to the surrounding livestock farms and game ranches?

References

Bailey, T. N. 2005. *The African leopard: Ecology and behaviour of a solitary felid.* Columbia University Press, New York.

Balme, G., Hunter, L. & Slotow, R. 2006. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74: 589-598.

Bothma, J. Du P. & Le Riche, E.A.N. 1994. Scat analysis and aspects of defecation in Northern Cape leopards. *South African Journal of Wildlife Research:* 24 21-25.

Bothma, J. Du. P. & Le Riche, E.A.N. 1984. Aspects of the ecology and behaviour of the leopard *Panthera pardus* in the Kalahari Desert. *Koedoe (Suppl)* 27: 259-279.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131: 293-304.

Chase-Grey, J.N. 2011. Leopard population dynamics, trophy hunting and conservation in the Soutpansberg Mountains, South Africa. *Ph.D. Thesis*, Durham University.

Grimbeek, A.M. 1992. The ecology of the leopard (*Panthera pardus*) in the Waterberg. *MSc Dissertation*, University of Pretoria.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* (London) 270: 298-313.

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

Isbell, L.A. 1994. Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3: 61-71.

Jenny, D. & Zuberbühler, K. 2005. Hunting behaviour in West African forest leopards. *African Journal of Ecology* 43: 197-200.

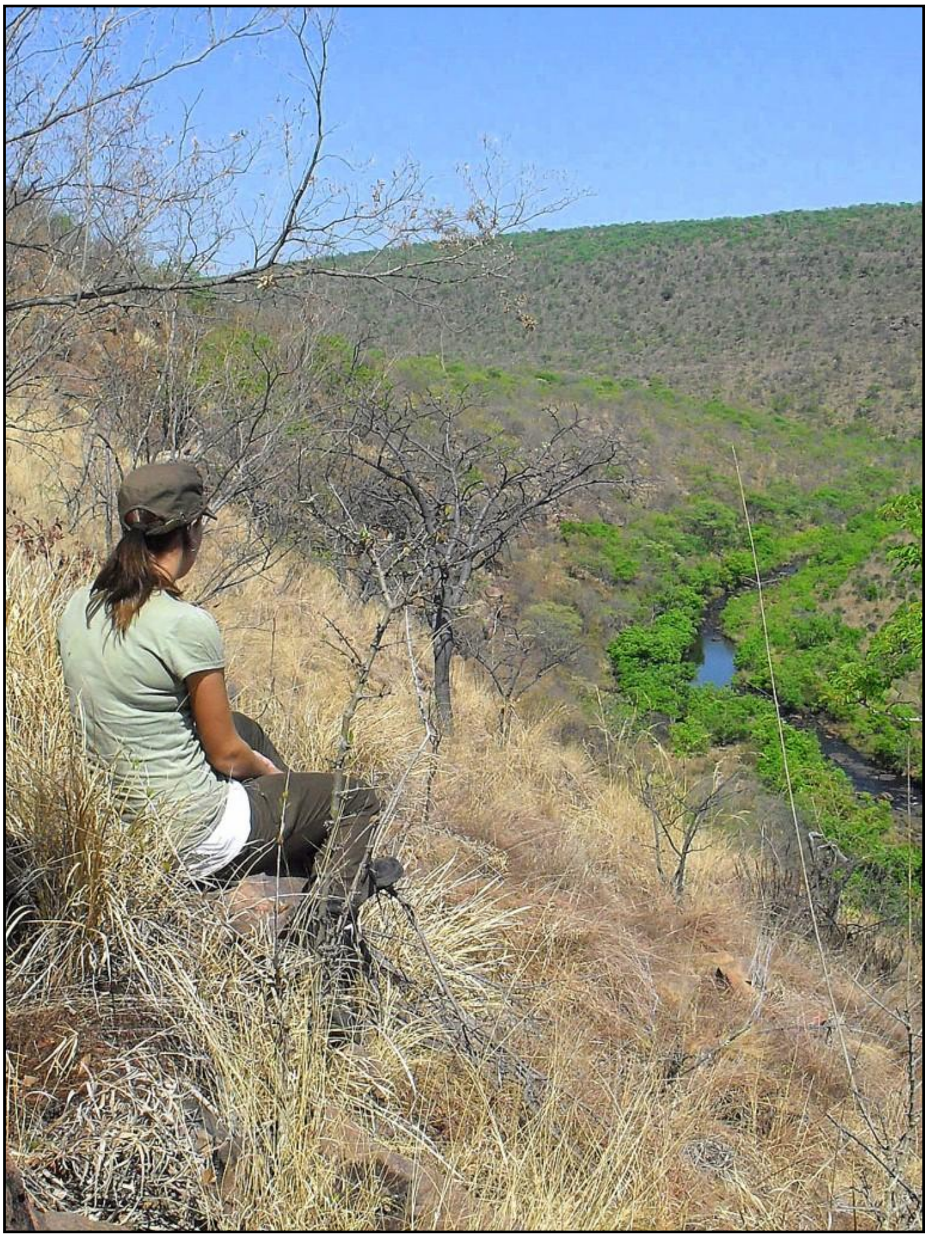
Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* (London) 283: 81-87.

Norton, P.M., Lawson, A.B., Henley, S.R. & Avery, G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Journal of Wildlife* Research 16: 47-52.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. 2007. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology* 42: 31-37.

CHAPTER 2:

STUDY AREA



CHAPTER 2:

STUDY AREA

Location

The study was conducted on Welgevonden Private Game Reserve in the Waterberg Mountains, Limpopo, South Africa (24°10’-24°25’ S; 27°45’-27°56’ E). The reserve lies approximately 20km west of the town Meetsheshela (formerly Vaalwater) and shares a 13km common boundary with the Marekele National Park. The reserve currently covers an area of approximately 37 500 ha and forms part of the Waterberg Biosphere Reserve that was declared by UNESCO in 2001. The reserve first started as a conservation area in 1993 through a private sector development that resulted in the consolidation of numerous private farms.

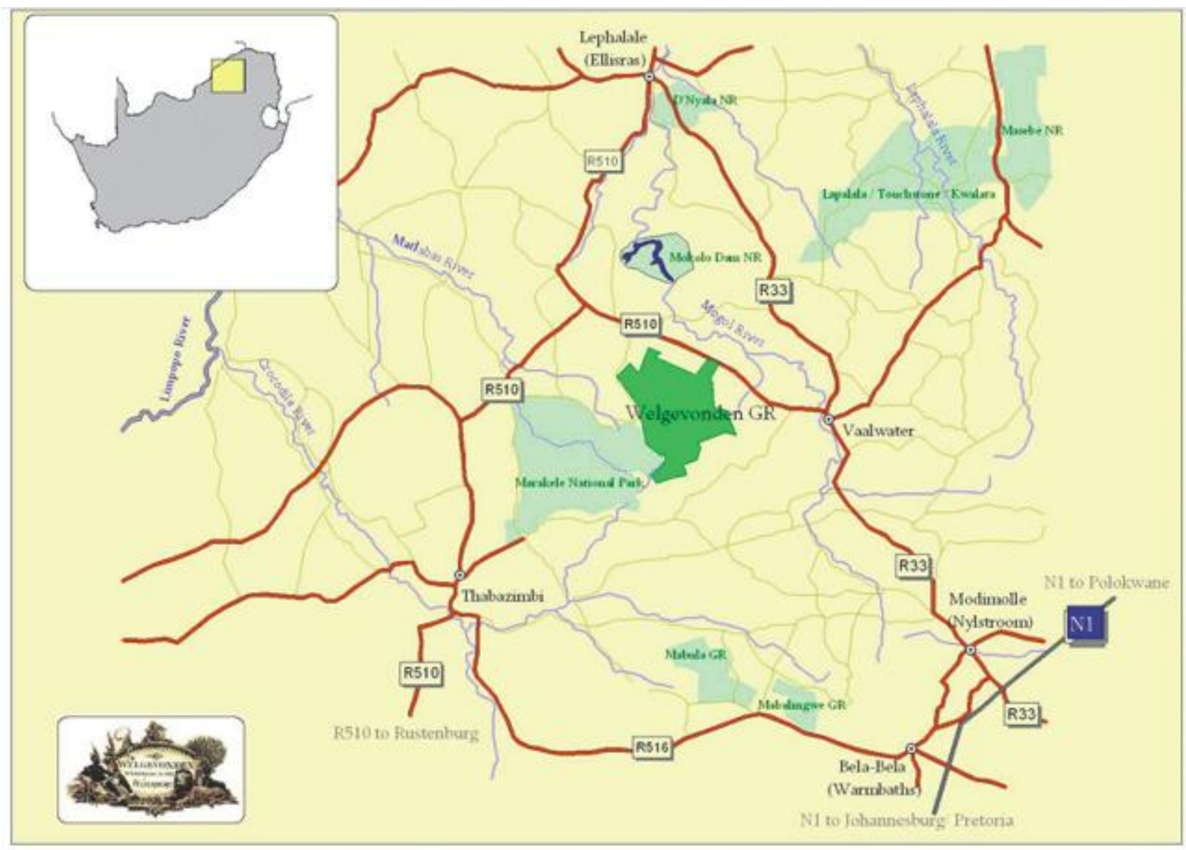


Figure 2.1 The study area located on Welgevonden Private Game Reserve in the Waterberg Mountains, Limpopo, South Africa.

Climate

The Waterberg region has distinct wet and dry seasons that stretch from October to March and April to September, respectively. Summers are hot and wet while winters are cold and dry. The mean annual temperatures range from a minimum of 11 to a maximum of 26.5°C (data from 1924-1999 at the Vaalwater Weather Station Station number: 0632/077LO; 24°17' S; 28° 03' E; Altitude 1215 masl). The mean annual rainfall is 670mm (Elandshoek Weather Station). Fire, caused predominantly by lightning strikes, is a regular occurrence on Welgevonden at the beginning of the rainy season (September-November) and such fires occurred during the study period.

Topography and drainage systems

The study area is located on the Waterberg Plateau at elevations of 1200-1500 masl. Eighty percent of the reserve is mountainous with numerous deep valleys. The reserve is drained by several ephemeral streams and five perennial rivers, of which the Sterkstroom is the largest. All rivers and streams on the reserve eventually lead into the Mogol River, which is an important branch to the Limpopo River. In addition to the streams and rivers, there are also seventeen artificial reservoirs on Welgevonden, of which the majority are perennial. Since the proclamation of the reserve, several smaller waterholes have also been created by landowners to attract game to lodges.

Soil and Vegetation

The reserve is situated on very acidic soils of the Sandriviersberg Formation of the Kransberg subgroup (Acocks 1988). The rocky hills and plateaus are dominated by

Mispah, Glenrosa, and Hutton forms and the rocky drainage lines by Oakleaf soils (MacVicar *et al*. 1977).

Vegetation in the study area is classified as Waterberg Moist Mountain Bushveld (Low & Rebelo 1996). Acocks (1988) classified it as Sour Bushveld (Veld type 20), with elements of Mixed Bushveld (Veld type 18). The tree layer is characterised by African Beechwood (*Faurea saligna*), Silver Cluster leaf (*Terminalia sericea*), Wild seringa (*Burkea Africana*), Stemfruit (*Englerophytum magalismontanum*), Red bushwillow (*Combretum apiculatum*), Velvet bushwillow (*Combretum molle*), and Horn-pod (*Diplorrhynchus condylocarpon*). Typical grass species include Crimson bluestem (*Schizachyrium sanguineum*), Common russet grass (*Loudetia simplex*), Spiked crinkleawn *(Trachypogon spicatus*), Wire grass *(Elionurus muticus*), and Red grass (*Themeda triandra*). Acocks (1988) described the grassveld as floristically rich, but with very low grazing value.

Mammal species

The reserve hosts more than 50 mammal species including the Big Five and various other carnivores like brown hyenas (*Hyaena brunnea*), black-backed jackals (*Canis mesomelas*), and cheetahs (*Acinonyx jubabtus*). There is high diversity of herbivore species, ranging in size from steenbok (*Raphicerus campestris*), mountain reedbucks *(Redunca fulvorufula*), and impala (*Aepyceros melampus*), to larger herbivores such as blue wildebeests (*Connochaetes taurinus*), plains zebras (*Equus quagga*), and giraffes (*Giraffa camelopardalis*). Other meso-mammals include warthogs (*Phacochoerus africanus*), baboons (*Papio ursinus*), vervet monkeys (*Cercopithecus aethiops*), and aardvark (*Orycteropus afer*). Smaller mammals include Jamson's red rock rabbits (*Pronolagus randensis*), rock hyraxes (*Procavia capensis*), and several species of mongoose.

Leopards on Welgevonden

Although Welgevonden is encircled by a boundary fence, leopards move freely between neighbouring properties, as one of the study leopards occasionally did. The adjacent land consists of Marekele National Park on the southwestern side, private game farms and protected areas on the south and east, and livestock farms on the remainder where leopards are seen as potential damage-causing animals.

At the time of the study, the density of leopards on Welgevonden was approximately 4.5 adult leopards/100km^2, as determined by mark-recapture models applied to camera trapping data (L. Swanepoel, unpublished data).

References

Acocks, J. P. H. 1988. Veld types of South Africa. *Memoirs of the botanical survey of South Africa* 57: 1-146.

Low, A.G. & Rebelo, A.G. 1996. *Vegetation of Southern Africa, Lesotho and Swaziland.* Dept. of Environmental Affairs & Tourism, Pretoria.

MacVicar, C.N., De Villiers, J.N., Loxton, R.F., Verster, E., Lamprechts, J.J.N., Merryweather, F.R., Le Roux, J., Van Rooyen, J.A. & Harmse, H.J. 1977. *Soil classification: a binomial system for SA*. Pretoria, 1st ed. Soil & Irrig. Res. Inst. Dept. Agric. Tech. Services.

CHAPTER 3:

GENERAL METHODS

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GENERAL METHODS

Introduction

The dissertation is prepared in such a way that each data chapter is an independent paper. Therefore, the methods, techniques, and statistics used will be discussed in more detail in the applicable chapters. Since all the data chapters deal with diet and behaviour of leopards (*Panthera pardus*), there is a big overlap in the methods used. This chapter will only give a broad summary of the methods used during the study.

Leopard capture and collaring

Leopards were captured using soft-hold foot snares (Frank *et al*. 2003) and immobilized with an intramuscular dose of teletamine-zolazepam (Zoletil ® 100, Virbac RSA (Pty) Ltd., Centurion, South Africa; 4–5mg.kg^{-1}). Condition and morphological characteristics were assessed whilst the leopards were sedated. After collecting biological samples, leopards were fitted with remote drop-off global positioning system (GPS) collars (Followit Tellus, Lindesberg, Sweden). Once fully recovered, leopards were released within close proximity to the capture site. Capturing and collaring was conducted under the University of Pretoria Animal Use and Care Committee ethics clearance protocol AO 22-06 with all its amendments and a Limpopo standing permit (no. S13631) for scientific institutional research. All collars were released from the leopards on completion of the study.

Locating leopard feeding sites

It has been reported that leopards stay near a kill until it is completely consumed (Bailey 2005). Therefore, it is predictable that if a leopard is fitted with a GPS-collar and stay near a kill, a cluster of GPS points would indicate a feeding site. Collars were scheduled to download GPS points every two hours, and send it to a server using the GSM network. Leopard feeding sites were located in the field using GPS cluster analysis (Tambling *et al*. 2010, Martins *et al*. 2011); this was achieved by manually inspecting GPS spatial clusters using ArcGIS v.9.2 (ESRI, Redlands, CA, USA). Clusters were located with the use of a hand-held GPS device (Garmin eTrexVenture® Cx, Garmin International, Kansas, USA) and inspected for prey remains for a maximum of 30 minutes. When present, prey remains were photographed and collected for later identification. Prey was identified by microscopic examination of cuticular hair scale patterns and cross sections (Dreyer 1966, Keogh 1979, 1983, Buys & Keogh 1984) and compared to reference samples housed at the Centre for Wildlife Management, University of Pretoria, South Africa.

Determination of age and mass of prey species

Jaw bones, horns, hooves and other indicative bones were used to determine the gender, age, and consequently weight of prey species. In the absence of bones at feeding sites, the mean weight for the specific prey species was used for each individual leopard separately. Mean time of birth was recorded for group birthing animals (e.g. impala *Aepyceros melampus*, plains zebra *Equus quagga*) and was used to assist in determining the age of juvenile animals where bones were absent. With the rare exception of finding a jaw bone, all small prey (Jameson's red rock rabbits *Pronolagus radensis*, banded mongooses *Mungos mungo*, and birds) were assumed to be adult.

References

Bailey, T. N. 2005. *The African leopard: Ecology and behaviour of a solitary felid.* Columbia University Press, New York.

Buys, D. & Keogh, H.J. 1984. Notes on the microstructure of hair of the Orycteropodidae, Elephantidae, Equidae, Suidae and Giraffidae. *South African Journal of Wildlife Research* 14: 111-119.

Dreyer, J.H. 1966. A study of the hair morphology in the family Bovidae. *Onderstepoort Journal of Veterinary Research* 33: 379-472.

Frank, L., Simpson, D. & Woodroffe, R. 2003. Foot snares: An effective method for capturing African lions. *Wildlife Society Bulletin* 31: 309-314.

Keogh, H.J. 1979. An atlas of hair from southern African mammal species with reference to its taxonomic and ecological significance. *DSc Thesis*, University of Pretoria.

Keogh, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research* 13: 89-132.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* (London) 283: 81-87.

Tambling, C.J., Cameron, E.Z., Du Toit, J.T. & Getz, W.M. 2010. Methods for locating African lion kills using global position system movement data. *Journal of Wildlife Management* 74: 549-56.

CHAPTER 4:

EFFECT OF PREY MASS AND SELECTION ON PREDATOR CARRYING CAPACITY ESTIMATES

EFFECT OF PREY MASS AND SELECTION ON PREDATOR CARRYING CAPACITY ESTIMATES

In Review at European Journal of Wildlife Research

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Abstract

The ability to determine the prey-specific biomass intake of large predators is fundamental to their conservation. In the absence of actual prey data, researchers generally use a 'unit mass' method (estimated as 3/4 adult female mass) to calculate the biomass intake of predators. However, differences in prey preference and range across geographic regions are likely to have an influence on biomass calculations. Here I investigate the influence of estimated prey mass on leopard (*Panthera pardus*) biomass calculations, and subsequently carrying capacity estimates, in an understudied mountain population. Potential leopard feeding sites were identified using global positioning system (GPS) location clusters obtained from GPS collars. I investigated 200 potential leopard feeding sites, of which 96 where actual feeding sites. Jaw bones, horns, hooves, and other indicative bones were used to determine gender and age of prey items, which were subsequently used to calculate mass of each prey item based on previously published values. There were significant differences in the biomass values calculated using the traditional unit mass method and the calculated prey masses obtained from leopard feeding sites. However, there were no considerable differences in the carrying capacity estimates using the preferred prey species model and leopard density estimates calculated using a non-

biased spatial approach, which suggests that estimating carnivore carrying capacity based on 3/4 adult female masses is a reliable method, also for a mountain population.

Key Words biomass calculation, carnivore ecology, carrying capacity, diet, GPS, *Panthera pardus*

Introduction

Large carnivores play an important role in regulating natural terrestrial ecosystems (Estes *et al*. 2011). However, on small enclosed reserves, large carnivores can reduce prey populations and destabilize ecosystems (Smith 2006). Therefore, knowledge of carnivore numbers and carrying capacity are important for management of small enclosed reserves (Fuller & Sievert 2001, Hayward *et al*. 2007). Predator-prey relationships serve as a foundation to determine the prey-specific biomass intake of predators which can then be used to estimate the carrying capacity of large carnivores (Hayward *et al*. 2007). Carrying capacities of several large carnivores (e.g., lions *Panthera leo*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, spotted hyenas *Crocuta crocuta*, and African wild dogs *Lycaon pictus*) have been predicted and tested for small reserves by regressing carnivore density to the abundance of their preferred prey (Hayward *et al*. 2007).

Although prey preference and abundance are key factors in calculating the carrying capacity of large predators, availability and range of prey species are also important factors to consider, especially across different geographic study areas. For example, leopards preferentially prey on species within the range of 10–40 kg (Hayward *et al*. 2006). However, in certain mountainous regions, such as the Cederberg Mountains of South Africa, leopards mostly have access to smaller species, like klipspringers (*Oreotragus oreotragus*, ± 12.5 kg) and rock hyrax (*Procavia capensis*, ± 3.2 kg) (Martins *et al*. 2011). These differences in the average mass of available prey likely affect biomass calculations, and subsequently carrying capacity estimates of large predators.

In this study, I collected leopard prey remains to estimate actual age and mass of the prey species consumed. I then used these masses to calculate biomass consumed by leopards and thus estimate leopard carrying capacity in a mountain population. To assess the implications of using various metrics of biomass consumption, I also calculated carrying capacity based on the widely used technique of ignoring the gender and age of each prey item and simply calculating the biomass as 75% of the mass of adult females of preferred prey species.

Methods

Study Area

The study was conducted on Welgevonden Private Game Reserve in the Waterberg Biosphere in South Africa. The reserve, which caters mainly for wildlife safaris, currently covers an area of approximately 37,500 ha at an elevation of 1200-1500 masl. Eighty percent of the reserve is mountainous with numerous deep valleys (Kilian 2003).

The reserve hosts more than 50 mammal species, including lions, leopards, cheetahs, and numerous smaller carnivores like brown hyenas (*Hyaena brunnea*), and black-backed jackals (*Canis mesomelas*). Herbivores range in size from giraffes

(*Giraffa camelopardalis*), plains zebras (*Equus quagga*), and blue wildebeests (*Connochaetes taurinus*), to smaller antelope such as impala (*Aepyceros melampus*), mountain reedbucks *(Redunca fulvorufula*), and steenbok (*Raphicerus campestris*).

Welgevonden is encircled by a boundary fence, but fences rarely act as barriers to leopards (Hayward *et al*. 2007b) and they are able to move freely between neighboring properties. The reserve is bordered by Marekele National Park on the southwestern side, private game farms on the south and east, and livestock farms on the remainder where leopards are seen as potential damage-causing animals.

Prey and leopard abundance

I estimated prey abundance with annual aerial counts conducted in the dry season when wildlife is most easily detected. Welgevonden was divided into grids that were systematically inspected to improve accurate detection of prey species. Each count was conducted over a 4-day period. I estimated prey abundance by using the most recent aerial count (2010). Aerial census techniques are biased against smaller, cryptic animals, so correction factors previously applied in Kruger National Park were used to adjust counts for these species (Owen-Smith & Mills 2008).

I used both a spatial and non-spatial approach to estimate leopard density on Welgevonden. I applied mark-recapture camera trapping data to the software package CAPTURE (Rexstadt & Burnham 1991) using ½ MMDM as well as to the R package *secr* (Efford *et al*. 2009). Spatially explicit methods such as *secr*, doesn't make any assumptions with regard to the effective survey area (Noss *et al.* 2012).

Leopard capture and collaring

Leopards were captured from May to August 2010 using soft-hold foot snares (Frank *et al*. 2003). Leopards were immobilized with teletamine-zolazepam (Zoletil ® 100, Virbac RSA (Pty) Ltd., Centurion, South Africa; dosage 4-5mg/kg) and examined for general health and condition. The leopards were weighed, measured, and examined for general health, and three females and one male were fitted with GPS/GSM cellular collars (Followit Tellus, Lindesberg, Sweden). The male leopard damaged and dropped his collar shortly after capture; thus, data in this paper concern only the three females. Immobilized leopards recovered in a wooden crate and were released near the capture site. The study was conducted under the University of Pretoria Animal Use and Care Committee ethics clearance protocol AO 22-06 with all its amendments and a Limpopo standing permit (no. S13631) for scientific institutional research. All collars were released from the leopards on completion of the study using a remote controlled drop-off function.

Locating leopard feeding sites

I programmed collars to record a GPS location every two hours and downloaded GPS locations via the cellular network on a daily basis. Potential predation GPS clusters were identified and mapped in ArcGIS v.9.2 (ESRI, Redlands, CA, USA) to locate possible leopard feeding sites (Valeix *et al*. 2011, Martins *et al*. 2011, Tambling *et al*. 2010). A GPS location from each potential predation site was used to navigate to clusters on foot and searched for prey remains for a maximum of 30 minutes. I excluded three occurrences of scavenging (all blue wildebeest), as indicated by the lack of typical signs of a leopard feeding/kill site (e.g., plucked hair, blood, drag marks, fighting circle), and two unidentified prey species from the analysis. Prey remains were photographed *in situ* and collected for later identification. I identified prey by either microscopic comparison of cuticular hair scale patterns and cross sections to reference keys (Dreyer 1966, Keogh 1979, 1983, Buys & Keogh 1984), or by macroscopic prey remains like horns and skin.

Estimation of age and mass of prey species

I used two methods to estimate the biomass of prey consumed by leopards. First, I applied the widely used convention of a generalized "unit mass", defined as ¾ of the average adult female body mass for each species (referred to as the "unit mass method" herein; e.g., Van Orsdol *et al*. 1985, Radloff & Du Toit 2004, Hayward & Kerley 2005, and Hayward 2006). This method was proposed to adjust biomass calculations assuming that some calves and sub-adults are also preyed upon (Schaller 1972). It is a popular technique because difficulty locating kills, species characteristics (e.g., a lack of sexual dimorphism), and the condition of prey remains make estimating the biomass consumed by carnivores difficult.

Second, I attempted to directly estimate the biomass by determining the gender and age of each prey item. I relied on hard tissue (e.g., jaw bones, horns, hooves, and other indicative bones) to determine gender and age of prey items captured by leopards. Teeth wear, replacement, and horn growth served as the most reliable indicators of age. Mean time of birth was recorded for group-birthing animals (e.g., impala, plains zebra) on the reserve and was used to assist in determining the age of juveniles. I used the mean mass of the species when suitable aging samples were absent at feeding sites. There were no abundance estimates available for smaller species i.e., red rock rabbits (*Pronolagis radensis*), banded mongooses (*Mungos* *mungo*), African civets (*Civettictis civetta*), and several bird species. I therefore excluded them from the carrying capacity estimates but their small size suggests they would not have increased the estimates using the actual dietary data.

The following studies were used to estimate age and mass of prey species: Roettcher & Hofmann 1970, Child 1964 (impala); Simpson 1966, Wilson 1965 (kudu *Tragelaphus strepsiceros*); Smuts 1972, 1974 (zebra); Wilson & Child 1965 (klipspringer *Oreotragus oreotragus*); Stoltz 1977 (baboon *Papio ursinus*); Seydack 1983 (bushpig *Potamochoerus larvatus*); Norton & Fairall 1991 (mountain reedbuck); and Wilson, Schmidt & Hanks 1984 (duiker *Sylvicapra grimmia*). Data from Skinner & Chimimba (2005) were used to estimate the age and mass of common reedbuck *Redunca arundinum.*

Statistical analysis

I estimated the carrying capacity of leopards using the equation

$$K = -2.248 + 0.405x$$

where x is $\log_{10}$ biomass of the prey. First, I estimated biomass as ¾ of the adult female mass of the three most preferred prey species of leopards: impala, bushbuck, and duiker (Hayward *et al*. 2007). Second, I calculated biomass as the mean mass of actual prey consumed by leopards on Welgevonden. I compared the resulting estimates of carrying capacity against the population estimate obtained from mark-recapture methods (L.H. Swanepoel, unpublished data).

I used chi-square tests to evaluate overall differences between prey biomass calculated directly and estimated by the unit mass method. I also used Strauss' linear index of selection (L_i = *unit mass*$_i$ – *direct estimation*$_i$; Strauss 1979) to determine if the unit mass method over- or underestimated my direct calculations of the consumed biomass of each prey species. Strauss' linear index of selection gives values from -1, representing a large underestimation, to 1, representing a large overestimation of prey biomass with the unit mass method.

Results

Over a period of five months, I visited 200 potential feeding sites of three female leopards, 96 of which were determined to be actual leopard feeding sites. Leopards preyed upon a total of 14 species with the most commonly taken prey items being baboons (20.2% of all identified prey), impala (20.2%), and klipspringers (12.4%) (Table 4.1). Duiker (n = 1) and bushbuck (*Tragelaphus scriptus*) (n = 0), which are often considered to be preferred prey of leopards, were rarely or never consumed in this study. Smaller prey species like banded mongooses, red rock rabbits, African civets, and several bird species accounted for 3.5% of the leopard's biomass intake. Distinct age preferences were seen in some prey, like zebras, where only foals were preyed upon.

Table 4.1 Prey item remains located at leopard feeding sites. The determined biomass was calculated with consideration of gender and age of the prey actually consumed. The unit mass method estimates body mass of each species as ¾ of adult female body mass.

			Biomass	
Species	Number	% of Kills	Determined	Unit Mass
Impala	18	20.22	20.42	15.77
Kudu	4	4.5	25	13.8
Mountain reedbuck	7	7.9	7.2	3.6
Common reedbuck	1	1.1	2.6	1.5
Klipspringer	11	12.4	5.6	3.1
Zebra	8	9	12.2	51.3
Baboon	18	20.22	18.7	6
Bushpig	2	2.25	4.8	2.4

Chi-square analysis revealed a highly significant difference in estimated prey biomass killed between the two methods ($\chi_8^2 = 37.6$, $P < 0.0001$). The biomass of killed zebras was overestimated by the unit mass method (linear selection index: 0.391) (Figure 4.1), which is caused by the exclusive predation on zebra foals by leopards on Welgevonden (Table 4.2). All of the other species were slightly underestimated with baboons (-0.127) and kudu (0.112) being the most underestimated (Figure 4.1). Estimating leopard density using CAPTURE yielded an estimate of 17 leopards (4.5 per 100km^2); *secr* yielded an estimate of 13 leopards (3.26 per 100km^2, SE = 1.42, CL = 1.44-7.36).

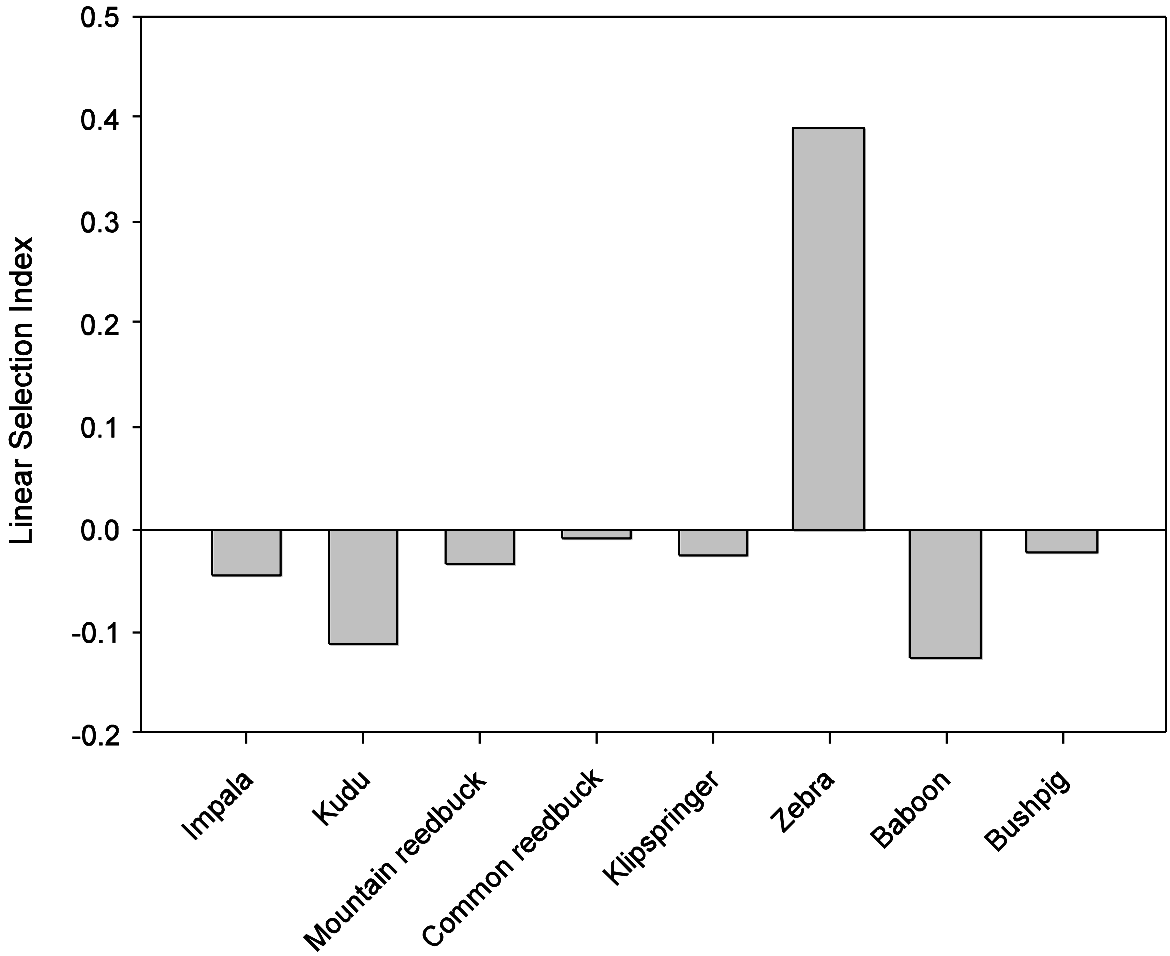

Figure 4.1 Strauss' linear index of selection illustrating the over/underestimation by the ¾ adult female mass method in calculating leopard biomass intake on Welgevonden Private Game Reserve.

Table 4.2 Minimum, maximum, and average masses of prey taken by leopards on Welgevonden represent the published values for the ages and genders of individuals found at feeding sites. The ¾ adult female masses are used in calculations of carrying capacity assuming we had no knowledge of genders and ages of taken prey. The percentage of kills estimated refers to the % of kills where age-indicative prey remains were located. Ratio refers to the ratio of juvenile to sub-adult to adult for prey species where age-indicative prey remains were located.

Species	Minimum mass	Maximum mass	Average mass	% of kills estimated (n)	Ratio	Unit mass
Impala	10	45	25.71	50 (9)	4:2:3	31.5
Kudu	99	190	143	100 (4)	0:2:2	123.75
Mountain reedbuck	8	31	23.5	43 (3)	1:0:2	18.375
Common reedbuck	60	60	60	100 (1)	0:0:1	52.5
Klipspringer	11	12	11.5	55 (6)	0:0:6	10.125
Zebra	35	35	35	100 (8)	8:0:0	230.625
Baboon	16	35.5	23.79	50 (9)	0:1:8	12
Bushpig	55	55	55	100 (2)	0:0:2	42.75

Using the preferred prey species model (Hayward *et al.* 2007) of leopard carrying capacity and calculating biomass as ¾ adult female body mass yielded an estimate of 11 leopards (3.1 per 100 km^2; Table 4.3), which is six below the CAPTURE estimate of 17 and two below the *secr* estimate of 13. Calculating carrying capacity based on the calculated biomass of the actual prey consumed (i.e., accounting for all species consumed as well as the age and gender of each individual) yielded an estimate of carrying capacity of 22.

Table 4.3 Abundance and biomass data (based on actual kills and ¾ adult female body mass) from Welgevonden. While all actual prey items were used in our refined calculations of the carrying capacity, only those significantly preferred prey species with asterisks (*) were used in estimations of carrying capacity using the traditional method.

Species	Abundance estimate	Owen-Smith & Mills (2008) correction factors	Biomass based on body mass of actual prey individuals (kg km^{-2})	Biomass based on ¾ adult female body mass (kg km^{-2})
Baboon	828	1.2	52.5	24.8
Bushpig	129	3	0	15.5
Common duiker	3	1	0	0.1 *
Impala	1105	1.7	75.8	60.2 *
Klipspringer	16	1	0.5	0.4
Kudu	275	1.8	105	99.1
Reedbuck, common	159	3	25.4	16.2
Reedbuck, mountain	45	3	2.8	2.7
Zebra, plains	728	1.2	68	339.9

Discussion

Taking into consideration only the species for which population estimates were available, leopards on Welgevonden consumed prey species ranging in size from 8-190 kg (Table 4.2). There were obvious differences in the estimated mass of several prey species when using the unit mass method and direct estimation. For example, since the leopards in this study mostly preyed upon adult baboons rather than sub-adults (Jooste *et al*. In press), I estimated an average mass of nearly 24 kg, compared to 12 kg as specified by the unit mass method. The leopards in this study preyed commonly on baboons (Table 4.1), and these estimated mass differences (which lead to substantial underestimates of biomass intake in the unit mass method) strongly affected estimated carrying capacity estimates. The same holds for kudu where I estimated an average of 143 kg compared to the previously used 123.75 kg.

I found the standard method of using ¾ of the adult female body mass to estimate the biomass eaten by large carnivores underestimated the leopard carrying capacity at Welgevonden when using the CAPTURE estimate (11 vs. 17); however, it was within closer range to the *secr* estimate (11 vs. 13). There are two possible reasons for this underestimation. First, the average masses of almost all prey species taken by leopards in this study were underestimated by the unit mass method except for plains zebra, which was overestimated. The most underestimated mass were those of kudu, baboon, and mountain reedbuck, all because mostly adults were taken. Conversely, all plains zebras preyed upon were foals, which resulted in an overestimation of biomass from the unit mass method. Predation on zebras mainly occurred after the onset of the first summer rains, which may have forced plains zebras into the mountains where juveniles were especially susceptible to predation. Given intraspecific differences in the mass of prey species, I recognize that calculations of prey biomass based on studies done in other areas may lead to biases in my Strauss' index values, but I believe this bias is minor compared to the apparent bias of the unit mass method. Second, basing calculations of density on the biomass of species preferentially taken by leopards elsewhere (bushbuck, common duiker, and impala) as suggested by Hayward *et al*. (2007) seems to create a substantial bias in the estimate because of differences in prey taken. Prey abundance estimates from Welgevonden suggest that common duiker and bushbuck are present in negligible densities; thus leopards can't prey on them. Therefore, such estimates underestimate the biomass available to support leopards and thus the estimated carrying capacity. However, when using the *secr* leopard density estimate, the preferred prey species model proved reliable. An alternative explanation for the underestimation by the model is that leopards may be above the reserve's carrying capacity, especially if leopards are hunting livestock on adjacent farmland and using Welgevonden as a refuge, allowing a higher population to be sustained with reduced food availability on site. However, I didn't locate any livestock remains at leopard feeding sites in this study.

My study demonstrates that two important variables in biomass computation, namely prey selection and prey mass, can influence carnivore carrying capacity predictions. While Hayward *et al*. (2007) successfully predicted a range of carnivore carrying capacities across South Africa, I suggest that for leopards at least some local populations might be over- or underestimated using the generalized unit mass rather than site specific kill information. Leopard feeding ecology has been biased towards the more mesic parts of South Africa, with few studies in mountainous areas. However, the recent advances in GPS telemetry systems will undoubtedly improve dietary studies for data poor areas, which will greatly improve biomass computations and predictions for carnivore carrying capacity. However, taking into consideration the advances of spatially explicit density prediction methods (Noss *et al*. 2012), I recognize that predator carrying capacity can reliably be predicted using the preferred prey species model, even in a mountain population.

Although my study contributes firsthand knowledge to large carnivore predation and carrying capacity prediction, I acknowledge some shortcomings of my study. First, the model predicts carrying capacity and not population size; thus, to test the predictive success of the model, I need several years of data. In addition, I make the assumption that the current leopard population estimate is accurate. Using a non-spatial approach such as CAPTURE could have overestimated the population size (Noss *et al*. 2012). Second, I only have a sample size of three females which may result in a biased record of prey selection in the population as a whole. If this bias leads to underestimating prey biomass (because leopards are size-constrained predators and females are smaller than males), my carrying capacity predictions may be too high. Conversely, if larger males can prey upon a wider range of species, my estimates may have underestimated biomass available and therefore carrying capacity. Third, the annual aerial counts could have undercounted the small, cryptic prey species which leopards do eat on Welgevonden (e.g., klipspringer), which could lead to an underestimation of carrying capacity estimates. Although correction factors (Owen-Smith & Mills 2008) were applied to adjust prey counts, differences in vegetation types in Kruger National Park and my study area could have caused potential biases. Fourth, I was unable to collect data year round (late winter – midsummer) and prey selection is likely to change (e.g., zebra foals are obviously only seasonally available). Finally, the body masses I used were obtained from studies of savanna prey species, which may be different than body masses of these species in more nutrient-deficient, mountainous areas. Nevertheless, I still show that biomass computation can vary greatly from the unit mass method and should be taken into account in estimating predator carrying capacities, especially for understudied areas or populations.

Management Implications

Using the unit mass method could potentially lead to biased estimates in large carnivore carrying capacity and seems to be strongly affected by variation in prey species available and age-dependent predation on prey. Thus, estimated carrying capacities using the unit mass method, which may be the best information available in some cases (particularly where no information about the actual diet is available), may result in incorrect management decisions. Conversely, using data on the actual diet of large predators, as I have done here, is time consuming and logistically difficult, but is likely to improve carrying capacity estimates, and therefore management decisions, however, to test its predictive success, long term data is required. It is possible that inclusion of more study animals over several seasons would potentially eliminate the discrepancy between methods in predator abundance estimates and therefore general consensus needs to be reached regarding sampling intensity. In addition, I caution wildlife managers and scientists to use equal surface areas when regressing carrying capacity estimates and comparing it to predator abundance estimates from camera trapping data, as this may influence the results. Where detailed annual information on the diet of predators is unavailable, the coarser unit mass method is likely to continue to yield viable estimates of carrying capacity.

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References

Buys, D. & Keogh, H.J. 1984. Notes on the microstructure of hair of the Orycteropodidae, Elephantidae, Equidae, Suidae and Giraffidae. *South African Journal of Wildlife Research* 14: 111-119.

Child, G. 1964. Growth and ageing criteria of impala, *Aepyceros melampus*. *Arnoldia* 27: 128-135.

Dreyer, J.H. 1966. A study of the hair morphology in the family Bovidae. *Onderstepoort Journal of Veterinary Research* 33: 379-472.

Efford, M.G., Borchers, D.L. & Byrom, A.E. 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods In: *Modeling demographic processes in marked populations*: pp 255-269. Thompson, D.L., Cooch, E.G. & Conroy, M.J. (Eds.). New York: Springer.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. and Wardle, D.A. 2011. Trophic Downgrading of Planet Earth. *Science* 333: 301-306.

Frank, L., Simpson, D. & Woodroffe, R. 2003. Foot snares: An effective method for capturing African lions. *Wildlife Society Bulletin* 31: 309-314.

Fuller, T.K. & Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. In: J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne, (Eds). *Carnivore Conservation*. Cambridge University Press and the Zoological Society of London, Cambridge

Hayward, M.W. 2006. Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* (London) 270: 606-614.

Hayward, M.W., Adendorff, J., Moolman, L.C., Hayward, G.J., Kerley, G.I.H. 2007b. The successful reintroduction of leopard *Panthera pardus* to the Addo Elephant National Park. *African Journal of Ecology* 45: 103-104.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* (London) 270: 298-313.

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

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

Jooste, E., Pitman, R.T., Van Hoven, W. & Swanepoel, L.H. 2012. Unusually high predation on Chacma baboons by female leopards in the Waterberg Mountains, South Africa. *Folia Primatologica*: In Press.

Keogh, H.J. 1979. An atlas of hair from southern African mammal species with reference to its taxonomic and ecological significance. *DSc Thesis*, University of Pretoria.

Keogh, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research* 13: 89-132.

Kilian, P.J. 2003. The ecology of reintroduced lions on the Welgevonden Private Game Reserve, Waterberg. *MSc Dissertation*, University of Pretoria.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* (London) 283: 81-87.

Norton, P.M. & Fairall, N. 1991. Mountain reedbuck *Redunca fulvorufula* growth and age determination using dentition. *Journal of Zoology* (London) 225: 293-307.

Noss, A.J., Gardner, B., Maffei, L., Cuéllar, E., Montaño, R., Romero-Muñoz, A., Sollman, R. & O'Connell, A.F. 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. *Animal Conservation* doi:10.1111/j.1469-1795.2012.00545x

Owen-Smith, N. & Mills, M.G.L. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77: 173–183.

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

Rexstadt, E. & Burnham, K. 1991. *User's guide for interactive program CAPTURE*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado 80523, USA

Roettcher, D. & Hofmann, R.R. 1970. The ageing of impala from a population in the Kenya rift valley. *East African Wildlife Journal* 8: 37-42.

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

Seydack, A.H.W. 1983. Age assessment of the bushpig *Potamochoerus porcus* Linn. 1758 in the Southern Cape. *MSc Dissertation*, University of Pretoria.

Simpson, C.D. 1966. Tooth eruption, growth and ageing criteria in greater kudu – *Tragelaphus strepsiceros pallas*. *Arnoldia* 2: 1-12

Skinner, J.D. & Chimimba, C.T. (Rev) 2005. *The mammals of the southern African subregion*. 3rd ed. Cambridge University Press, Cambridge

Smith, D.W. 2006. Re-introduction of gray wolves to Yellowstone National Park, USA. *Re-introduction NEWS* 25: 29-31.

Smuts, G.L. 1972. Seasonal movements, migration and age determination of Burchell's zebra (*Equus burchelli antiquorum*, H. Smith, 1841) in the Kruger National Park. *MSc Dissertation*, University of Pretoria.

Smuts, G.L. 1974. Growth, reproduction and population characteristics of Burchell's zebra (*Equus burchelli antiquorum*, H. Smith, 1841) in the Kruger National Park. *DSc Thesis*, University of Pretoria.

Stoltz, L.P. 1977. The population dynamics of *baboons Papio ursinus* Kerr 1792, in the Transvaal. *DSc Thesis*, University of Pretoria.

Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity Index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* 108: 344-352.

Tambling, C.J., Cameron, E.Z., Du Toit, J.T. & Getz, W.M. 2010. Methods for locating African lion kills using global position system movement data. *Journal of Wildlife Management* 74: 549-56.

Valeix, M., Chamaille´-Jammes, S., Loveridge, A.J., Davidson, Z., Hunt, J.E., Madzikanda, H. & Macdonald, D.W. 2011. Understanding patch departure rules for large carnivores: Lion movements support a patch-disturbance hypothesis. *The American Naturalist* 178: 269-275.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology* (London) 206: 97-112.

Wilson, V.J. 1965. Observations on the greater kudu *Tragelaphus strepsiceros pallas* from a tsetse control hunting scheme in Northern Rhodesia. *East African Wildlife Journal* 3: 27-37.

Wilson, V.J. & Child, G. 1965. Notes on Klipspringer from Tsetse fly control areas in Eastern Zambia. *Arnoldia* 1: 1-19.

Wilson, V.J., Schmidt, J.L. & Hanks, J. 1984. Age determination and body growth of the common duiker *Sylvicapra grimmia* (Mammalia). *Journal of Zoology* (London) 202: 283-297.

CHAPTER 5:

UNUSUALLY HIGH PREDATION ON CHACMA BABOONS (*PAPIO URSINUS*) BY FEMALE LEOPARDS (*PANTHERA PARDUS*) IN THE WATERBERG MOUNTAINS, SOUTH AFRICA

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ABSTRACT

Leopards (*Panthera pardus*) do not preferentially favour baboons as prey, but they are considered the primary predators of baboons across Africa. Even in areas where baboons are abundant, their contribution to leopard diet seldom exceeds 5% of biomass. It is suggested that the extreme aggressiveness of baboons, group vigilance and their high mobility when escaping may limit leopard predation. Male baboons are particularly aggressive and retaliation often leads to the death of the leopard. However, evidence suggests that leopards may learn to catch and kill certain dangerous prey. This study reports predation on Chacma baboons by three female leopards on a private game reserve in the Waterberg Mountains of South Africa. Potential leopard feeding sites were identified using global positioning system (GPS) location clusters obtained from GPS collars. Over a five month period, I investigated 200 potential leopard feeding sites and located 96 leopard feeding/kill sites. Baboons constituted 18.7% of the leopards' biomass intake. The majority of baboons preyed upon were adults and 70% of the kills were diurnal. In terms of the

measured variables, there were no significant differences in the way the leopards preyed upon baboons, compared to the rest of the prey species.

Key words: *aggression, baboon, feeding ecology, leopard, primate predation*

Introduction

Studies on the predation of primates are scarce and frequently restricted by small sample sizes (e.g. Morino 2010, D'Amour *et al*. 2006, Isbell 1994). Simple biological fact (e.g., primates are rarely preyed upon) interacts with logistical realities (e.g., data on the subject are difficult to collect) and leads to this scarcity of knowledge on predation of primates. Given this, it is not surprising that most studies on the predation on primates by carnivores rely on indirect evidence and opportunistic reports (Morino 2010, Isbell 1994). This is unfortunate because predation is likely to have an important impact on population dynamics of primates, which tend to have relatively slow life histories (Charnov & Berrigan 1993).

Leopards (*Panthera pardus*) have a diverse diet and will prey on animals ranging in size from insects, rodents and birds to large ungulates (e.g. Hayward *et al*. 2006, Skinner & Chimimba 2005, Bothma & Le Riche 1984). However, the level of specialisation in a leopard's diet is unclear. Bailey (2005) reports more than 90 different species in the leopard's diet, while Balme *et al*. (2006) suggest that leopards might be more specialised than previously thought, especially with regard to the selection of hunting habitat. It appears that leopards prefer to prey on animals that occur in small herds, in dense habitats, and which present minimal risk of injury, such as impala (*Aepyceros meplampus*), which is generally the most frequently taken prey (preyed on in 100% of study areas where they occur) (Hayward *et al*. 2006).

A misconception about leopards is that they prefer baboons as a prey item (Hunter 1999). Even in areas where baboons are abundant and are likely to be encountered frequently, they are avoided by leopards (Hayward *et al*. 2006). Baboons exhibit several characteristics likely to limit leopard predation, most notably extreme aggressiveness and high mobility when escaping onto the smaller branches of trees (Bailey 2005). Male baboons are particularly aggressive and retaliation often leads to injury or even death of the leopard (Cowlishaw 1994); on rare occasions when leopards do hunt baboons, it usually occurs at night while the baboons are at rest (Busse 1980). Numerous studies from South Africa illustrate this avoidance of baboons by leopards. In the Baviaanskloof region, leopards did not prey on baboons at all, despite them being abundant throughout the study area (Ott *et al*. 2007). In the Cederberg Mountains, baboons comprised only 6.4% of the leopard's biomass intake (Martins *et al*. 2011). In the Soutpansberg Mountains, baboons comprised between 4.2% (Chase-Grey 2011) and 6.7% of the leopard's biomass intake (Schwarz & Fischer 2006); and in the Waterberg Mountains, baboons contributed to less than 2.7% of all kills found (Swanepoel 2009, Grimbeek 1992). Savannah primates—like baboons—are preyed on so infrequently that they are often left off the prey lists by researchers of terrestrial carnivores such as leopards (Isbell 1994).

Here, I report unusually high predation on Chacma baboons (*Papio ursinus*) by female leopards in the Waterberg Mountains of South Africa and evaluate temporal features associated with baboon kills to determine if leopards hunt baboons differently than other species. This is one of very few studies on the predation of primates by carnivores where I could focus on the predator instead of the prey, and this allowed me to record all the kills made by the study leopards and not just occasional kills in a specific troop of baboons.

Methods

Study area

The study was conducted on Welgevonden Private Game Reserve in the Waterberg Mountains of South Africa (24° 18' S, 27° 50'E). Eighty percent of the reserve is mountainous with numerous deep valleys and ravines (Kilian 2003). Although the reserve is encircled by a boundary fence, leopards are still able to move freely between neighbouring properties. At the time of the study, the density of leopards on the reserve was approximately 4.5 adult leopards/100km^2, as determined by mark-recapture models applied to camera trapping data (L. H. Swanepoel, unpublished data).

The reserve hosts more than 50 mammal species, including various carnivores such as lions (*Panthera leo*), brown hyenas (*Hyaena brunnea*), black-backed jackals (*Canis mesomelas*), and cheetahs (*Acinonyx jubatus*). A high diversity of herbivore species exists, ranging in size from giraffes (*Giraffa camelopardalis*), plains zebras (*Equus quagga*) and blue wildebeests (*Connochaetes taurinus*) to smaller antelope such as waterbucks (*Kobus ellipsiprymnus*), mountain reedbucks (*Redunca fulvorufula*) and steenbok (*Raphicerus campestris*). The most abundant species on the reserve is impala (*Aepyceros melampus*). The mountainous terrain of the reserve provides an ideal habitat for baboons and, during the course of the study, there were approximately 25 troops on the reserve, with some comprised of as many as 100 individuals as determined by annual aerial censuses.

Leopard capture and collaring

Leopards were captured using soft-hold foot snares (Frank *et al*. 2003) and immobilized with an intramuscular dose of teletamine-zolazepam (Zoletil ® 100, Virbac RSA (Pty) Ltd., Centurion, South Africa; 4–5mg.kg^{-1}). Condition and morphological characteristics were assessed whilst the leopards were sedated. After collecting biological samples, leopards were fitted with remote drop-off global positioning system (GPS) collars (Followit Tellus, Lindesberg, Sweden). Once fully recovered, leopards were released within close proximity to the capture site. Capturing and collaring was conducted under the University of Pretoria Animal Use and Care Committee ethics clearance protocol AO 22-06 with all its amendments and a Limpopo standing permit (no. S13631) for scientific institutional research. All collars were released from the leopards on completion of the study.

Locating leopard feeding sites

Collars were programmed to download GPS points every two hours (except at noon) and upload them to a server via cellular phone networks whenever the animal was in range of a tower. I located leopard feeding sites in the field using GPS cluster analysis (Tambling *et al.* 2010, Martins *et al*. 2011); this was achieved by manually inspecting GPS spatial clusters using ArcGIS v.9.2 (ESRI, Redlands, CA, USA). Clusters were navigated to using a hand-held GPS device (Garmin eTrexVenture® Cx, Garmin International, Kansas, USA) and searched for prey remains for a maximum of 30 minutes. When present, prey remains were photographed and collected for later identification. I identified prey by microscopic examination of cuticular hair scale patterns and cross sections (Dreyer 1966, Keogh 1979, 1983, Buys & Keogh 1984) and compared it to reference samples housed at the Centre for Wildlife Management, University of Pretoria, South Africa. Prey remains were analysed to determine gender, age, and subsequently mass of prey species. Together these data were used to estimate prey biomass intake of the leopards. I categorized rarely eaten species, Jameson's red rock rabbits (*Pronolagus radensis*), banded mongooses (*Mungos mungo*), rock hyraxes (*Procavia capensis*), common duikers (*Sylvicapra grimmia*), African civets (*Civettictis civetta*) and bird species, in one category labelled 'other'. Three occurrences of scavenging, indicated by the lack of typical signs of a leopard feeding/kill site (e.g. plucked hair, blood, drag marks, fighting circle) and two unidentified prey species, have been excluded from the analysis.

Statistical analysis

Time of kill was taken as the first GPS location of a confirmed leopard feeding site and was categorised into day and night (8am–6pm = day) for statistical analysis. A two sample Kolmogorov-Smirnov test was used to determine if the distribution of the time of kills shows a significant difference from uniformity. A binomial test was used to determine whether leopards selected for a specific gender of baboon and Pearson's correlation test was used to measure correlation between the number of baboon- and non-baboon kills each month. Statistical analyses were conducted with R v.2.10.1 (R Development Core Team 2011).

Results

GPS data were collected from three female leopards. Over a period of five months, I visited 200 potential leopard feeding sites as indicated by GPS-clusters, and located 96 actual leopard feeding sites. Impala (20.2%), baboon (20.2%) and klipspringer (12.4%) were the species most frequently preyed upon, while kudu made the biggest contribution to the leopards' biomass intake (25%) (Table 5.1).

Table 5.1 Prey item remains located at leopard feeding sites using GPS location clusters.

	Scientific name	Number	% of Kills	% Biomass
Impala	*Aepyceros melampus*	18	20.2	20.4
Baboon	*Papio ursinus*	18	20.2	18.7
Klipspringer	*Oreotragus oreotragus*	11	12.4	5.6
Plains zebra	*Equus quagga*	8	9	12.2
Mountain reedbuck	*Redunca fulvorufula*	7	7.9	7.2
Kudu	*Tragelaphus strepsiceros*	4	4.5	25
Bushpig	*Potamochoerus larvatus*	2	2.2	4.8
Common reedbuck	*Redunca arundinum*	1	1.1	2.6
Other	-	20	22.5	3.5

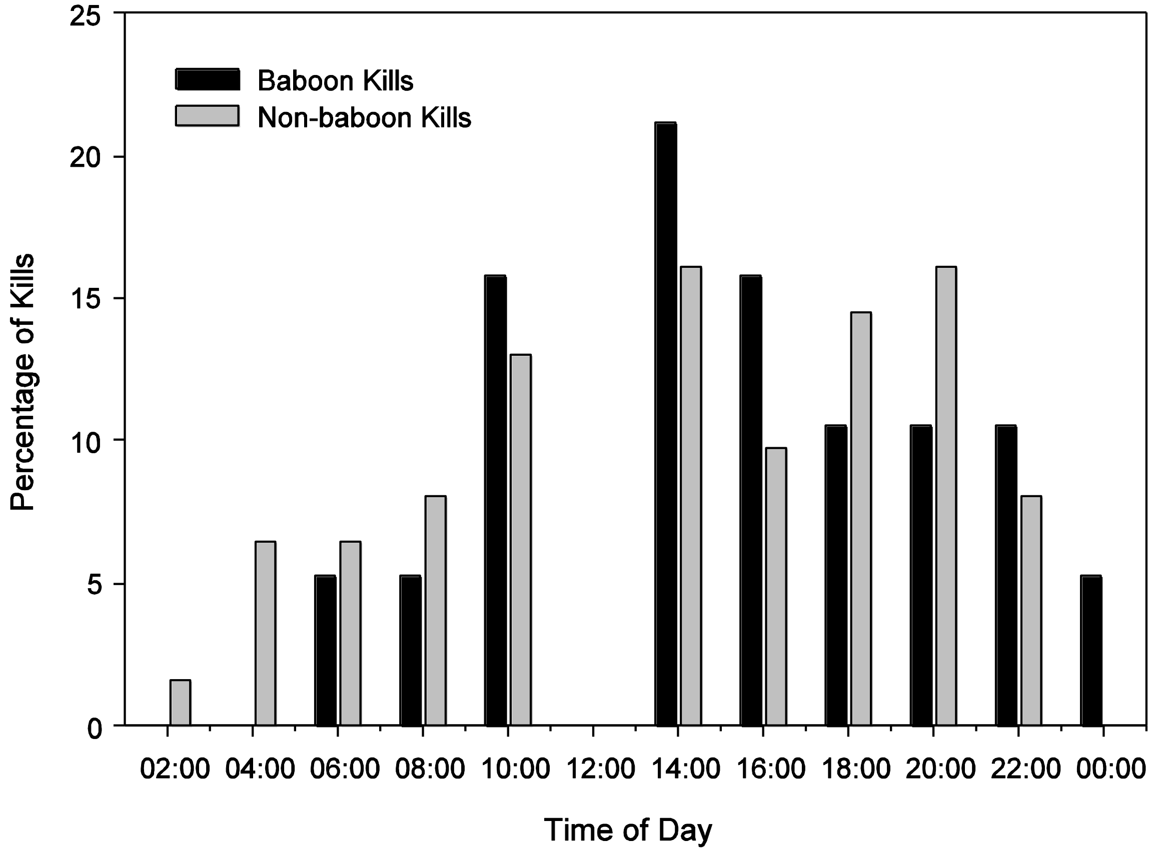

Figure 5.1 Comparison between the time of baboon (*Papio ursinus*) kills and the rest of the kills made by female leopards (*Panthera pardus*) on a private game reserve in the Waterberg Mountains. GPS locations were downloaded every two hours, except at noon, which explains the lack of data at 12:00 and high value at 14:00.

There was no selection by the study leopards for a specific gender of baboons among the small number of individuals for which gender could be determined (Binomial test; n = 8; P = 0.64). With the exception of one sub-adult, all the baboons preyed on were adults. Over time, the distribution of baboon kills showed no significant deviation from uniformity (n=19, P=0.4, D=0.2) (Figure 5.1), but the distribution of combined leopard kills did differ significantly from uniformity (n=81, P=0.02, D=0.2). There were no significant relationship between the number of baboon kills and the number of non-baboon kills each month (Pearson's correlation; n=6, r=0.32, P=0.56) (Figure 5.2).

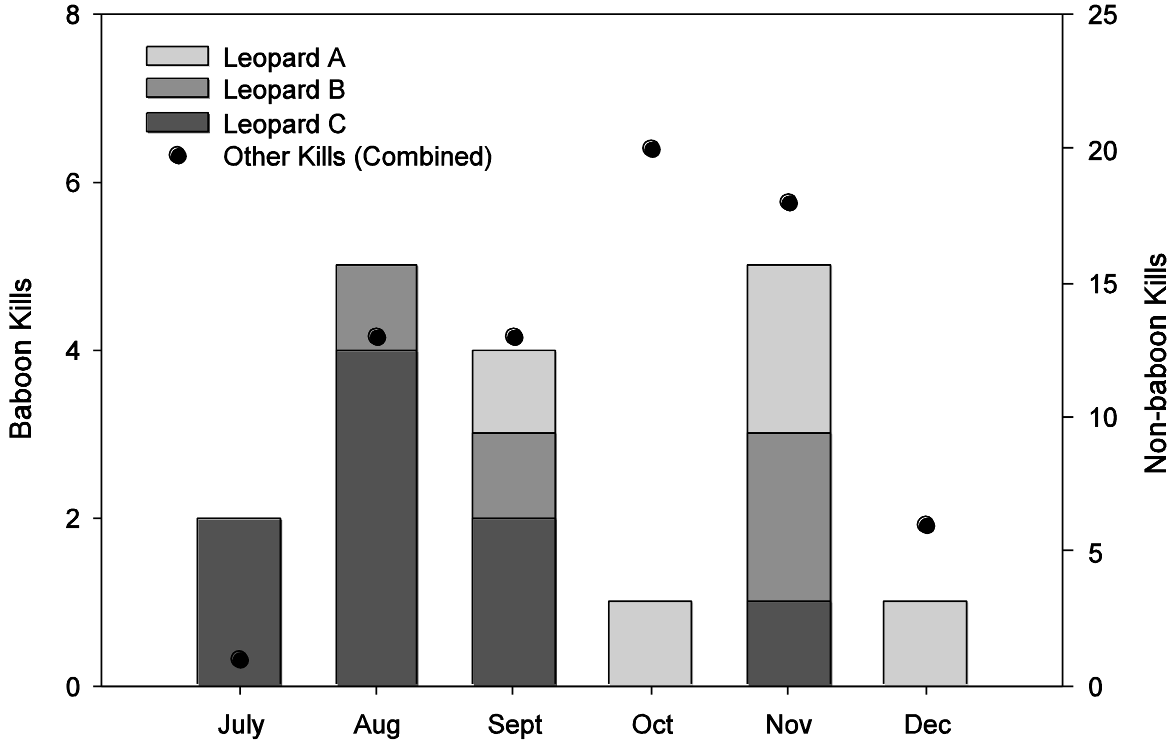

Figure 5.2 Baboon (*Papio ursinus*) kills by each leopard (*Panthera pardus*) per month (bars) and non-baboon kills by all leopards combined per month (dots).

Table 5.2 Weight, developmental stage, and baboon capture data of the study leopards.

Leopard	Weight (kg)	Description	% of diet comprising of baboons
A	30	Young sub-adult female	31.5%
B	43	Adult female	8.8%
C	41	Adult female with young cubs	23.5%

Discussion

While an overwhelming majority of literature on leopard diet confirms they prefer to prey on medium sized ungulates that afford them minimal risk of injury (Hayward *et al*. 2006), there is evidence suggesting leopards may catch and kill certain dangerous prey, as has been shown in several other carnivore species (Power & Compion 2009; Richardson & Andriashek 2006; French & French 1990). Leopards in the southern Kalahari have acquired the skill to kill porcupines by ambushing them just as they emerge from their burrows (Bothma & Walker 1999). A well observed leopard in the Ngorogoro Crater preyed on 11 jackals in less than a month (Hunter 1999) and in arid regions of southern Africa there are records of leopards killing cheetahs (Bothma & Walker 1999; Hunter 1999). However, throughout the literature, it is clear that leopards do not favour baboons (e.g. Hayward *et al*. 2006, Ott *et al*. 2007). In this study, 20.2% of the leopards' diets and 18.7% of their biomass intake consisted of baboons (Table 5.1), the highest values of predation on baboons ever recorded.

Cowlishaw (1994) investigated patterns of predation in baboons and found that leopards are more likely to take adults than juveniles and more likely to take males than females. It was speculated that adult male baboons are more predated on by leopards than any other age-sex class because they tend to spend more time on the periphery of the troop and further away from their nearest neighbour. Adult males also undertake solitary periods while transferring between troops. While leopards in our study also focused heavily on adults, we found no preference for one gender over the other.

Attempts to explain how the leopards managed to kill such a high number of baboons are speculative. Busse (1980) suggested that leopards only attack baboons at night or at dusk, likely because nocturnal hunts on baboons may be more successful (Cowlishaw 1994). However, 70% of all kills on baboons in this study were made during the day (Figure 5.1), thus questioning the widely accepted notion that leopards are primarily nocturnal. The lack of temporal differences in baboon and non-baboon kills suggest that the leopards in this study likely hunt baboons opportunistically, or at least in patterns similar to how they hunt their prey as a whole. However, deviation from uniformity of the combined kills (baboon and non-baboon) suggests that the leopards did not hunt prey at random. The non-significant distribution from uniformity in the baboon kills can possibly be attributed to small sample size, however, the distribution in Figure 5.1 is atypical for leopards (Hayward & Slotow 2009) and it should therefore be considered that this may be learned behaviour by the local leopard population. The high predation on baboons at this study site can also possibly be attributed to an optimal number of baboons; small isolated groups would be too hard to find, while a large population, with large group formations, would potentially be too dangerous to hunt.

For a leopard to catch and kill a baboon still requires a certain level of skill that is likely to vary among individuals, as has been shown among not only leopards (e.g. Bothma & Walker 1999), but also other carnivores hunting dangerous prey (e.g. Power & Compion 2009). Leopard A (a young sub-adult female), despite being inexperienced (Table 5.2), successfully caught and killed five adult baboons (Figure 5.2). This leopard was at the age where she would have only very recently left her mother, it is possible that she acquired this skill while still learning to hunt. Genetic tests (E. Jooste, unpublished data) revealed no maternal or sibling relationship between the study leopards, so this theory was beyond evaluation in this study. However, this raises the question of how leopards acquire skills to kill dangerous prey and to what extent such skill is passed on to members of the population and should be studied in the future.

I acknowledge that a shortcoming to my study is the inability to interrogate the effect of leopard predation on baboon population structure and density. Unfortunately I could not gather such data because of logistical constraints, difficult terrain and skittish baboon troops. However, I have shown the highest level of predation on baboons by leopards to date, which could possibly have significant effects on the population structure of these baboon populations. Significant research is needed to determine the demographic effects of this predation on baboons as well as the behavioural implications of predation of such a dangerous prey item by leopards.

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References

Bailey, T. N. 2005. *The African leopard: Ecology and behaviour of a solitary felid.* 2nd Ed. Columbia University Press, New York.

Balme, G., Hunter, L. & Slotow, R. 2006. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74: 589-598.

Bothma, J. du. P. & Le Riche, E.A.N. 1984. Aspects of the ecology and behaviour of the leopard *Panthera pardus* in the Kalahari Desert. *Koedoe (Suppl.)* 27: 259-279.

Bothma, J. du. P. & Walker, C. 1999. *Larger carnivores of the African savannas*. J.L. van Schaik Puplishers, Pretoria.

Busse, C. 1980. Leopard and lion predation upon Chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes & Records* 12: 15-21.

Buys, D. & Keogh, H.J. 1984. Notes on the microstructure of hair of the Orycteropodidae, Elephantidae, Equidae, Suidae and Giraffidae. *South African Journal of Wildlife Research* 14: 111-119.

Charnov, E.L. & Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology* 1: 191-194.

Chase-Grey, J.N. 2011. Leopard population dynamics, trophy hunting and conservation in the Soutpansberg Mountains, South Africa. *PhD Thesis*, Durham University.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131: 293-304.

Dreyer, J.H. 1966. A study of the hair morphology in the family Bovidae. *Onderstepoort Journal of Veterinary Research* 33: 379-472.

D'Amour, D.E., Hohmann, G. & Fruth, B. 2005. Evidence of leopard predation on bonobos *(Pan paniscus). Folia Primatologica* 77: 212-217.

Frank, L., Simpson, D. & Woodroffe, R. 2003. Foot snares: An effective method for capturing African lions. *Wildlife Society Bulletin* 31: 309-314.

French, S.P. & French, M.G. 1990. Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986-88. *International Conference on Bear Research and Management* 8: 335-341.

Grimbeek, A.M. 1992. The ecology of the leopard (*Panthera pardus*) in the Waterberg. *MSc Dissertation*, University of Pretoria.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* (London) 270: 298-313.

Hayward, M. W. & Slotow, R. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research* 39: 109-25.

Hunter, L.T.B. 1999. The quintessential cat. *Africa: Environment & Wildlife* 7: 32-42.

Isbell, L.A. 1994. Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3: 61-71.

Keogh, H.J. 1979. An atlas of hair from southern African mammal species with reference to its taxonomic and ecological significance. *DSc Thesis*, University of Pretoria.

Keogh, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research* 13: 89-132.

Killian, P.J. 2003. The ecology of reintroduced lions on the Welgevonden Private Game Reserve, Waterberg*. MSc Dissertation*, University of Pretoria.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* (London). 283: 81-87.

Morino, L. 2010. Clouded leopard predation on a wild juvenile siamang. *Folia Primatologica* 81: 362-368

Ott, T., Kerley, G.I.H. & Boshoff, A.F. 2007. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology.* 2: 31-37.

Power, R.J. & Compion, R.X.S. 2009. Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *African Zoology* 4: 36-44.

Richardson, E.S. & Andriashek, D. 2006. Wolf (*Canis lupus*) predation of a polar bear (*Ursus maritimus*) cub on the sea ice of Northwestern Banks Island, Northwest Territories, Canada. *Arctic* 59: 322-324.

Schwarz, S. & Fischer, F. 2006. Feeding ecology of leopards (*Panthera pardus*) in the western Soutpansberg, Republic of South Africa, as revealed by scat analysis. *Ecotropica* 12: 35-42.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the southern African subregion*. Cambridge University Press, Cambridge.

Swanepoel, L.H. 2009. Ecology and conservation of leopards, *Panthera pardus,* on selected game ranches in the Waterberg region, Limpopo, South Africa. *MSc Dissertation*, University of Pretoria.

Tambling, C.J., Cameron, E.Z., Du Toit, J.T. & Getz, W.M. 2010. Methods for locating African lion kills using global position system movement data. *Journal of Wildlife Management* 74: 549-56.

CHAPTER 6:

EVALUATING DIETARY SPECIALIZATION OF LEOPARDS (*PANTHERA PARDUS*) IN SOUTH AFRICA

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Abstract

Leopards (*Panthera pardus*) are opportunistic large carnivores and are known to feed on a wide variety of animals, ranging in size from small rodents to large ungulates. However, recent studies have suggested that leopards might be more specialized than previously thought, especially with regard to the selection of hunting habitat. Depending on availability, the species leopards prey on may differ between habitats. In this study I collected leopard dietary data and calculated the dietary breadth of leopards in different areas of South Africa. Analyses suggest that leopards in mountainous areas are less specialized than leopards in the Lowveldt and Kalahari. My results may have important implications for wildlife managers when making choices regarding the species that should be kept on reserves where leopards are present.

Key words: *Leopard, feeding ecology, dietary breadth, DDI*

Introduction

Determining carnivore diet is essential in understanding their interspecific-dynamics i.e. competition with other carnivores and impact on prey populations (Klare *et. al*. 2011). In addition, management choices regarding the species that should be kept on fenced reserves are very often based on the feeding behaviour displayed by the carnivores present. The most common methods to determine carnivore diet are direct observations and scat- analysis. In recent years the use of global positioning system (GPS) clusters have also greatly improved our ability to study the diet of carnivores (e.g. Martins *et al*. 2011, Tambling *et al*. 2010). Despite these advances, restrictions such as remote or rugged habitats and cryptic behaviour damper the collection of dietary data in certain species.

Leopards (*Panthera pardus*) are opportunistic large carnivores and will prey on animals ranging in size from small rodents to large ungulates (e.g. Skinner & Chimimba 2005, Hayward *et al*. 2006; Bothma & Le Riche 1984). More than 90 prey species have been reported in the leopard's diet (Bailey 2005), however, the level of specialization is still unclear. Balme *et al*. (2006) suggested that leopards might be more specialized than previously thought, especially with regard to selection of hunting habitat, which is mostly limited to thick vegetation. Analysis of several leopard diet studies suggests that leopards prefer to prey on medium sized ungulates, such as impala (Hayward *et al.* 2006). This appears to be the case in Kruger National Park where 77% of the leopards' diet consists of impala (Pienaar 1969). In mountainous regions, where impala is less abundant, smaller species, such as klipspringer and rock hyrax, feature more prominent in the leopards' diet.

Here I evaluate the dietary specialization of leopards in different regions of South Africa. By comparing the dietary breadth calculated using the Dietary Diversity Index (DDI) I am able to assess the range of prey species utilized in different habitats.

Methods

Dietary Diversity Index (DDI) and statistical analysis

I collected leopard dietary data from 18 different study areas in South Africa. I only included published studies that reported each prey type as a % of the entire diet. Study areas included five studies in the Waterberg Mountains, four in the Cederberg Mountains, two in the Gamka Mountains, two in the Soutpansberg Mountains, two from Kruger National Park, one from the Baviaanskloof, one from Londolozi, one from Sabi Sand, one from Phinda, and one from the southern Kalahari. Due to the novelty of GPS location clusters to locate leopard kills, studies reporting data obtained from scat analysis and direct observations have also been included in the analysis. I calculated the dietary breadth for each study area using a dietary diversity index (DDI) (McArthur 1972), also referred to as Levin's index (Safi & Kerth 2004) or Simpson's reciprocal index:

$$DDI = 1/\Sigma V_i^2$$

where V_1 represents the proportional volume of each prey species in the diet. I considered 47 potential prey species, including most of the generally preyed on ungulates, primates, carnivores, lagomorphs, large rodents (e.g. porcupine), large birds (e.g. ostrich) and livestock. Small birds were categorised into one category, as well as small rodents. A DDI value of 1 would indicate a dietary specialist, whereas a DDI value of 47 would indicate an extreme generalist. However, since all 47 potential prey species doesn't occur together in any of the study areas, a DDI value of 47 would technically not be possible. Dietary data were obtained from Jooste et al. (*in press*), Chase-Grey (2011), Martins *et al*. (2011), Rautenbach (2010), Swanepoel (2009), Ott *et al*. (2007) Schwarz & Fischer (2006), Balme *et al*. (2006), Bailey (2005), Grimbeek (1992), Le Roux & Skinner (1989), Norton *et al*. (1986), Mills (1984), Graupner & Graupner (1971), and Pienaar (1969). A standard Chi-squared test was used to assess whether the diet of leopards in the mountainous regions of South Africa are more specialized than those of the Lowveldt.

Results

The dietary diversity index (DDI) values ranged from 1.42 in to 11.15 (Table 6.1). Chi-squared analysis revealed a highly significant difference between the dietary breadth of leopards in mountainous areas and the Lowveldt ($p < 0.0001$). The Waterberg Mountains (8.1) and the Baviaanskloof (DDI = 8.8) had the highest DDI values, and the Kruger National Park the lowest (DDI = 1.8) (Figure 6.1).

Table 6.1 Details of the study areas, method of determining leopard diet, and average dietary diversity index (DDI) value for each specific study site.

Study	Area	Method	Average DDI
Jooste(this study)	Waterberg	GPS	8
Swanepoel (2009)	Waterberg	Scats, GPS	7.18
Grimbeek (1992)	Waterberg	Scats	9.09
Chase-Grey (2011)	Soutpansberg	Scats	3.83
Schwarz & Fischer (2006)	Soutpansberg	Scats	3.98
Martins *et al*. (2011)	Cederberg	Scats, GPS	3.29
Rautenbach (2010)	Cederberg	Scats	5.79
Norton *et al*. (1986)	Cederberg	Scats	2.23
Rautenbach (2010)	Gamka	Scats	7.15
Norton et al. (1986)	Gamka	Scats	3.02
Ott *et al*. (2007)	Baviaanskloof	Scats	8.84
Balme *et al*. (2006)	Phinda	VHF, Direct obs.	4.32
Bailey (2005)	Kruger National Park	Scats, Direct obs.	1.87
Le Roux & Skinner (1989)	Londolozi	Direct obs.	2.15
Mills (1984)	Southern Kalahari	Direct obs.	2.32
Graupner & Graupner (1971)	Sabi Sand	Direct obs.	1.42
Pienaar (1969)	Kruger National Park	Direct obs.	1.66

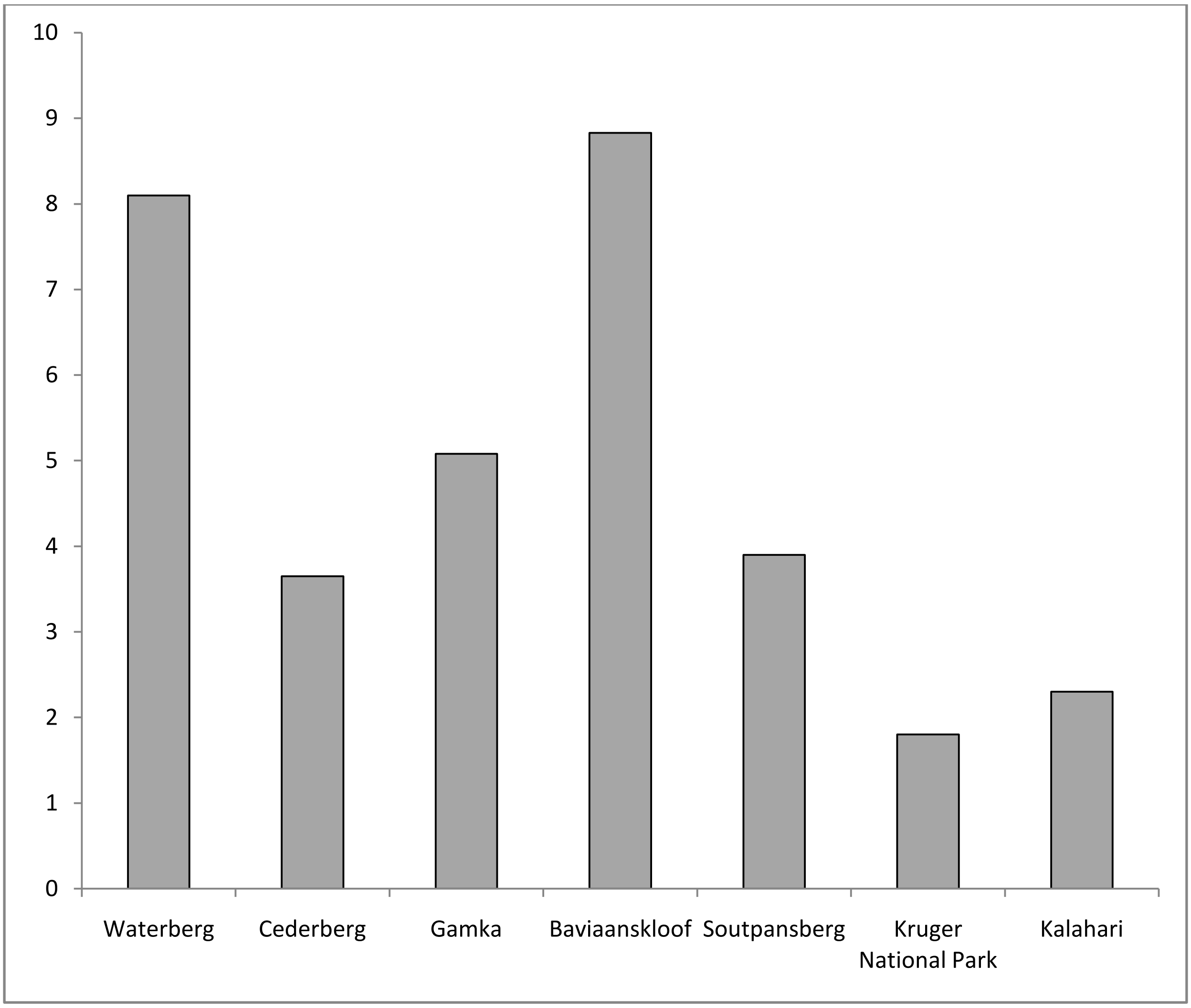

Figure 6.1 Comparison of leopard (*Panthera pardus*) dietary breadth between different regions of South Africa.

Discussion

It has been suggested that leopards might be more specialized than previously thought, especially with regard to hunting habitat (Balme *et al*. 2006), however, little is known about leopards' dietary specialization. Leopards in Kruger National Park have access to at least 90% of the 47 potential prey species used in the DDI calculation, but still had the narrowest dietary breadth. The anomaly can possibly be explained by the high predation on impala in the park (87%, Bailey 2005). In mountainous- or forested areas, leopards typically feed on smaller animals, mainly because larger ungulates are less abundant (Bothma & Le Riche 1984; Norton *et al*. 1986). Leopards in the Baviaanskloof (DDI = 8.8) and the Waterberg Mountains (DDI = 8.1) had the widest dietary breadth. The less specialized and thus more opportunistic behaviour by the mountain leopards can possibly be explained by lower biomass intake per prey item, and leopards therefore need to hunt more often. However, due to small sample size, especially from the Baviaanskloof region, these results should be viewed with caution. In addition, impala and other larger antelope are abundant, and preyed upon on some mountain reserves. The wider dietary breadth of leopards in these areas can therefore not exclusively be attributed to predation on a wider range of smaller mammals.

Previous research suggests that a dietary overlap exists among Africa's large carnivores (Hayward & Kerley 2008). My results suggest that leopards may have narrower dietary breadths in areas where they are competing with other large carnivores, such as lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*). That would explain the low dietary specialization in the Baviaanskloof and certain areas of the Waterberg Mountains.

Although a dietary diversity index can give a good idea of the specialization, or lack thereof in the feeding habits of large carnivores, it doesn't provide any information on specific prey species preferred or avoided. In order to make educated management decisions, prey abundance-, as well as habitat- data should be considered.

References

Bailey, T. N. 2005. *The African leopard: Ecology and behaviour of a solitary felid.* 2nd Ed. Columbia University Press, New York.

Balme, G., Hunter, L. & Slotow, R. 2006. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74: 589-598.

Bothma, J. du. P. & Le Riche, E.A.N. 1984. Aspects of the ecology and behaviour of the leopard *Panthera pardus* in the Kalahari Desert. *Koedoe (Suppl.)* 27: 259-279.

Chase-Grey, J.N. 2011. Leopard population dynamics, trophy hunting and conservation in the Soutpansberg Mountains, South Africa. *PhD Thesis*, Durham University.

Graupner, E.D. & Graupner, O.F. 1971. Predator-prey interrelationships in a natural big game population. *Final Rep*. Nature Conservation Division, Subproj. TN. 6.4.1/4F. Pretoria, Rep. So. Afr.: Transvaal Provincial Administration.

Grimbeek, A.M. 1992. The ecology of the leopard (*Panthera pardus*) in the Waterberg. *MSc Dissertation*, University of Pretoria.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G & Kerley, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* (London) 270: 298-313.

Hayward, M.W. & Kerley, G.I.H. 2008. Prey preferences and dietary overlap amongst Africa’s large predators. *South African Journal of Wildlife Research* 38: 93-108.

Jooste, E., Pitman, R.T., Van Hoven, W. & Swanepoel, L.H. 2012. Unusually high predation on Chacma baboons by female leopards in the Waterberg Mountains, South Africa. *Folia Primatologica* (*In Press*).

Klare, U., Kamler, J.F. & MacDonald, D. 2010. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41: 294-312.

Le Roux, P.G. & Skinner, J.D. 1989. A note on the ecology of the leopard (Panthera pardus Linnaeus) in the Londolozi Game Reserve, South Africa. *African Journal of Ecology* 27: 167-171.

MacArthur, R.H. 1972. *Geographical Ecology*. New York: Harper and Row. 269 p.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* (London) 283: 81-87.

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

Norton, P.M., Lawson, A.B., Henley, S.R. & Avery, G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Journal of Wildlife* Research 16: 47-52.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. 2007. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology* 2: 31-37.

Pienaar, U. De V, 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12: 108-76.

Rautenbach, T. 2010. Assessing the diet of the Cape leopard (*Panthera pardus*) in the Cederberg and Gamka Mountains, South Africa. *MSc Dissertation*, Nelson Mandela Metropolitan University.

Safi, K. & Kerth, G. 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology* 18: 1293–1303.

Schwarz, S. & Fischer, F. 2006. Feeding ecology of leopards (*Panthera pardus*) in the western Soutpansberg, Republic of South Africa, as revealed by scat analysis. *Ecotropica* 12: 35-42.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the southern African subregion*. Cambridge University Press, Cambridge.

Swanepoel, L.H. 2009. Ecology and conservation of leopards, *Panthera pardus*, on selected game ranches in the Waterberg region, Limpopo, South Africa. *MSc Dissertation,* University of Pretoria.

Tambling, C.J., Cameron, E.Z., Du Toit, J.T. & Getz, W.M. 2010. Methods for locating African lion kills using global position system movement data. *Journal of Wildlife Management* 74: 549-56.

CHAPTER 7:

MANAGEMENT RECOMMENDATIONS

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Introduction

When the free movement of large migrating mammals like lions and elephants are constrained by a boundary fence, such as on Welgevonden Private Game reserve, the active monitoring and management of these populations becomes crucial (Bothma 2010). Studies of predator-prey relationships serve as a good foundation to determine the ecological condition of an area and the ability to determine the prey-specific biomass intake of predators is fundamental in their conservation (Hayward *et al*. 2007). Habitat requirements, physical attributes, feeding behaviour, and present and historical distributions are all vital factors to take into consideration when making decisions regarding the selection of species to be kept on a reserve (Bothma *et al*. 2010). While the leopards on Welgevonden are able to move freely between neighbouring properties, significant dangers exist outside the reserve and most of the resident leopards have established home ranges and utilise the natural prey within the reserve. Therefore, leopards on Welgevonden are likely subject to many of the same constraints and pressures as other large mammals on small reserves.

This study provides the most comprehensive documentation of the diet of female leopards in the Waterberg Mountains, with the ultimate goal of aiding in decision making and management choices regarding leopards kept on Welgevonden and other small mountainous reserves.

Leopard prey selection as evidence for habitat selection

Compared to other populations, the leopards in this study displayed truly unique prey selection habits. Baboons, impala, klipspringers, Jameson's red rock rabbits, mountain reedbucks, and kudus were commonly preyed upon species. Most of these species prefer mountainous terrain with rocky patches and cliffs (Skinner & Chimimba 2005; Bothma *et al*. 2010), which suggests that the leopards on Welgevonden also preferred rocky, rugged areas. Waterbuck and bushbuck, both abundant on Welgevonden, were never found in the diet of the study leopards. These species prefer denser vegetation near water above rocky slopes, suggesting that leopards may not frequent these areas or that these habitats are not suitable for hunting.

Interestingly, however, was the occasional predation by leopards on animals that do not normally frequent mountainous regions, such as plains zebras. Plains zebras occur on open savanna plains and are predominantly grazers. Even though young zebras may be seasonally abundant, leopards do not generally prey on them, as stalking prey on open plains is difficult and unlikely to be successful (Bailey 2005). Unlike other areas with plains zebras, Welgevonden Private Game Reserve is a very mountainous reserve with limited plains. As a result the zebras frequently wander into the rocky mountain slopes thereby subjecting them to possible predation by leopards. Plains species are not agile running over rugged, rocky terrain, as evidenced by at least one occurrence of a zebra breaking its leg while trying to run from a helicopter on Welgevonden. The leopards likely exploit the poor agility of zebras in rocky areas, as evidenced by a total of eight zebra foals found in the diets of leopards located at these feeding sites. However, this was only a seasonal occurrence after the first summer rains and is unlike to have any negative effects on plains zebra populations.

Impala appear to be a favourite prey item of leopards range-wide because they are reported in leopards' diets in 100% of studies where they occur (Hayward *et al*. 2006). The high biomass intake of impala (20.4%) by the study leopards on Welgevonden is an indication that this pattern holds in this mountainous region as well. Despite the study leopards frequently preying on juvenile impala, there is no indication from the yearly census data that impala numbers are decreasing. In the Kruger National Park, impala populations are stable (or even growing) despite a mortality rate of more than 85% in the annual lamb crop (Bothma 2010). This seems to be the case on Welgevonden as well.

One of the most interesting observations from my study was the heavy predation by leopards on Chacma baboons. During the course of the study, there were approximately 25 troops of baboons on the reserve, some as large as 100 individuals. Despite baboons being a very dangerous and high-risk prey species, they were probably encountered frequently by the study leopards because of overlaps in habitat selection. My results suggest that leopards are able to kill baboons, even dangerous males. This contradicts all previous leopard predation studies, including those from areas with high baboon densities. Although the aim of this study was not to investigate the effect of leopard predation on baboon troop size, group composition, or sex ratio, this unusually high predation may have significant effects on the population structure of these baboon populations.

Calculating biomass

Determining the carrying capacity of large predators is essential in their conservation, especially in small fenced areas (Hayward *et al*. 2007). According to Hayward *et al*. (2007) the carrying capacity for every predator that preys on large, readily surveyed wildlife can be calculated based on the abundance of its preferred prey. This technique has been applied to lions, leopards, cheetahs, spotted hyenas, and African wild dogs in ten conservation areas in South Africa. However, I believe that an accurate calculation of leopard carrying capacity on Welgevonden is unlikely for several reasons. First, as shown in Chapter 4, the commonly used technique to estimate the biomass intake was unreliable in the case of leopards on Welgevonden. Second, the high levels of predation on cryptic antelopes such as klipspringers and common duikers make calculations of prey biomass difficult. Finally, leopards on Welvegvonden are able to move freely between neighbouring properties and the boundary fence serves as little impediment. Thus, calculating the carrying capacity of leopards on the reserve with the intention of removing or adding leopards is likely a futile undertaking. Conversely, yearly wildlife censuses can give a good indication of whether management actions such as the enhancement of food sources are necessary to support the otherwise naturally occurring populations of leopards on the reserve (Hayward *et al*. 2007).

Genetic diversity and human-leopard conflict

During the course of the study, biological samples from six leopards were collected and genetically analysed to determine possible relatedness between the study leopards. Apart from two female leopards that possibly had the same grandmother, there was no relatedness between the study leopards. Although the leopard population on Welgevonden appears small, the allele frequency was relatively diverse (pers. com. Dr. C. Harper). Much of Welgevonden Private Game Reserve is bordered by cattle farms and leopards occasionally leave the reserve and protected areas and are thus subject to persecution by cattle farmers. Although the number of leopards killed by farmers is unknown, it may be substantial. When a leopard is killed or removed from a certain area, it creates the opportunity for another leopard to occupy that home range (Balme 2010). This may lead to a constant influx and replacement of leopards resulting in low relatedness and high allele diversity.

During the course of the study, one of the study leopards did occasionally leave the reserve. However, no livestock remains were identified from any of the 96 leopard feeding sites. There was also no evidence of livestock hair in the 80 leopard scats collected on Welgevonden. This clearly suggests that the presence of leopards near or on a cattle farm does not necessarily mean they will prey on livestock. Likewise, Ott *et al*. (2007) found the remains of domestic animals in only two leopard scats collected in the Baviaanskloof region of South Africa, indicating that leopards do not preferentially prey on livestock in that area either. In the Cederberg Mountains of South Africa, Martins *et al*. (2011) also only located two kill sites where leopards preyed on livestock. Collectively, this evidence suggests that the view of leopards as problem animals for farmers near natural reserves may be overestimated and education of the farmers is of utmost importance.

References

Bailey, T. N. 2005. *The African leopard: Ecology and behaviour of a solitary felid.* Columbia University Press, New York.

Balme, G. 2010. Return of the leopard. *Africa Geographic* February: 35-41.

Bothma, J. Du. P. 2010. Predators. In: J. du P. Bothma & J.G. du Toit (Eds), *Game ranch management*, Van Schaik Publishers, Pretoria.

Bothma, J. Du P., Van Rooyen, N. & Du Toit, J.G. 2010. Antelope and other smaller herbivores. In: J. du P. Bothma & J.G. du Toit. (Eds), *Game ranch management*, Van Schaik Publishers, Pretoria.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* (London) 270: 298-313.

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

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology* (London) 283: 81-87.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. 2007. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology* 42: 31-37.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the southern African subregion*. Cambridge University Press, Cambridge.