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Diet, activity and spatial occupancy of leopards in the Soutpansberg Mountains.

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Abstract

Leopards, though broadly distributed, are highly variable in terms of their ecology. Recently, the Soutpansberg Mountains were identified as supporting one of the highest leopard populations in a non-protected area in Africa. This study aims to understand how these mountains can support such a high density of leopards, thus aiding in identifying the conservation potential of this environment and the species in it. Using a combination of camera trap and scat data collected over two years, research into leopard occupancy, diet and activity was conducted. This research represents the first of its kind to use this combination to investigate these factors in the Soutpansberg.

The occupancy analysis proved inconclusive in determining which variables influence the occupancy of leopards. It was found that camera trap data can be split into almost any number of sessions (groupings of trap days), which is a valuable finding as no previous study has provided evidence to support their choice of session number.

Leopards consumed 22 species of various sizes, with Artiodactyla species like bushbuck and bushpig contributing most to their diet. No livestock were found in the scats, indicating that leopards are preying on livestock at lower levels than landowners perceive. Some species, such as red duiker and common warthog, were consumed less than expected by leopards based on their availability.

Activity patterns indicate that leopards are active throughout the day and night, but their diet suggests they may hunt nocturnally as their most commonly consumed prey are active during this time. Evidence of temporal partitioning between leopards and their prey provides viable explanations for prey selection.

This study provides knowledge of elements, such as availability of prey and temporal overlap with prey, which make this environment suitable for a high density of leopards. The knowledge gained through this study of the ecology and behaviour of the Soutpansberg's top predator in relation to its prey should be valuable in future conservation planning there and in similar montane environments.

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indicated prey species are illustrated by the solid lines. The overlap coefficient (Δ_4) is indicated by the shaded area. These estimates of overlap are provided in each plot along with their 95% confidence intervals in brackets

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List of Abbreviations

PPP   Primate and Predator Project

The following species names have been abbreviated for ease of writing. At first mention their name is given in full and thereafter the following shortened versions of the name will apply unless otherwise stated;

Baboon   Chacma Baboon

Kudu   Greater Kudu

Porcupine   Cape Porcupine

Warthog   Common Warthog

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Chapter 1 – Introduction

1.1 Introduction

Mountainous regions often have high concentrations of endemic species, both floral and faunal, which makes them important biodiversity hot spots for conservation (Körner, 2004; Burgess et al., 2007). Their importance in species conservation is growing with the continued degradation of many low-land habitats by human activity. Assessing the biodiversity of such regions, particularly when they include rare, cryptic or nocturnal species, is notoriously difficult (Busby et al., 2009). However, conducting research in regions that have not yet been studied, or in areas where research is just beginning, is vital, particularly when these regions lie outside of protected areas.

This study focuses on the non-protected area of the Soutpansberg Mountains, South Africa, building on data collected there since 2003 by the Primate and Predator Project (PPP). The PPP are based in the western part of the Sountpansberg Mountains at Lajuma Research Centre (23°02′S, 29°26′E) where data were collected from a study site of approximately 60 km^2, including 12 surrounding properties. The top predator there is the leopard (*Panthera pardus*) and its population density has been estimated to be the highest density in Africa, outside of a state-protected area (Chase Grey et al., 2013).

The main aims of this study are to investigate the occupancy of leopards in the study area, to determine the main prey species consumed by leopards there, and to examine the activity pattern of leopards and their prey in order to understand how the Soutpansberg region can support such a high density of this large predator. Through examining leopard behaviour and ecology in relation to that of its main prey species, this study aims to gain an understanding of the ecology of the species in this montane environment and its conservation potential. Insights into how and why the Soutpansberg Mountains, in particular, are able to support a high density of leopards will be useful for future conservation planning initiatives, not only in the Soutpansberg but in similar unprotected montane regions worldwide.

1.2 Predator-Prey Interactions

Predators are an important part of every natural community and play a critical role in ecosystem functioning. Almost all animals are engaged in some form of predator-prey interaction which has played a key role in shaping their evolution and behaviour. Therefore,

if conservation strategies are to be successful in preserving natural ecosystems, we need to understand the dynamic interactions that occur between predators and prey, and how these interactions can shape populations.

Continuous arms races between predators and prey are ongoing, leading to the occurrence of predator and anti-predator adaptations (Eriksen et al., 2011). One such adaptation is temporal partitioning, where prey may avoid being active at the same time as predators in order to reduce the risk of being eaten but, similarly, predators may try to synchronise their activity with that of their prey to increase hunting success. There is evidence to support both adaptation strategies. Predators have been noted as mirroring the activity patterns of their main prey species (Kawanishi and Sunquist, 2004; Jenny and Zuberbühler, 2005). Conversely, prey species have also been found to alter their activity patterns to avoid being active at the same time as their main predators (Fenn and Macdonald, 1995; Ross et al., 2013), thus reducing predation risk.

One of the main constraints on carnivore density is prey availability and abundance, with carnivore densities being positively correlated with the abundance and biomass of their prey (Carbone and Gittleman, 2002; Karanth et al., 2004; Carbone et al., 2011; Bauer et al., 2014). Indeed, the positive relationship between prey biomass and leopard density is well established (Marker and Dickman, 2005). However, predictions of leopard density based on preferred prey biomass suggest it is prey biomass that sits within a suitable prey weight category that is the crucial factor, rather than prey biomass in general (Hayward et al., 2007a). Prey size is an important factor for leopards when selecting prey as the energy to find, catch and kill the animal has to match, but more preferably be outweighed by, the energy received from consuming the prey. Leopard prey density and composition may be affected by the presence of other predators. Exploitative competition can occur when predators share the same food supply (Caro and Stoner, 2003). There is evidence of competitive exclusion of leopards by tigers in Nepal due to a lack of availability of larger prey species usually eaten by the tigers (Seidensticker et al., 1990). In terms of kleptoparasitism (stealing food), leopards were the most vulnerable of 70 African carnivores studied (Caro and Stoner, 2003), despite the fact that leopards often cache their prey in trees or thick bush (Bailey, 1993). The method used for caching carcasses depends on the habitat and degree of interspecific competition. If the probability of detection of a kill on the ground is high then leopards will cache the carcass in a tree, otherwise dragging and hiding the

carcass is a more beneficial option for reducing the risk of kleptoparasitism (Stander et al., 1997).

While leopards are known to exist in many different habitats, reflecting their remarkable ecological flexibility, there is some evidence that they prefer certain habitat features that may not be the most profitable for their prey. Hayward et al. (2006) found that leopards preferred to hunt in densely vegetated environments. Balme et al. (2007) found that they prefer hunting in habitats where prey was easier to catch rather than where it was more abundant. They found that successful hunts occurred most often in areas with intermediate vegetation cover even though these areas contain lower prey densities than other areas. Similarly, leopards in a mountainous environment also exploited areas with high levels of vegetation cover to prevent detection during hunting and increase the probability of capture (Pitman et al., 2013). It seems that preferred areas are those where vegetation is dense enough to provide sufficient cover for a leopard to get close to its prey, without being so dense that it reduces visibility. Small ruminant density is also an important covariate in determining suitable leopard habitat (Swanepoel et al., 2013). It would seem that leopards require habitat which not only has high numbers of suitable prey to hunt but also favourable habitat features like vegetation cover to hunt successfully.

1.3 Human-Wildlife Conflict

A key aspect of conservation is to understand how animals co-exist with humans, in landscapes that are dominated by human activities. Every year thousands of cattle, sheep, goats, poultry & farmed fish are killed by carnivores worldwide (Breitenmoser et al., 2005). Livestock depredation is one of the main types of conflict between felids and rural communities (Zarco-Gonzalez and Monroy-Vilchis, 2014). Retaliatory killings can have significant effects on populations, particularly if breeding females are frequently killed. In fact, the population decline of many carnivore species can be traced back to direct conflicts with humans arising from livestock depredation (Mishra et al., 2002). The killing of animals that are considered pests has resulted in the extinction of several species, and has endangered many others (Woodroffe et al., 2005). The loss of large carnivores can result in mesopredator release, which may exacerbate human-carnivore conflict ever further (Treves and Naughton-Treves, 2005). Anthropogenic pressure can alter food webs through activities such as overhunting of potential prey, which can force carnivores to consume smaller prey and drive

them towards local extinction (Henschel et al., 2011). Habitat degradation and fragmentation are also consequences of human activity which can result in decreasing populations, not just of carnivores but of all animals. These anthropogenic conflicts can have as much of an effect on leopard populations as ecological factors such as availability of suitable habitat and prey.

Leopards often inhabit and thrive in areas greatly modified by people or within close proximity to human settlements (Pitman et al., 2013). However, leopards can impose significant costs on humans by inflicting damage that threatens their local livelihoods through predation on livestock or managed game. Nevertheless, the frequency and severity of livestock depredation varies greatly. Indiscriminate poaching of wild ungulates for meat, skins, horns, and medicine has caused decline of leopards' natural prey populations (Kala, 2005) in many areas. In a lot of cases, this lack of natural prey causes leopards to turn to hunting livestock in order to survive, resulting in conflicts with local communities. These leopards are then killed in retaliation, causing population levels to decrease. In India, the high predation rates of leopards on livestock were discovered to be a direct result of the low density of wild prey species available (Kala and Kothari, 2013). Leopards are also known to attack humans, with the largest number of attacks on humans by large cats in India being carried out by leopards (Singh, 2005; Athreya et al., 2011). In Namibia, it was concluded that the lower density of leopards outside of protected areas was a result of local persecution by landowners, as they are considered a threat both to the humans themselves and their livestock (Marker and Dickman, 2005).

Accessing many mountainous regions is difficult for humans, therefore, human activity is often lower there than in non-mountainous areas. This reduction of human activity provides more isolated habitats with lower human persecution than would occur in lower lying areas (Swanepoel et al., 2013). The potential for conflict between carnivores and humans is higher in poor rural areas where livestock production is the main economic activity (Mech et al., 2000). Even though livestock is assumed to represent only a small portion of felid diets in the Soutpansberg, retaliatory killing is one of the main factors affecting the local population (Chase Grey, 2011). This perceived threat often has little evidence to support it, but the fear, and often hatred, of leopards has been passed down through generations of landowners.

Leopard diet analysis in this study will aid in determining if the landowners around the study site are correct in thinking that leopards are to blame for their livestock being killed, or if they are targeting and persecuting the wrong offender. If the results show that leopards are indeed

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the culprit then techniques and ideas on how to protect landowners' animals without harming the leopards can be tried and tested in an attempt to reduce the number of killings made by leopards, which in turn would hopefully reduce the number of leopards killed by the landowners. If the scat analysis shows that leopards are not preying on livestock then this evidence can be shown to landowners to educate them about their perception of leopards as the problem.

1.4 Leopards

Leopards are one of the most iconic big cats of the world. They have a yellow or tawny coloured coat covered with a pattern of black rosettes and spots (Figure 1.1), unique to each individual. The African leopard (*Panthera pardus pardus*) is one of nine subspecies of leopard recognised by the IUCN (Henschel et al., 2008) and is the only subspecies present in Africa. Adult leopards can weigh anything between 20-90 kg (Stuart and Stuart, 2001), with adult African leopards averaging about 35-40 kg for females and 60 kg for males. Based on trappings conducted on site by the PPP of seven confirmed adult leopards, average weight of females was 37 kg (range = 36-38 kg) and 63 kg for males (range = 53-68 kg). Leopards are the most broadly distributed members of their family (Felidae) due to their ecological adaptability. They are the most successful and wide-ranging large felid in Africa and have the widest habitat tolerance of any African felid (Ray et al., 2005). They are found in a wide range of habitats throughout Asia and Africa from rainforest to savannah and from mountains to the edges of urban areas (Nowak, R.M., 1999). Their occurrence across this large geographic range can be partially explained by their highly adaptable feeding behaviour which allows them to live in any habitat that has a sufficient prey base and appropriate hunting cover (Hunter et al., 2003). This adaptable feeding behaviour is highlighted by their ability to survive on whatever they come across, including invertebrates and small vertebrates (Hayward et al., 2006) birds (Ott, 2004) and fish (Mitchell et al., 1965). They have a record of preying on up to 92 different species, typically ranging between 20-80 kg in weight (Mills and Harvey, 2001), (potential prey species in this study are discussed in more detail in Chapter 1.6). However in recent years, widespread conversion of suitable habitat into land for cultivation and human habitation has resulted in extensive habitat loss for many leopard populations (Chase Grey et al., 2013). As a result of this, leopards in the lower lying areas are being decimated and only refuge populations survive in these areas. Thus, greater population

densities are concentrated in areas that are less accessible for humans, such as montane environments (Swanepoel, 2008; Martins, 2010; Swanepoel et al., 2013).

Figure 1.1: Image of an African leopard taken during this study.

Modelling has identified that surface ruggedness is one of the top variables contributing to habitat suitability for leopards in South Africa (Swanepoel et al., 2013). Other studies on leopards (Gavashelishvili and Lukarevskiy, 2008), and on similar large felids such as cougars (*Puma concolor*) (Riley and Malecki, 2001) and jaguars (*Panthera onca*) (Hatten et al., 2005) have also found that rugged terrain is an important habitat variable.

Despite the adaptability of leopards, global population numbers have declined. The African subspecies has declined and disappeared from 37% of its historical range in Africa during the past 100 years (Ray et al., 2005). Loss of habitat and declines in prey remain the main threats to this species. Some of the most dramatic habitat loss has occurred in South Africa, with only 20% of the land now containing suitable habitat for leopards (Swanepoel et al., 2013). At the edges of their range and in large regions throughout their historic habitat, they currently occur only in small, fragmented populations (Ray et al., 2005). The IUCN (International Union for the Conservation of Nature) lists leopards as Near Threatened at present (IUCN, 2014), and research suggests that unprotected and mostly privately owned

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land is extremely important for the African leopard. In the Limpopo Province, where the study site is situated, 95% of suitable leopard habitat is situated outside of protected areas (Swanepoel et al., 2013). While the purpose of protected areas is to preserve ecosystems and the biodiversity they contain, many are not big enough for all resident species, making neighbouring areas just as important (Petracca et al., 2014).

1.5 Soutpansberg Mountains

The Soutpansberg Mountains are an isolated, quartzite mountain range in the Limpopo Province of north-eastern South Africa (Figure 1.2). They are situated between the Kalahari Desert in the west and the Kruger National Park in the east (Schwarz and Fischer, 2006) and cover a north-south distance of 60 km (Berger et al., 2003). Soutpansberg means "Salt Pan" in Afrikaans and the mountains get their name from the salt pan on their western side. The mountain formed as a result of faulting along three strike-faults, followed by the northwards tilting of the area (Hahn, 2006). The Soutpansberg Mountains are the furthest north mountain range in South Africa and lie between 23° 05' S - 29° 17' E and 22° 25' S - 31° 20' E (Berger et al., 2003). The mountains cover approximately 6, 800 km^2 in total and range in height from 250 m above sea level to the highest peak, Mount Lajuma, at approximately 1748 m (Mostert et al., 2008). Due to the extreme topographic diversity and altitude changes over short distances within the mountains (Mostert et al., 2008), the climate of the area varies dramatically. The mountains experience a cool, dry season from May to August with daytime temperatures from 12-22°C and a warm, wet season from December to February with temperatures from 16-40°C (Chase Grey et al., 2013). Rainfall ranges from 367 mm annually in the north to 1,874 mm in the south where mist precipitation due to the changing landscape can further increase annual precipitation up to 3,233 mm (Hahn, 2002).

Figure 1.2: Soutpansberg Mountain range (green) in Limpopo Province, South Africa.

The study site within the Soutpansberg Mountains, consisting of Lajuma Research Centre and the surrounding properties, is situated in a mountainous environment with varied on-site elevation levels and rugged terrain. Such topography may indicate that the area consists of prime leopard habitat. As human populations continue to rise and human activities convert and degrade lowland habitats, mountainous regions are becoming increasingly important for species conservation. The Soutpansberg Mountains are known to contain 56% of the bird and 60% of the mammal species of South Africa (Munyai and Foord, 2012). These species may inhabit a mosaic of available habitat types, which are composed of both structural and floral elements of the mistbelt forest, thicket, savannah, and grassland biomes (Von Maltitz et al., 2003). These habitats differ in terms of the availability of moisture in the soil (Bond et al., 2003) which leads to diversity in the vegetation of that area. With vegetation diversity comes diversity in animal species found in the region, many of which have not been formally studied in terms of their ecology.

Due to their rich species diversity, the Soutpansberg Mountains are recognized nationally as a centre of endemism and biodiversity. The mountains form the focal point of the recently established Vhembe UNESCO Biosphere Reserve and form part of the North-Eastern Escarpment Bio-region, a priority area for conservation research highlighted by the South African National Biodiversity Institute. The Kruger National Park borders the east side of the Soutpansberg Mountain range. This makes the unprotected Soutpansberg region even more

important as a conservation area for leopards as it may provide territory for the overspill of leopards from the Kruger National Park.

Despite this knowledge of Soutpansberg's diversity, the conservation significance of this area in terms of its abundance and diversity has yet to be fully investigated and understood. Uncontrolled hunting during the 19th century and habitat destruction due to farming practices has led to the decline and extinction of numerous animals (MacKenzie, 1988). The PPP have recently noted rising levels of human induced mortality of leopards (R. Hill, *pers. comms.)* suggesting that the leopard population may be in danger of heading towards the local extinction experienced by lion (*Panthera leo*) and other species in the Soutpansberg such as the African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*). Despite these rising levels of human-conflict, a healthy predator community prevails (Willems and Hill, 2009), for now, making species such as leopards a good candidate to use in raising awareness of the mountains' conservation value.

Leopards are the only large felids that still inhabit the study site at Lajuma and the surrounding region in the Soutpansberg Mountains, with the only other large carnivore present in significant numbers being the brown hyena (*Hyaena brunnea*). As a result of this, leopards suffer very little from inter-specific competition for prey in this area as hyenas are known to be scavengers more so than hunters and all other predators in the area are small-medium in size, hence pose no threat to the leopards. The flexible diet of leopards and their secretive nature has enabled them to survive here when other large carnivores have disappeared (Stuart and Stuart, 1993). They are present at one of the highest densities, 10.7 per 100 km^2, recorded in sub-Saharan Africa (Chase Grey, 2011; Chase Grey et al., 2013). This population density is the highest recorded for leopards outside of a state-protected area in Africa (Chase Grey et al., 2013), exceeding densities reported in other montane environments such as the Cederberg and Waterberg Mountains where density ranges from 0.62-3.0 per 100 km^2 (Swanepoel, 2008; Martins, 2010). Despite this, the conservation significance of the mountainous populations in the Soutpansberg is still poorly understood. Studying leopards in mountainous regions is challenging (Martins, 2010), resulting in a lack of ecological information on their behaviour in these types of habitats. This study aims to investigate various aspects of leopard ecology such as predator-prey activity patterns, human-wildlife conflict, diet and occupancy in an attempt to provide possible explanations behind the high density of leopards in this particular mountainous region.

1.6 Potential Prey Species

The Soutpansberg Mountains are home to a diverse range of species, especially vertebrates. Mammals are of particular interest in this study as they make up the majority of the leopard's diet (Mills and Harvey, 2001; Hayward et al., 2006). It has been estimated that 145 species of mammal occur in the Soutpansberg Mountains and the area is especially rich in hoofed mammals (Berger et al., 2003) which indicates it is also rich in potential prey for leopards. However, of the 27 herbivore species that once roamed this area, only 15 now remain due to local extinction (Hahn, 2006). This is a serious problem as antelope species are an important component of African ecosystems, fulfilling important ecological roles such as seed dispersal and as prey for top predators (Bowkett et al., 2008). Game farms have reintroduced some species, but these animals are confined rather than roaming freely through the mountain as they may have historically.

With leopards having such a broad diet, there is a large range of potential mammalian prey species found in the study site that they could prey upon, varying in mass from <1 kg to >300 kg. All five species of South African primate occur in this study area: chacma baboon (*Papio ursinus*), vervet monkey (*Cercopithcus aethiops*), samango monkey (*Cercopithecus mitis erythrarchcus*), thick-tailed bushbaby (*Otolemur crassicaudatus*) and lesser bushbaby (*Galago moholi*). Vervet monkeys have been recorded as a preferred prey species of the leopard at specific sites (Schwarz and Fischer, 2006) and baboon are also commonly preyed upon (Jooste et al., 2013). Two species of dassie (or hyrax), the rock dassie (*Procavia capensis*) and the yellow-spotted dassie (*Heterohyrax brucei*), can be found in the more rugged and rocky habitats of the area. Dassies are often found to be a major component in leopard diet and are commonly recorded as preferred leopard prey, especially in mountainous regions (Stuart and Stuart, 1993; Nemangaya, 2002; Martins et al., 2011). Leopards have the ability to feed on smaller species, when large prey are not available (Hayward et al., 2006). Therefore, the various abundant species of rodent in the area such as rats, mice and shrews, as well as the Cape porcupine (*Hystrix africaeaustralis*), may be frequently preyed upon. The most speciose order present in the Soutpansberg Mountains are the Artiodactyla, or even-toed ungulates. This order includes species such as bushbuck (*Tragelaphus scriptus*), common duiker (*Silvicapra grimmia*), mountain reedbuck (*Redunca fulvorufula*), klipspringer (*Oreotragus oreotragus*), greater kudu (*Tragelaphus strepsiceros*) and also many domestic livestock species such as cattle, sheep and goats. The pig family, Suidae, also belongs to this order and species such as the common warthog (*Phacochoerus aethiopicus*) and bushpig

(*Potamocherus larvatus*) are regularly recorded around the study site. Many studies report a species of Artiodactyla being the preferred prey or most common prey consumed by leopards (Hart et al., 1996; Ray and Sunquist, 2001; Henschel et al., 2005). Indeed, Hayward et al. (2006) found the globally preferred prey species of leopards all belong to this order, namely bushbuck, common duiker and impala (*Aepyceros melampus*).

1.7 Summary and Aims

Numerous studies have been conducted on leopards within protected areas (Marker and Dickman, 2005) however, more information regarding leopard ecology is needed outside such areas for effective conservation. Lajuma provides a study site where leopard behaviour and ecology can be investigated in an area with low human activity and interference and an absence of other, larger predators. Leopards can become part of a conservation initiative before becoming endangered, thus hopefully reducing the likelihood of them acquiring this status. Chase Grey et al. (2013) provide a density estimate for the leopards around Lajuma, but suggest longer term surveys are needed in order to conduct an examination of population fluctuations and determine the effects of factors such as seasonality on leopard population numbers.

While certain aspects of the Soutpansberg Mountains indicate that they are an important refuge for leopards, the leopards themselves are just as important for the mountains. They are the top remaining predator there and play an important ecological role within the environment. They also bring money and economic growth to the area through ecotourism. For these reasons, understanding the leopards' ecology and behaviour in this area will not only benefit the leopards themselves, but also the humans and wildlife they share this ecosystem with.

Using the high density Soutpansberg Mountain population as a model system, the main aims of this study are to investigate:

- The occupancy of leopards in the study area,

- The main prey species consumed by leopards,

- The activity patterns of leopards and their prey.

The data from these analyses will give insights into the ecology and behaviour of the leopards in the Soutpansberg Mountains. It will hopefully provide evidence of what drives this potentially significant population and aid in understanding the conservation significance of montane environments for leopards. Rather than waiting for leopard populations to start decreasing, studies done on populations now will provide baseline data for future conservation initiatives. Developing suitable management strategies for areas outside protected zones, like the Soutpansberg, could be a key factor in the future conservation of leopards (Marker & Dickman, 2005) and, therefore, more detailed knowledge is required of their ecology in such areas.

1.8 Thesis Structure

The next chapter, Chapter 2, provides a review of the specific study site in the Soutpansberg Mountains. The general method being used in each analysis, camera trapping, is introduced and details on camera trap set-up are provided.

Chapter 3 determines leopard occupancy in relation to the availability of prey, as well as the amount of human interaction, in the area. This occupancy estimate will aid in determining the role the Soutpansberg Mountains play in leopard conservation and, importantly, help understand why there is such a high density of leopards in this particular area. It is anticipated that the occupancy estimates for leopards may show particular patterns of coexistence with certain prey species and provide insight into what might be driving the high population density.

Chapter 4 investigates the diet of leopards using a combination of dietary analysis and prey availability analysis to determine what prey species are available and consumed by leopards in the Soutpansberg Mountains. Scat analysis will determine which species are most important to the leopard in terms of their diet and also help in resolving the growing conflict between leopards and landowners in the local area.

In Chapter 5, the activity patterns of leopards and prey species are studied using camera traps in order to detect any temporal avoidance and/or overlap between leopards and their prey, as determined via scat analysis. The information from both Chapters 4 and 5 will aid in deducing which prey species, if any, are most important to the leopard, which may prove vital in future conservation initiatives aimed at monitoring and maintaining these key prey species.

Finally, the main findings are reviewed in a final discussion in Chapter 6 to draw together the conclusions of the various analyses conducted during this study. General study limitations, along with suggestions for future research, are also outlined.

Chapter 2 – General Methods

2.1 Study Site

This study was carried out in conjunction with the PPP. The PPP was formalised in 2010 but their research has been conducted at the Lajuma Research Centre since 2003. The main aims of the project include: assessing the conservation potential of the Soutpansberg Mountains; evaluating the nature and extent of human-wildlife conflict within the mountains; and understanding the behavioural ecology of predator-prey interactions. Since the arrival of the PPP at Lajuma, viable management strategies for mammalian conservation in the region have been implemented and the ecology of key species such as leopards, brown hyenas, samango monkeys and baboons have been studied.

This study was conducted in the western part of the Soutpansberg Mountain range in South Africa. The study site includes 12 farms covering an area of approximately 60 km^2 and within this area one of the farms, Lajuma, served as a base for this research. The terrain of the study site consists of a mixture of wide open grass valleys with scattered trees, rugged cliffs and gorges, and small forest patches. The methods used in this study are all non-invasive methods. The farms were surveyed using camera traps and leopard scat was collected randomly across all 12 of the properties.

The Lajuma Research Centre (or Lajuma) (Figure 2.1) is a privately owned research and retreat centre situated in the western part of the Soutpansberg Mountains, South Africa (23°02′S, 29°26′E) between the villages of Vivo and Makado (Louis Trichardt). Lajuma has an average annual rainfall of 700 mm (Schwarz and Fischer, 2006) and covers an area of 4.3 km^2. It has a varied topography with deep valleys and high cliffs. In fact, the highest peak of the entire mountain range, Mount Lajuma, is within its area, hence the Centre's name. Lajuma has been declared a Natural Heritage Site and forms part of the Luvhondo Nature Reserve within the Vhembe Biosphere Reserve. Before being turned into a dedicated ecotourism and research station in 1996, Lajuma was a farm with cattle and plantations of macadamia, orange, banana & avocado (Gerdel, 2008).

Figure 2.1: Map of Lajuma's position in the Soutpansbergs range (red icon), between the villages of Vivo and Makado.

Land use in the western Soutpansberg, surrounding Lajuma, consists of a patchwork of private cattle and game farms, ecotourism properties, conservancies and communal farm land (Chase Grey et al., 2013). Lajuma is surrounded by 11 other properties (Figure 2.2), eight of which are ecotourist or holiday properties, two are communal land and one is a fruit farm (Table 2.1). Three of these properties also use their land for cattle farming. More intensive livestock farming can be found in the lower areas of the mountain range.
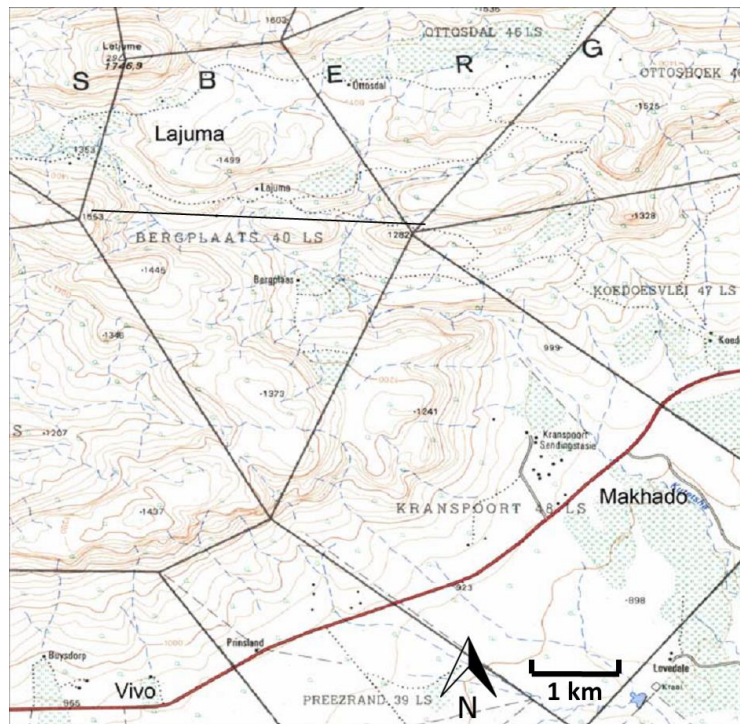
Figure 2.2: Ground plan of Lajuma with adjoining farms (Gerdel, 2008)

Table 2.1: List of properties and the use of their land.

Property	Land Use
Bergplaas	Holiday
Buysdorp	Communal land
Diepkloof	Holiday
Koedoesvlei	Ecotourism / Cattle farming
Kranspoort	Communal land
Lajuma	Ecotourism / Research
Llwelyn	Holiday
Louisville	Holiday / Cattle farming
Ontmoet	Holiday
Ottosdaal	Fruit farming / Cattle farming
Ottoshoek	Holiday
Sigurawana	Ecotourism / Holiday

There is no official hunting in the area, although occasionally a very small amount of game is shot on the Buysdorp and Ontmoet properties. There are, however, known problems of illegal hunting, snaring and poaching of leopards within the area, particularly by livestock owners that derive no economic benefit, such as gains from trophy hunting, from the presence of leopards (Chase Grey, 2011).

Hunting in the past has wiped out most of the large mammals of the area (MacKenzie, 1988). The only large carnivore species that remain resident in Lajuma and the western part of the mountain range are leopards, brown hyena and spotted hyena (*Crocuta crocuta*), although the latter are not present in significant numbers. Transient cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) have also occasionally been encountered. Smaller carnivores that can be found include African civet (*Civettictis civetta*), common genet (*Genetta genetta*), serval (*Leptailurus serval*), caracal (*Felis caracal*), honey badger (*Mellivora capensis*), Cape or African clawless otter (*Aonyx capensis*) and several mongoose species – the dwarf *(Helogale parvula),* slender *(Galerella sanguinea*), banded (*Mungos mungo*) and water mongoose (*Atilax paludinosus*). The most speciose order present in the study site are the Artiodactyla, some of which occur naturally throughout the study site, and others that were exterminated in the past but have now been reintroduced by private game farms in the area such as Sigurawana. The largest antelope species found naturally in Lajuma today is the waterbuck (*Kobus ellipsiprymnus*). However, larger, and sometimes rarer, species such as giraffe (*Giraffa camelopardalis*), sable (*Hippotragus niger*), zebra (*Equus*

quagga), nyala (*Tragelaphus angasii*), eland (*Taurotragus oryx*) and impala can be found on these game farms.

2.2 Camera Trapping

Studying wild carnivores is extremely difficult using direct methods, such as line transects or tracking. Their large home ranges, low population densities (Silver et al., 2004) and often cryptic and nocturnal nature make them especially difficult to survey using the more conventional methods. Indirect methods such as camera trapping have become increasingly important for these species and are beginning to replace traditional methods of population study. The use of camera traps for studying elusive species was pioneered by George Shiras III in the early 1900s (Sanderson and Trolle, 2005), and has since become a readily available and affordable method for studying such animals. The technique has become a main-stream methodology for collecting data for conservation and/or ecology purposes (Rowcliffe and Carbone, 2008).

There are many advantages associated with the use of camera traps;

1) They are non-invasive, meaning the species can be studied without physical interference,

2) They are ideal for studying nocturnal animals, which could not be studied as easily at night using traditional methods,

3) They are less likely to disturb the animal, therefore providing data on the species behaving naturally,

4) They can survey a large area simultaneously, therefore reducing survey time, effort and cost,

5) They are low on labour effort and cost, traps can be set with little training and left for a couple of weeks before being revisited,

6) They provide extra material/photographs on other species that may be used in future studies.

Due to these advantages, camera traps are especially useful for surveying felids. Camera traps have been successfully used for surveying elusive large cat species such as tigers (*Panthera*

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tigris) (Karanth, 1995), jaguars (Maffei et al., 2004), leopards (Henschel and Ray, 2003) and snow leopards (*Panthera uncia*) (Jackson et al., 2006).

Most modern wildlife cameras use infrared flashes to capture images at night, which allow the photographs to be taken in a less obtrusive manner than a regular flash, often without the animal even noticing. This is an extremely important feature, as a visible flash may disturb the animal and bias the resulting data if the animal avoids that area in the future. There are two types of camera systems that are used in camera trapping surveys: active and passive. Active systems have a transmitting unit that sends an infrared beam and a receiving unit that is set across the target area (Kelly and Holub, 2008). These traps take a picture every time an animal or object breaks the infrared beam. Passive systems are single units that use heat or motion detectors to trigger the camera (Kelly and Holub, 2008). Both camera systems may be prone to capturing images of non-target objects such as moving leaves or rain. The cameras used in this study are Reconyx Hyperfire ™ HC500 digital passive infrared motion detector cameras. They use motion detectors to detect the slightest movement between an object and its background, within the camera's frame, which then triggers a picture to be taken. They also have an infrared flash for capturing images of animals at night. Animal/Movement-triggered systems like this are more appropriate for capturing images of species that may occur infrequently or unpredictably (Cutler and Swann, 1999) rather than, for example, using time-lapse equipment where the event of interest occurs repeatedly. Kelly and Holub (2008) compared the efficiency of different camera trap types and noted that the Reconyx performed better than all other cameras in their study. Its high sensitivity, due to a wider infrared beam, lead to a higher trap success, especially for medium and small species. Furthermore, Reconyx traps had zero malfunctions and there was no delay between detection of movement and the photograph being taken.

Camera traps have been used at the study site since 2006 for various surveys. Since the arrival of the PPP, a permanent array of camera traps has been established to survey predators in the area. The PPP possess an extensive archive of hundreds of thousands of camera-trap images, both of leopards and other carnivores in the area, as well as potential prey species. These camera trap data, along with data collected from scat analysis (Chapter 4), will form the basis of this study and will allow a comparison of potential changes in leopard occupancy and activity patterns throughout different seasons, as well as assessing the role that specific prey species may have played in these changes.

2.3 Camera Trap Set-Up

The guiding principles set out by Meek et al. (2014) were used to aid in reporting camera trap methods and results. Forty-eight Reconyx Hyperfire ^{TM} HC500 digital motion sensitive cameras were set up at 24 stations around Lajuma and neighbouring properties, covering an area of 60 km^2 (Figure 2.3). Additionally, Table 2.2 gives a list of which camera stations were assigned to each property. The camera-trapping research protocol is based on Pollock's (1982) 'robust' design and follows protocols employed by Karanth's (1995) long-term tiger monitoring project in Nagarahole National Park, India (Karanth et al., 2011). The advantages of such long-term studies of a population arise from the opportunities they provide to derive estimates of survival, recruitment and movement rates as well as being able to assess differences in abundance levels over several years (Williams et al., 2002).
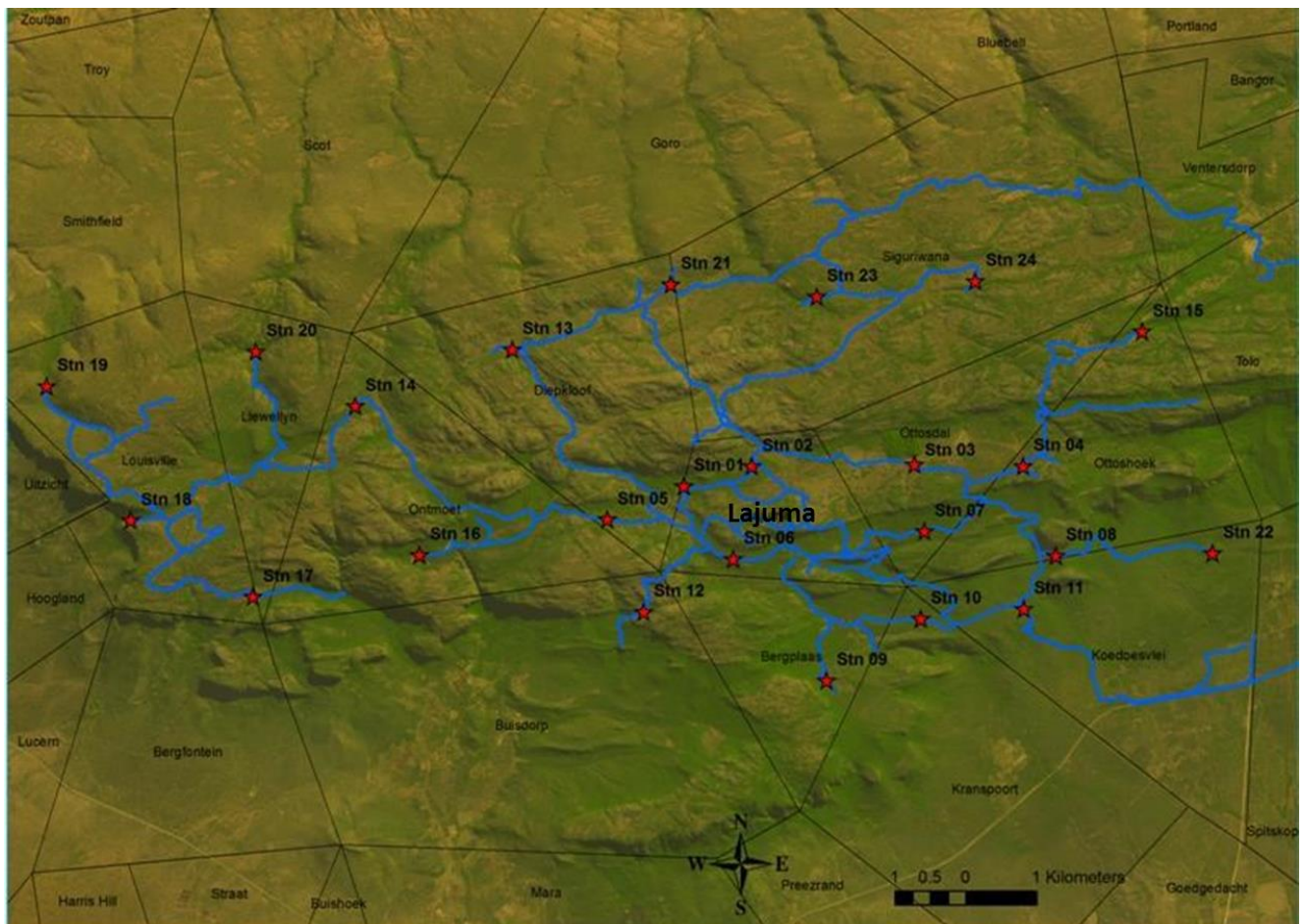
Figure 2.3: Map showing the camera trap array and locations of the 24 camera trap stations around Lajuma and 11 neighbouring farms.

Table 2.2: Camera station numbers assigned to each property.

Property	Camera Station
Bergplaas	9
Buysdorp	12
Diepkloof	5, 13
Koedoesvlei	8, 11, 22
Kranspoort	10
Lajuma	1, 2, 6
Llwelyn	20
Louisville	17, 18
Ontmoet	14, 16
Ottosdaal	3, 7, 15
Ottoshoek	4
Sigurawana	19, 21, 23, 24

Camera stations were set out in a way that ensured the maximum number of leopard captures while also covering the maximum area possible to ensure a good sample of the population. In order to ensure that all individuals had a non-zero probability of capture and that no area existed that was large enough to enclose the entire home range of an adult female leopard (Karanth and Nichols, 2002), recorded by Grassman (1999) as a minimum of 9 km^2, distances between cameras were kept as similar as possible. There was a maximum distance of 2.75 km between any two stations, thus establishing a continuous sampling area. Ideally, the area being studied should be large enough to contain parts of several individuals' home ranges (Henschel and Ray, 2003). During a previous camera trapping survey of the area, it was found that random placement of cameras was not possible due to the montane topography of the study site (Chase Grey et al., 2013). Using this type of placement would have resulted in many stations being situated on cliff edges or other inaccessible areas. Therefore, a method was implemented that has been recommended by Karanth and Nichols (2002) and used in many studies previously (Karanth, 1995; Henschel and Ray, 2003; Silver, 2004; Wegge et al., 2004; Jackson et al., 2006); the key feature of this method is that it does not involve the use of a grid formation. Using this method, an array of camera trap stations was set up on roads and trails known to be regularly travelled by leopards, in order to maximise leopard capture probability. Cameras remained fixed in their positions as to move them around regularly in a mountainous environment would have been impractical. The term "study site" is used in this thesis to describe the area covered by camera traps and the term "station" refers to the location of each of the 24 pairs of cameras. No baits or lures were used.

Previous studies (Silver, 2004; Soisalo and Cavalcanti, 2006) have shown that effective camera stations have two cameras opposite each other, one on either side of the road or trail. Cameras in this study were set up in this way. This ensured the animal was photographed on both sides which aids in identification of the animal and also reduced the risk of missing an individual should one of the cameras stop working. Cameras were attached to trees or fence posts, where possible. Where neither of these was available, a bamboo stake was driven into the ground and a camera was securely attached to it. Cameras were set approximately 2-3m from the centre of the road or trail, at a height of 40cm from the ground (Henschel and Ray, 2003). This height corresponds to the shoulder height of an adult leopard and placing cameras at this height ensured images of the whole body were taken. Cameras were set at a slight offset, rather than directly opposite, each other to avoid infrared flash interference, but remained aimed at the same focal point. Cameras with fast trigger speed are critical to avoid missing passing animals (Rovero et al., 2013). The particular cameras used in this study can take images at speeds of up to two frames per second and were set to run continuously so that even an animal passing the camera at speed would be captured. Although leopards are thought to be mostly nocturnal animals, they are regularly seen during the day. Therefore, running the cameras 24 hours a day ensured that images of all leopard activity at the station were captured regardless of time of day. Images imprinted with date, time, temperature and lunar phase were saved onto secure digital (SD) memory cards within the camera device. Cameras were checked once every 10 to 14 days to replace batteries and download images from the SD cards.

2.4 Data Analysis

All data analyses in this thesis were carried out using the free statistical software package 'R 3.1.2' (R Core Team, 2014), which allows statistical and graphical techniques to be undertaken. Significance was determined by a p-value of less than 0.05. A p-value is an estimate of the probability that, given the null hypothesis, a particular result could have occurred by chance (Crawley, 2005). The ΔAIC is a measure of goodness of fit of a statistical model and is a proven method of model selection (Burnham and Anderson, 2002). The lower the ΔAIC, the better the model fit (Crawley, 2005).

Chapter 3 - Leopard Occupancy

3.1 Introduction

Owing to their position at the apex of food webs, carnivores can have significant effects on the structure and composition of the ecosystems they occupy (Palomares and Caro, 1999). It is, therefore, important to understand the elements that may make an area more or less attractive for a carnivore to occupy. Occupancy is defined as the proportion of an area, patch or site occupied or used by a target species (MacKenzie et al., 2002; 2006) i.e. the probability that the species is present in that area. Fundamentally, it looks at the variables that dictate how and where animals are distributed (Royle and Dorazio, 2006). Occupancy is clearly related to abundance, with the proportion of areas occupied by a species increasing with its average abundance (He and Gaston, 2003). In essence, occupancy estimation/modelling involves repeatedly sampling a number of units over a short period of time (Bailey et al., 2013) and the observed occupancy 'state' (occupied or not) of the unit is recorded for each survey. The occupancy modelling design is similar to that of Pollock's design in mark-recapture models (Pollock, 1982). Occupancy modelling is often used when capture of animals is difficult, or when densities are expected to be low (O'Connell et al., 2011) but it can also be used as a surrogate for abundance estimation for some species (MacKenzie and Nichols, 2004). Recently, it has become a more commonly used tool for understanding how animals are distributed in their environment using data from camera trap surveys (MacKenzie et al., 2005; Linkie et al., 2007; Thorn et al., 2009; Sollmann et al., 2012; Bender et al., 2014). Occupancy models use data that are relatively easy to collect and generate unbiased estimates (O'Connell et al., 2011). They also correct for imperfect species detection and allow the probability of a species occupying and being detected at a site to vary in response to covariates (Carter et al., 2012). These qualities make occupancy models ideal for analysis of camera trap data. Programmes designed to estimate occupancy require less effort than those designed to estimate abundance, while still providing an efficient and robust means of assessing populations (Thorn et al., 2009). This combination of using camera traps and occupancy modelling has become a well-established tool for sampling and making inferences about animal populations (O'Connell et al., 2011).

Occupancy estimates can be used to aid in animal management programmes and inform people interested in conservation of the focal species. They can provide information about habitat suitability (Long et al., 2011), as well as the importance of different prey species and

human-induced impacts. Habitat features have been used as variables in previous occupancy studies (Negrões et al. 2010; Sollmann et al., 2012) as a means of understanding why the focal animal occurs where it does. Negrões et al. (2010) additionally included indicators of prey species richness and the type of trail the cameras were located on as variables.

Leopards are not only the sole species of big cat in and around Lajuma but are also the largest carnivore found there, which adds to the importance of understanding which variables of the ecosystem are most important to them in terms of their occupancy. There is a particularly high density of leopards at Lajuma (10.7 per 100 km^2) (Chase Grey et al., 2013). Therefore, it is expected that there will also be a high estimate of occupancy for leopards in this area. Building on reasons for the high density suggested by Chase Grey et al. (2013), such as a high density of bushbuck, this study includes many different variables that may have an effect on which areas leopards choose to occupy, such as habitat features, prey abundance and human-influenced factors. This study aims to identify which variables most affect leopards through occupancy modelling. This may aid in understanding and explaining the reasons behind the high leopard density in the Soutpansberg. A key difference to note between this occupancy study and that of Chase Grey et al.'s (2013) density survey is that this study is taking a multi-season approach, using camera trap data from four 60-day seasons, two winter and two summer, over a two year period, which should be more informative than using just a single season. Using data from four seasons will produce four different occupancy estimates which can be compared to determine if leopard occupancy changes between seasons in the same year. It also allows a comparison of data from the same season in two different years, allowing a more detailed investigation into the factors influencing leopard occupancy.

3.1.1 Sampling Design

There are a number of ways to conduct repeated surveys (MacKenzie et al., 2006):

   i. Visit each site multiple times and conduct one survey each time,

   ii. Conduct multiple surveys within a single visit ensuring survey sessions are separated by sufficient time to make them independent,

iii. Have multiple surveys conducted simultaneously by independent surveyors during a single visit,

iv. Within a larger site, conduct surveys at multiple smaller plots.

Camera trapping is most comparable to option ii, where a single visit in this case is the entire season and capture events are subsequently determined to be independent or not. It is important that data are collected in such a way that the probability of detecting the species during a survey can be estimated (MacKenzie et al., 2006). This requires repeated surveys to be conducted so that when the species is detected at a site, the repeat surveys will provide information on the chances of detecting that species again at an occupied site, i.e. the detection probability. A key aspect of designing occupancy studies is determining the number of repeated surveys that should be conducted (MacKenzie and Royle, 2005). Unlike the usual survey methods used with occupancy estimates such as point counts or distance sampling, camera trap data are collected as a continuous data set. When capture numbers are low, the data may become highly zero-inflated if each single day is defined as one trapping occasion. Therefore, several trapping days may be grouped together and labelled as one trapping occasion, as suggested by Henschel and Ray (2003). Ultimately, the researcher must, therefore, choose the number of survey sessions that the data set should be divided into. As an example, a study may be designed to observe a species during a three month (single-season) time-frame. Cameras are set to take photographs continuously at each sample site over this three month period. At the end of the study, the data are one continuous survey. In order to carry out occupancy analysis the data need to be split into a number of trapping sessions and each session will contain the same number of trapping days. For example, a three month (90 day) data set could be split into 10 sessions of nine days each, 15 sessions of six days, or 30 sessions of three days. However, no clear guidelines exist regarding the optimum number of survey sessions. It has been recommend that each sample site should be surveyed a minimum of three times (MacKenzie and Royle, 2005), but no further details on choosing a number of sessions were provided. Field et al. (2005) suggest that when occupancy is low it is better to sample more widely across an area in order to maximise the number of occupied sites. They note that sampling widely is of less concern than sampling intensively, and will aid in reducing uncertainty in areas where the species is not detected.

Surveying more sites less intensively (less repeats) is needed for rare species whilst, for common species, fewer sites should be surveyed more intensively (MazKenzie and Royle,

2005). However, no definition exists for "surveying intensively", i.e. how many sessions would be considered enough for studying any particular species. Most studies state the way in which their sampling sessions where split, for example Tobler et al (2009) used ten 6-day sessions, Negrões et al. (2010) split their 42 days of trapping into six 7-day sampling sessions and Sollmann et al. (2012) used five 16-day sessions. Thorn et al. (2009) simply regarded each individual day as a single sampling session. However, in none of these cases were any reasons given for the choice of session length, nor were references cited that might give an insight into these choices.

MacKenzie et al. (2002) conducted simulations to test the effects of various factors, one of which was the number of survey sessions to perform. They looked at using two, five and ten sessions and found that increasing the number of sampling sessions improves the accuracy and precision of estimates of the probability of occupancy, although, in their case there was not much difference between using five or ten sessions. Similarly, Tyre et al. (2003) used simulation results in an attempt to shed some light on the number of sessions required at a sampling area/site. They recommend that when detection probability is high, it is better to increase the number of sites being surveyed then to increase the number of sessions per individual sample site, but as detection probability decreases, number of sessions for each site should be increased. While some effort has been made to explain the choice of survey session number, there is still no clear cut answer as to how, or if, the number of sessions affects model results, which makes it particularly difficult when it comes to analysing camera trap data.

For this reason, this study was divided into two parts. In the first, a number of data simulations were carried out in order to determine whether changes in survey session number have an effect on the occupancy estimates and best fit model results. Simulations are useful when there are questions about the validity of different sampling approaches (MacKenzie et al., 2006) and so should reduce the uncertainty surrounding how to split continuous data into survey sessions. Based on the simulation results, the second part of this study then analyses the real camera data collected in this study, to investigate which variables, if any, have an effect on the areas that leopards occupy.

3.2 Occupancy Analysis

3.2.1 Terminology and Assumptions

In this study, primary sampling periods are referred to as seasons, and define the long intervals where occupancy status could change from one interval to the next due to local extinction or colonisation. Secondary sampling periods are referred to as survey sessions and define the shorter intervals within a season where occupancy status is not expected to change. Therefore, in keeping with traditional occupancy terminology (Bailey et al., 2013), the term "session" is used rather than "occasion" which is used when discussing camera trapping, and "sample site" is used instead of "camera station". At any given time during the season, a leopard may be randomly present in the study area as it travels through its territory but on any single day it is either present or absent at a particular sample site. Thus, when studying occupancy, it is generally regarded that the study area as a whole is much larger than the sampling sites and inferences are made about the population of the study area, not of each individual sample site.

Single-season occupancy models were used to analyse the camera trap data, based on the original model by MacKenzie et al. (2002). A few main assumptions are associated with this model (MacKenzie et al., 2006):

- The occupancy state of areas being sampled is closed during the sampling season,

- Probability of occupancy is equal at all sites,

- Probability of detection, if present, is equal at all sites,

- Detection of the species in each survey is independent of detections in other surveys.

Sample sites having an occupancy state of 'closed' implies that they are either occupied or not during the season, no new sites become occupied after surveying has begun and none are abandoned during the season until surveying has been completed. But occupancy state can, and is expected to, change between seasons. Unoccupied sites may become colonised due to immigrations/births, and occupied sites may become unoccupied due to local extinction/migration events. These changes in occupancy between seasons may occur for a variety of reasons including changes in habitat, human disturbance or prey availability. Probability of detection is the probability that at least one individual of the target species will be detected, if it is present, at the site (MacKenzie et al., 2006) and non-detection at a site

does not always imply that it is truly absent. This may be influenced by many factors including abundance, visibility in the habitat or skill of the observer. Cameras were set up in the same way at each site thus insuring equality of probability of detection across sites.

3.2.2 Data Analysis

Occupancy analysis in this study was carried out using the R package *unmarked* (Fiske and Chandler, 2011) which fits hierarchical models of animal abundance and occurrence to data collected from various survey methods for data from unmarked animals. The *unmarked* package allows parameters that govern the state and observations to be modelled as functions of covariates (Fiske et al., 2014). The specific function from *unmarked* that was used was the "occu" function. This function fits the single season occupancy model of MacKenzie et al (2002) by fitting occurrence models with no linkage between abundance and detection.

Rather than running each of the four seasons separately, a multi-season model could be run which would run the variables for each season and compare them to each other. The "colext" function in the *unmarked* package of R can perform these multi-season models but does not allow for more than one predictor variable to be used in the model. As a result, this function was not used in this study since an objective was to examine the effect of multiple variables in determining leopard occupancy. Since particular variables may have different influences on leopard occupancy during each separate season, it was decided to run models for the seasons independently in order to get an accurate overview of the important variables for each season. This made comparisons between seasons easier as it was clear if, and why, there were any common variables.

Many occupancy studies record a species as either present or absent in order to estimate occupancy (MacKenzie et al., 2002; Nichols et al., 2008; Thorn et al., 2009; Schuette et al., 2013) but the aim of this study is not only to determine if leopards are occupying the study site or not, but also why they are occupying it and how often they use the area. These aims can be measured by looking at the independent photo events for leopards during different seasons and also at the events of various prey species to determine if these have an impact on leopard occupancy. More independent photos captured at each camera station, implies that leopards are using these stations more regularly. It is for this reason that data in this study

were input not as present or absent recordings but as numbers of independent trap events for each variable per camera station per day.

All variables were standardised by z-scoring prior to analysis which removed the scale effect and ensured each variable got equal prominence in the test by being centred around zero. Z-scores are calculated by subtracting the mean of the variable from the value and dividing by its standard deviation. Models were compared based on their AIC (Akaike's Information Criterion) values. The lower the AIC, the better the model fit (Crawley, 2005). However, the best model is not always a good model; hence, a common approach is to test the most general model in the set and, if this is deemed adequate, to proceed with model selection (MacKenzie et al., 2006).

3.3 Simulations

3.3.1 Methods

Simulation tests were carried out to test the effect of various survey session numbers on the accuracy of occupancy estimates (see Chapter 3.1.1). A data set was created to represent a typical camera trap data set for leopards, with the season length set to 60 days in order to fit the assumptions of site closure. The number of sample sites surveyed could vary. To represent the independent capture events of typical prey species, 4 variables were created and named; Species A, Species B, Species C and Species D. The strength of the relationship between each of these variables and leopard occupancy could be altered to make it a strong or weak relationship. A strong relationship indicated that the species had a strong influence on leopard occupancy, while no relationship at all meant the species had no effect on leopard occupancy. Table 3.1 gives the study design used for the simulations, each of which were set to represent various data sets that may be collected through camera trapping. All variables were standardised by z-transforming prior to analysis in each simulation. These simulations tested various session lengths during this 60 day season; 2, 3, 4, 5, 6, 10, 12, 15, 20, 30, and 60. A session length of 2 indicated that the camera data were split into two 30-day sessions, and on the other extreme 60 indicated that each of the 60 days were counted as a separate survey, so there were 60 1-day sessions. If an area is surveyed just once, there is a chance that the species may not be recorded during this survey, especially if the species is rare. To counter the effect of imperfect detection, one solution is to conduct multiple or repeated

surveys within a relatively short timeframe to minimize the possibility of a false absence (MacKenzie and Royle, 2005). Occupancy modelling tools, therefore, are made to be able to, and expect to, read data in the form of multiple surveys. The "occu" function is no exception and would be unable to read data from a single 60-day survey, hence a session length of one was not included in this analysis as it does not fit occupancy data requirements.

Table 3.1: The study design of each of the four simulations including the number of days and sites the data were split into and the strength of each species relationship with leopard occupancy.

Simulation	No. of Days	No. of Sites	Strength of Relationship			
			Species A	Species B	Species C	Species D
1	60	25	Strong	Weak	None	None
2	60	25	Strong	Strong	Weak	None
3	60	100	Strong	Strong	Weak	None
4	60	100	Strong	Weak	None	None

Models were ranked according to their AIC values, with higher ranking models having lower AIC's. However, AIC values change with each model, and so the delta AIC and the Akaike weight were used to compare between models. Delta AIC is a measure of each model relative to the best model. Typically, values < 2 suggest strong evidence for the model, values between 3-7 indicate the model has less support and values > 10 mean that the model is unlikely (Burnham and Anderson, 2002). The Akaike weight of a model expresses the probability that the model is the best out of all the candidate models and is another measure of the strength of evidence for a model. An Akaike weight of 0.80 implies that that particular model has an 80% chance of being the best model. High model selection uncertainty is noted if many models in the set have some Akaike weight, whereas model selection uncertainty is low if most of the weight lies with one particular model.

3.3.2 Results

The general results of the four simulations are provided in Table 3.2 (Appendix A provides more detailed results for each session length in the simulations).

Table 3.2: Results of the four simulations in terms of session lengths 2-30 and 60, with the best model and weight range provided for the 2-30 group.

Simulation	2 - 30	Weight range	60
1	Species A	0.283-0.284	Errors
2	Species A & B	0.411-0.427	Errors
3	Species A & B	0.411-0.414	Errors
4	Species A	0.192-0.201	Errors

For session lengths 2, 3, 4, 5, 6, 10, 12, 15, 20 and 30 days, the best fit model was as expected, ranking the variables with the strongest relationships highest, and the order of best models remained the same regardless of session length. This indicates that the model selection was correctly able to identify the coefficient that matched the definition of the relationship. For example, Simulation 1 was set to have a strong relationship with Species A and the best model comprised of only this variable. Delta AIC values of 0 suggests strong evidence for the models and these values remained similar for each model despite varying session length. The Akaike weight varied between session lengths for each model, however, these variations were quite small.

Session lengths of 60 produced errors, hence model results could not be provided. A list of best fit models were produced, but errors occurred with some models which meant that this list was unreliable as it did not include all possible combinations of model variations.

3.4 Camera Trap Data

3.4.1 Collecting Data

The PPP camera trap grid has been set up and run continuously for a number of years. However, the potential for change within the ecosystem being surveyed increases the longer it takes to collect the data, therefore it is ideal to survey all stations as quickly as possible (MacKenzie and Royle, 2005) while still ensuring enough data are collected. Taking this into account, data were taken from four 60-day periods, representing two consecutive winter and summer seasons in the years of 2012 and 2013, in order to look at changes in leopard occupancy between seasons (Table 3.3). This period of 60 days is long enough to assume that an individual will be present for sampling at any given station if that station lies within its home range.

Table 3.3: Season type, dates, average day and night temperatures (°C) and number of camera stations in operation for each of the four periods, Season 1-4.

	Season	Dates	Average Night Temp (°C)	Average Day Temp (°C)	No. Stations
Season 1	Summer	21/01/12 - 20/03/12	17.13	23.24	24
Season 2	Winter	24/06/12 - 22/08/12	10.07	15.3	24
Season 3	Summer	19/01/13 - 19/03/13	16.56	20.18	21
Season 4	Winter	18/05/13 - 16/07/13	8.87	14.73	22

There were 24 camera stations set up, however during Seasons 3 and 4 only 21 and 22 stations, respectively, were in operation for the entire 60 day duration of the study period. During Season 3 both cameras at stations 6, 21 and 22 malfunctioned and were out of action for a period of time during the season and during Season 4 the same issues occurred at stations 12 and 22. Even though this period of time may have only been a week, it was long enough to make these stations incomparable to the others and therefore they were removed from the occupancy data sets for their respective seasons.

Seasons of 60 days aided in ensuring that the assumptions of population closure during each season were likely to be met; i.e. no births, deaths, immigration or emigration occurred, which avoids overestimating the population size. This agrees with similar research on large felids which suggest two to three months is an adequate sampling period (Silver, 2004) to meet these assumptions. Using seasons of 60 days also leads to a higher probability of more individual leopards being photographed during that time. Each sampling event in the area is defined as a 'trapping occasion' (Karanth, 1995; Karanth and Nichols, 1998). When working in remote or difficult to access areas, it is advised that cameras remain fixed in their positions (as in this study), due to impracticality of moving them, and trapping occasions may be defined later (Henschel and Ray, 2003).

When each station was checked and data were downloaded from the SD cards, images were tagged with a species label using Windows Live Photo Gallery. As with many large felids, leopards can be identified by their unique pelage markings (Figure 3.1) particularly along the flank, and were given an additional tag to note which individual was in the image. As well as identifying and tagging all naturally occurring species, humans and domestic animals were tagged as well as vehicles. These images were used to determine the role, if any, human activity has on leopards in the area.
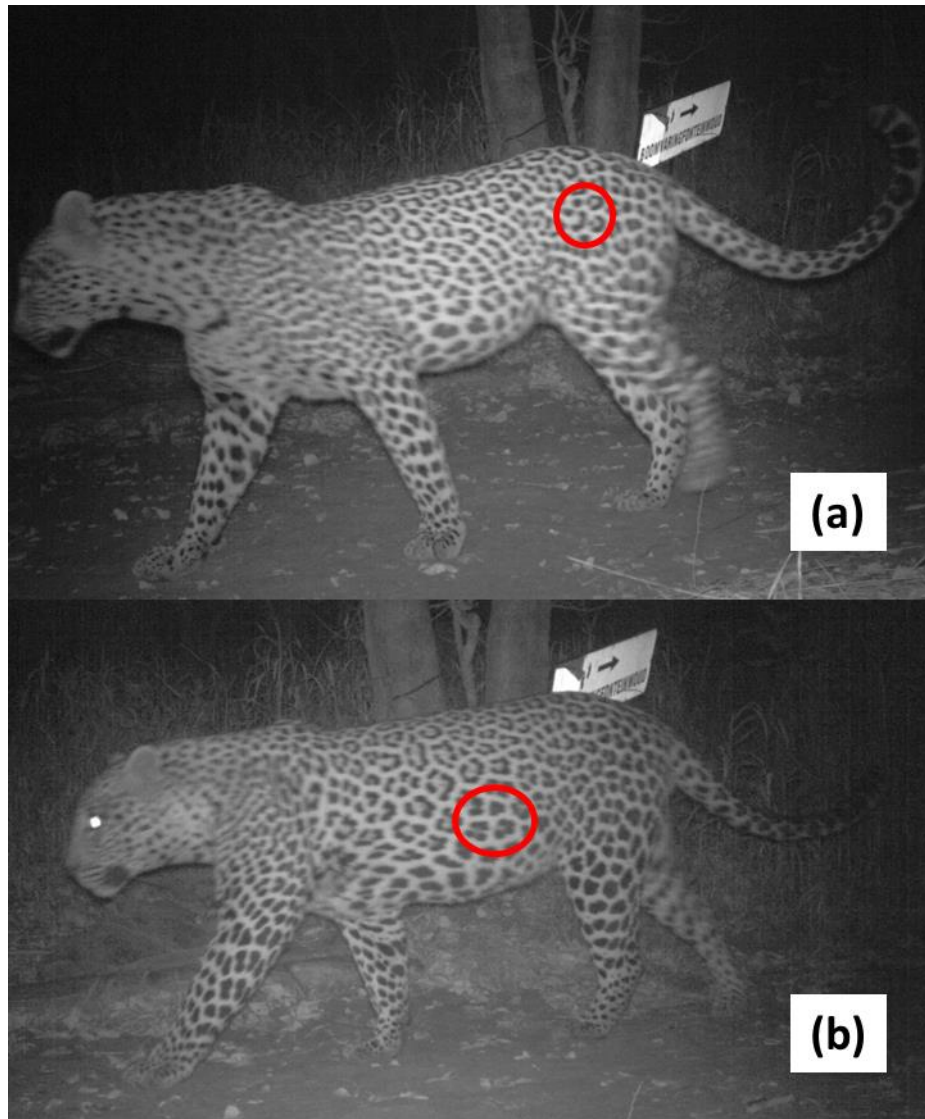
Figure 3.1: Images of two different leopards (a) and (b) identifiable by their unique pelage markings, characteristic differences are indicated (red).

Images were tagged and double checked by a second person to ensure no false positive (misidentifying a species causing it to be reported as detected when it actually is not present) or false negative (failing to detect an animal when it is present) errors occurred. Blank images, i.e. images that were certain not to contain any animal or vehicle, were deleted. The Exif Tool programme was used to extract the metadata, e.g. date, time, species ID, temperature, etc., from each photograph. After identifying the species in each image, the images were categorised as an independent or dependent capture event, which allows them to be used as an index of abundance. An event was considered independent if there were

consecutive images of different species or if a specified amount of time had passed between consecutive photographs of the same species. This time limit has been defined differently in various studies. Some studies consider a photograph to be independent if it is captured more than 30 minutes apart from the previous image (O'Brien et al., 2003; Datta et al., 2008; Kelly and Holub, 2008), whereas others considered an independent event to be one in which images are separated by more than one hour (Tobler et al., 2009; Chase Grey et al., 2013; Wearn et al., 2013). This study adopted a similar approach to the latter, and defined an independent event as one in which consecutive images of the same species are captured more than one hour apart. Consecutive photographs of leopards were considered independent if they showed different individuals, differentiated by their unique pelage, regardless of the time between them. Data were stored as numbers of independent trap events for each prey species, as well as humans and vehicles, per camera station per day.

3.4.2 Preparing for Analysis

Data were analysed by dividing the period of 60 days for each season into ten separate sessions comprising of six consecutive trap days each (i.e. ten 6-day sessions). By grouping trap days together in this way, more captures can be produced per single occasion than if the days were analysed individually. However, results from the simulations performed (Chapter 3.3.2) indicate that any number of survey sessions from 2 to 30 could have been chosen to run the model. By having repeated sessions this provides multiple opportunities to observe the true occupancy state for each given season (Bailey et al., 2013).

Based on previous literature (Negrões et al. 2010; Sollmann et al., 2012), various variables were used in the occupancy models to determine what may influence leopards to occupy an area or not. Habitat type, altitude, and being situated on a road (or not) were included as variables, as well as using independent capture rates from potential prey species, derived from the camera traps, as additional variables. These independent capture rates give an indication of the abundance of each species, with high capture rates suggesting the species is common in that area. Human-related variables were also included using the independent captures rates of humans, vehicles and domestic animals, to examine the effects human presence may have on the leopards' occupancy of the area.

Habitat type was split into two categories, Forest and Savannah. An area was considered to be a forest habitat if it was densely packed with vegetation, usually trees, and a savannah habitat if it was an area of grassland with widely spaced trees and shrubs. Road was a binary variable, categorised as either 'Yes' the camera station/sample site was situated on a road fit for vehicle use, or 'No' it was on a smaller game trail. Altitude was recorded as metres above sea level using a Garmin GPSMap 60CSx device. This handheld GPS device has a high-sensitivity receiver that gives satellite reception even in heavy tree cover or deep canyons. Independent capture events of different prey species were included as separate variables. Camera traps are commonly used to detect multiple species, but none can detect all species with equal efficiency (Gompper et al., 2006; O'Connell et al., 2006; Tobler et al., 2009). Due to limitations associated with the traps being set to primarily capture leopards, some prey species, particularly small ones, were not captured. The species used as variables in the occupancy modelling were: aardvark (*Orycteropus afer*), bushbuck, bushpig, porcupine, baboon, common duiker, dassie, Gambian rat (*Cricetomys gambianus*), kudu, impala, klipspringer, rabbit, red duiker (*Cephalophus natalensis*), tree squirrel (*Paraxerus cepapi*), vervet monkey and warthog. These species were chosen either because they had the highest numbers of independent capture rates for their various taxonomic groups or because they represented a size of prey that was not otherwise included. Human, vehicle and domestic animal were also included to determine the effect human presence may have on leopard occupancy, either directly through walking or travelling though the sample sites or indirectly by allowing domestic animals to roam in these areas. By modelling these key variables it was hoped that reasonable explanations for the patterns of leopard occupancy would be provided.

All variables were standardised by z-scoring prior to analysis. Prior to running the main models, variables were firstly run on their own for each season to determine their AIC values independently and get a feel for which variables had the most impact on leopard occupancy in each season. Model combinations were then run using multiple variables.

3.4.3 Results

There were a total of 5,460 trap nights (1,440 in Seasons 1 and 2, 1,260 in Season 3 and 1,320 in Season 4). Analysing only the photos of the variables that were considered in this study, a total of 13,855 independent photo events were obtained during this time, which produced an overall trap success rate of 253.75 per 100 trap nights. A total of 488

independent leopard events were recorded during the four seasons (Table 3.4), resulting in a trap success of approximately 9 leopards per 100 trap nights. The two variables with the highest numbers of independent events, and therefore trap successes, during the study were human and, the human-related variable, vehicle (Table 3.4). Prey species with the highest event records (>1000) include bushbuck, porcupine and baboon. The smaller rodent species such as rabbit and Gambian rat had the lowest event records (<30) of the study.

Table 3.4: The total number of independent photo events for each variable per season and for the entire study, as well as the trap success (per 100 trap nights) of each variable during the study.

Variables	Season 1	Season 2	Season 3	Season 4	Total	Trap Success
Human	776	1007	602	792	**3177**	**58.19**
Vehicle	531	855	851	761	**2998**	**54.91**
Bushbuck	366	819	274	440	**1899**	**34.78**
Porcupine	524	435	187	347	**1493**	**27.34**
Baboon	374	370	242	161	**1147**	**21.01**
Red duiker	140	175	54	128	**497**	**9.10**
Leopard	122	117	102	147	**488**	**8.94**
Warthog	103	107	118	99	**427**	**7.82**
Bushpig	104	94	92	62	**352**	**6.45**
Domestic animal	36	164	69	38	**307**	**5.62**
Kudu	78	85	53	35	**251**	**4.60**
Vervet monkey	59	97	27	37	**220**	**4.03**
Aardvark	72	17	43	15	**147**	**2.69**
Common duiker	41	53	31	18	**143**	**2.62**
Dassie	37	43	19	23	**122**	**2.23**
Tree squirrel	40	18	10	1	**69**	**1.26**
Impala	3	24	15	1	**43**	**0.79**
Klipspringer	19	3	7	4	**33**	**0.60**
Gambian rat	10	7	0	9	**26**	**0.48**
Rabbit	1	9	1	5	**16**	**0.29**

Season 2 had the highest number of events for a number of variables including bushbuck, humans, red duiker, vervet monkeys and domestic animals. Numbers of leopard, warthog, common duiker, bushpig and dassie remained relatively stable between seasons compared to other variables. Over the course of the four seasons, leopards were caught at every camera station. Some species, such as impala or dassie, were only captured at one or two particular camera stations due to their locations in a specific property such as Sigurawana or near a favourable habitat feature such as rock crevices.

None of the prey variables had strong effects in any of the seasons, therefore when models were run using multiple variables only the human-influenced and natural variables were used. These six variables were human, domestic, vehicle, road, habitat and altitude. Adding on any of the prey variables never resulted in a lower AIC value for any season, hence they were excluded from the analysis.

Table 3.5: The main occupancy results for each of the four seasons including the variables in the best fit model, along with their occupancy estimates, and their respective p-values.

Season	Best Model Variables & Corresponding Estimates			p-values
1	Human 175.4	Habitat (Savannah) -12.6	Altitude 6.9	0.303, 0.819, 0.652
2	Domestic -13.1	Altitude -11.8		0.656, 0.725
3	Human 269.5	Road (Yes) 18.4		0.281, 0.893
4	Null Model Best			-

For Season 1, human and altitude had a positive effect (175.4 and 6.9, respectively) meaning as number of humans increased or as altitude got higher, leopard occupancy increased (Table 3.5). The savannah factor of the habitat variable had a negative effect meaning that leopard occupancy decreased in savannah areas. Both the domestic and altitude variables in Season 2 had a negative effect. In Season 3, human had a very strong positive effect on leopard occupancy and the Yes factor of the road variable also had a positive effect. The best model in Season 4 was the null model, meaning that none of the variables measured had a significant effect on the occupancy of leopards. With that said, it must be noted that none of the analysed variables in models of any season had significant results.

3.5 Discussion

Based on the simulations performed in this study, researchers now have information to aid in deciding how to split camera trap data into a number of sessions and evidence to support the decision that, as long as the number of sessions is adequate, the results will be valid.

The main finding of this occupancy study was that leopards were ubiquitous, so any model that worked well in a season was likely a random outcome of the properties of that site (or a couple of sites) where, by chance, leopards were not detected during that season. The high and constant occupancy of leopards in the study site throughout the seasons made it impossible to determine which explanatory variables may have an effect on occupancy.

Both of these findings are discussed in more detail in the following sections. Study limitations and suggested future research, specific to studying occupancy, are outlined before the findings of this chapter are brought together in a final concluding section.

3.5.1 Simulations

Simulation data were produced for a variety of different situations, with varying number of sample sites and strengths of relationships between variables. These simulations provided evidence that the number of sessions into which data were split did not have an effect on the results. Notwithstanding one exception, the number of sessions the 60-day survey was split into did not affect the result. The resulting top models always reflected the relationships that the variables were given with leopard occupancy. This was the case whether the number of sample sites was 25 or 100. The only exception to this was when data were split into 60 1-day sessions. While this exception may seem obvious or trivial, 1-day sessions have previously been used for studying occupancy (Thorn et al., 2009), hence their inclusion in this study. When the data were split into 60 1-day sessions, there was insufficient data in these single day sessions to produce accurate occupancy estimates. Estimates and models were produced but they contained errors and differed noticeably from the models produced by all the other session lengths, which matched each other in terms of the variables included.

These results suggest that while there needs to be a number of sessions greater than one, each session still needs to contain enough information for accurate models to be produced. In terms of camera trapping, data collected for some species in one day of surveying could be zero, depending on the animal's activity patterns or behaviour. Grouping days together into sessions, even if it is just combining two survey days, produces a much more reliable data frame for the occupancy tools to work on. Based on these results, researchers now have information to aid in deciding how to split camera trap data into a number of sessions and evidence to support the decision that, on a whole, whatever choice is made will produce valid occupancy estimates. As long as there are an adequate number of sessions, the results are robust to decisions made about this.

3.5.2 Camera Trap Data

In Season 1 the Human and Altitude variables had positive effects on leopard occupancy implying that as humans increased or altitude got higher, leopard occupancy increased in the study area. This result is unusual as it would be expected that the greater the presence of humans, the less leopards would occupy the area. When the data were examined it was clear that out of the 24 sample sites, only two recorded no leopards at all during the season. At both of these sites the number of human events recorded was lower than average. Similarly, altitude at these sites was also lower than average and both sites were situated in a savannah habitat. It is important to note, however, that leopard events were recorded at other sites with similar human, altitude and habitat recordings. Therefore, it seems that the occupancy model simply picked up on any variable that was higher or lower than the average and associated this variable with having an effect on leopard occupancy. This effect is not significant and merely highlights that leopard occupancy in this study was too high and constant for any of the explanatory variables to have a meaningful effect. It also highlights the issue that the "best" model from a model selection process is not necessarily a good model and interpretation of this model needs careful consideration.

This was also the case for Season 2 and 3, where there were one or two stations which recorded no leopards and had below/above average levels of another variable (or two). The model then picked up this correlation as being important even though leopards were recorded at other sites with similar levels of these variables. This pattern of the occupancy model producing results based on a correlation is highlighted by the fact that the best model for Season 4 was the null model. The reason for this was that of the 22 sites in operation during Season 4, all of them recorded leopard events. Therefore, the model could not distinguish any variable that had a significant impact on leopard occupancy because regardless of whether the variable was low or high, one category or the other, leopards still occurred, making it impossible to find a relationship between any of them. The occupancy level of leopards in this study, regardless of season, was clearly very high, making it impossible to detect any consistent significant pattern between particular explanatory variables and occupancy. Had occupancy been lower, a comparison between variables in occupied areas versus non-occupied areas could be made which would aid in explaining which variables are most important to leopards.

3.5.3 Study Limitations and Future Studies

One main limitation affected the collection of data and, therefore, the results. The camera stations were set up as part of a long term study by the PPP, hence their locations could not be changed. Camera stations were set up mainly to optimise data collection for density estimations of leopards and brown hyena. However, an array optimised for density estimation often violates some of the assumptions of occupancy estimating. According to Rovero et al. (2013) if home ranges are larger than the spaces between camera stations, the same individual could appear at many different stations and data would be unusable in terms of estimating occupancy. Ideally for occupancy studies, distances between sample sites should be larger than the average adult leopard home-range to ensure a true measure of occupancy is measured (Karanth et al., 2011). Future studies like this one must ensure that their camera trap array is set up to optimise occupancy modelling which may lead to differing results.

One of the main issues with this study was that leopards' occupancy throughout the study area was very high, making it impossible to determine which variables may affect their occupancy. To overcome this issue, camera traps would need to be placed in similar areas where it is known for definite that leopards *do not* occur. Variables would be measured and recorded in these areas and then compared to the areas that leopards do occupy to see if there are any main differences between the variables at each site. These differences would then aid in explaining the reasons why leopards occupy certain areas and which factors of an area are most important to them. However, finding similar locations in the Soutpansberg where it is known for sure that leopards do not occur may prove difficult. Even if leopards have not been captured on camera traps or evidence of them has not been obtained it does not mean that they are not present. Determining that they do not occur at a site could be a study in itself.

3.5.4 Conclusions

There are two main conclusions to this study;

1) That the number of sessions a camera trap data set is divided into does not matter, provided there is sufficient data in each session,

2) In and around Lajuma, there was no individual covariate in any of the four seasons that had a significant and important effect on the occurrence of leopards.

Based on the first conclusion, future camera trap research can now be split into almost any number of sessions with the knowledge and evidence to support that this won't affect the results of that study.

The second conclusion highlights that there are challenges when attempting to model occupancy in an area where general occupancy is very high. Leopards occur almost everywhere throughout the study site, which makes it difficult to determine which variables, if any, are responsible for influencing leopards to occupy the area.

This occupancy study has been a good example of the well-known scientific maxim "correlation does not imply causation". Had the individual camera stations for each season not been looked at in more detail, the variables that occurred in each of the top models could have been taken as an accurate measure of the factors influencing leopard occupancy during each season. However, it became clear that the model correlated any variable that was particularly higher or lower than the average, at sites where leopards were not recorded, as being the reason for the lack of leopards. These variables were found to have no significant evidence to support them as the causes behind the absence of leopard events, thus reinforcing the maxim.

Chapter 4 - Leopard Diet

4.1 Introduction

Leopards are known to have the broadest ranging diet of all the large predators in sub-Saharan Africa, with 92 different prey species recorded, typically ranging in weight between 20-80 kg (Mills and Harvey, 2001). This suggests that leopards are highly adaptable in the range of prey they can hunt but have specific preferences which lie within the 20-80 kg weight range. They are morphologically equipped to kill larger prey species, but during difficult times they may rely on abundant smaller species to survive (Hayward et al., 2006), thus demonstrating their adaptable and opportunistic nature. Indeed, Kittle et al. (2014) found that Sri Lankan leopards in the central hills hunted large prey where available but also smaller, more specialised prey when necessary. Leopards require between 1.6 and 4.9 kg of meat per day to sustain their body mass (Bothma and Le Riche, 1984; Stander et al., 1997) and studies have shown that leopards need to kill between 40-60 prey items per year to achieve this (Chase Grey, 2011). They are adapted to a famine or feast lifestyle and can eat a quarter of their body weight in a single day if the opportunity arises (Sunquist and Sunquist, 2002). Generally, leopards make a kill every 4-5.5 days, returning to feed on large kills over a number of days (Stander et al., 1997). Limitations on the size of prey they can capture may be imposed by the hunting strategies available to them, which depend on their habitat (Hayward et al., 2006). Current literature records a broad range of prey weights for the leopard which varies according to habitat. In general, preferred prey weight ranges between 10-40 kg, with a preferred mean prey weight of 23 kg (Hayward et al., 2006). In African forest ecosystems mean prey weight ranges from as high as 29.2 kg (Henschel et al., 2005), to as low as 7.3 kg (Ray and Sunquist, 2001). Karanth and Sunquist (1995), recorded a higher mean prey weight of 37.6 kg for leopards in their study area in an Indian tropical forest, with prey weights ranging from 30-175 kg. In the Cederberg Mountains, where leopards are known to be half the mass of leopards elsewhere in South Africa, it was recorded that leopards preyed upon small to medium-sized species, <20 kg, perhaps because larger prey species are unavailable (Martins et al., 2011).

Hayward et al. (2006) noted that preferred prey species are found in small herds that occur in densely vegetated habitat that provides leopards with minimal risk of injury during hunting, but also maximum cover to limit detection. As ambush predators, leopards in the Kalahari require at least 20cm of cover, making tall grasses (>30cm) and thick vegetation sufficient

(Bothma and LeRiche, 1984). Vegetation must not be not so dense that it reduces the ability to see prey or to stalk, but still dense enough to provide sufficient cover for a leopard to get close enough without being detected. The skill of stalking undetected is the key to a successful leopard hunt, as once detected, leopards have very little chance of capturing the target prey (Rice, 1986). Main prey species in most studies are ungulates, with primates and large rodents also regularly preyed upon, but to a lesser extent (Hart et al., 1996; Schwarz and Fischer, 2006; Braczkowski et al., 2012; Selvan et al., 2013).

4.1.1 Analysing Leopard Diet

Leopards have the widest distribution of all large cats in Africa and yet, their habits and feeding ecology outside of savannah habitats are still poorly understood (Martins et al., 2011; Jooste et al., 2013). Although leopards have a broad dietary niche (Hayward and Kerley, 2008), it is known that carnivore populations are generally limited by their food supply (Macdonald, 1983). Hayward et al. (2007a) found leopard density was strongly correlated with preferred prey biomass. In addition, Chase Grey et al. (2013) suggested that the probable high abundance of bushbuck, a preferred species of prey for leopards at Lajuma, may account for the high density of leopards found there. However, neither this reason nor others that were hypothesised, have been formally tested. As potential prey species in the Soutpansberg Mountains range from <10 kg to species >60 kg, it will be interesting to determine the prey preferences of leopards in this area and see if they concur more with those of Martins et al. (2011) where leopards in a similar mountainous environment mostly consumed prey less than 20 kg, or with studies done in other habitats where the mean prey weight was typically larger. Leopards in the Soutpansberg Mountains have fewer carnivore competitors than populations which co-exist with other large felid species. Thus, it will also be interesting to see if diets of the leopards here are different due to the lack of inter-specific competition for prey. Knowledge of any predator's diet is crucial for their management (Hayward et al., 2007b) thus, this study employed a combination of dietary analysis and prey availability analysis to determine what prey species are available and consumed by leopards in the Soutpansberg Mountains. Prey availability governs the movements, abundance and population viability of large carnivores (Hayward et al., 2007a), hence, it was hoped that the investigation of leopard diet would provide insights into possible explanations for the high density of leopards in this region. A large prey base of species from a variety of taxa and a range of different sizes

would provide a wide choice of prey for leopards to hunt, regardless of their hunting preferences. This variety of available prey, if found in the scats and on the camera traps, would indicate that the environment has sufficient prey to support a high density of leopards

A diet profile of the leopard was described using scat analysis, the identification and quantification of undigested materials that have passed through the digestive systems of the species of interest (Trites and Joy, 2005). Scat analysis has become the primary method of assessing carnivore diets (Klare et al., 2011) due to the ease of collecting samples and its non-invasive nature, compared to more intrusive methods such as analysing stomach contents. The frequency of occurrence of each prey species among scat collections can be easily determined to describe the average diet of leopards (Trites and Joy, 2005). A comparison study by Klare et al. (2011) found that frequency of occurrence methods were used in 94% of reviewed papers, and were the sole method used in 50% of the papers. Although frequency of occurrence indicates how common an item is in the diet, Klare et al. (2011) concluded that it has the least ecological significance and can provide misleading results about a species' ecology. This is due to the surface to volume issue that occurs when prey sizes are highly variable, creating a tendency for frequency of occurrence estimates to overestimate the number of smaller species consumed and underestimate the number of larger species (Henschel et al., 2005). Due to the relatively greater surface area in relation to volume in smaller prey types their, often complete, consumption results in the production of more scats containing indigestible material, such as hair, than larger prey types where mostly just meat, and relatively little hair, is consumed. Therefore, smaller prey items have a greater representation in scats per unit ingested than larger prey (Floyd et al., 1978). Here, scat contents were quantified using both estimates of frequency of occurrence and relative biomass consumed. Calculating the percentages of food items in the diet of leopards is an essential element in understanding the role they play in this montane environment, as well as the impacts they may have on prey populations and local farming communities.

Prey availability was determined using camera trap images, a method which had yet to be used in the Soutpansberg. Conducting game count surveys has previously been the most common method for estimating prey abundance for comparison with diet, with techniques such as aerial counts (Hayward et al., 2006; Jooste et al., 2013) or road transects (Hunter, 1998; Walker, 1999; Balme et al., 2007) being used. However, these studies are often limited by the surveyor's visibility (Hunter, 1998), a disadvantage that is overcome by the use of

camera traps. Previous studies often use camera trap data as a measure of abundance (Balme et al., 2010; Henschel et al., 2011). However, as noted by Cutler and Swann (1999), a number of photos is rarely an index of abundance as it is usually impossible to determine whether multiple photos represent repeated events from one individual or single events from various individuals. Furthermore, the number of photos obtained depends on the movement behaviour of the focal species and, thus, cannot be compared among species. Here, instead of assuming that the number of independent capture events is proportional to abundance, the more realistic assumption is made that it is proportional to the probability of encounter. By using this encounter rate, rather than relative abundance rate, in combination with scat data, Manly's selectivity index (α) (Manly et al., 1972; Chesson, 1983) was evaluated for each of the main prey species. This index measures the degree to which a predator is more likely to take one kind of prey rather than another (Manly et al., 1972) and is commonly used in the literature to determine whether a predator preys on a species more or less than expected by chance (Escamilla et al., 2000; Teixeira and Cortes, 2006; Davis et al., 2012; Klecka and Boukal, 2012). A value of $\alpha = (1/n)$ (where n = the total number of species), means the specific prey species is consumed in proportion to its availability in the environment, $\alpha > (1/n)$ indicates preference and $\alpha < (1/n)$ indicates avoidance (Teixeira and Cortes, 2006). This index will be valuable in determining whether leopards are preying on species they encounter regularly or have preferences in their diet.

Camera trap data were also used with scat data to produce Independent Event Rates (IERs) which provide data on the average number of independent events for a scat location for a species, based on the events at the surrounding camera stations. The IERs of a number of species were then used to explain the presence or absence of a species in a given scat, for example if the presence or absence of baboon in a scat can be explained by the event rates of baboon and other species. The purpose of using more than one species' IER to predict occurrence in a scat is that the focal species' abundance might be expected to affect occurrence but, equally, so might the abundances of other common species in the area be expected to reduce it.

4.2 Methods

4.2.1 Scat Preparation and Analysis

Leopard scats have been collected opportunistically across the study site by the PPP since 2011. When a scat was found, it was individually bagged in a plastic zip-lock bag to avoid contamination. The date, altitude and GPS co-ordinates of the collection site were recorded on the bag. Leopard scats are recognisable due to their large hair and bone mass. They are usually deposited along roads/trails and are coiled, elongated and tapered at one end. Generally, they are found in several pieces which measure between 6–13 cm in length and 2.5-4 cm in diameter (Chase Grey, 2011), anything less than 2 cm in diameter was disregarded (following Schwarz and Fischer, 2006). African civet and hyena scats can look very similar to leopard scats, but civet scat can be distinguished from leopard as they will often contain evidence of the ingestion of arthropods, fruit and seeds (Henschel and Ray, 2003). In contrast, hyenas often deposit their scats in specialised latrines and they usually have a higher bone content than leopard scats giving them a white, chalky appearance. To ensure accurate identification, all collected scats were also checked by a field guide qualified by the Field Guide Association of South Africa (FGASA). Once confirmed as leopard, scats were washed in water using a fine sieve with a mesh width of 1mm, and biological remains such as hairs, teeth and bones were separated and left to dry in the sun. These remains were then washed and sun-dried a second time to ensure only undigested material remained. Each scat's remains were stored in an individual plastic zip-lock bag labelled with its GPS location, date of collection and date of preparation.

Undigested hair was used to identify consumed prey species because unlike tooth and bone fragments, hair remains relatively undamaged during the digestion process (Keogh, 1983). In some instances it is possible to identify, macroscopically, which species the hairs belong to, but this is not always the case and may be unreliable if used as the sole method of analysis. As a consequence, microscopic analysis was also used. Two main microscopic methods dominate the literature: cuticular scale impressions and cross-sections. Cross-sections have been shown to be a more definitive tool, as cuticular impressions are inadequate in identifying hairs to species level (Kent, 2004). Thus, cross-sectioning was the method chosen for this study. A cross-section of the shaft of the hair can be divided into 3 layers;

1) The cuticle or outer layer,
2) The cortex is the middle layer,

3) The medulla is on open area that runs through the centre of the cortex. (Kent, 2004).

The cortex and medulla are the main layers used for identification during cross-section analysis. Some species, such as impala and klipspringer (Figure 4.1 a & b), have very obvious shapes or features when cross-sectioned which make identifications easy. Others, such as giraffe and baboon (Figure 4.1 c & d) can be more difficult to distinguish between.
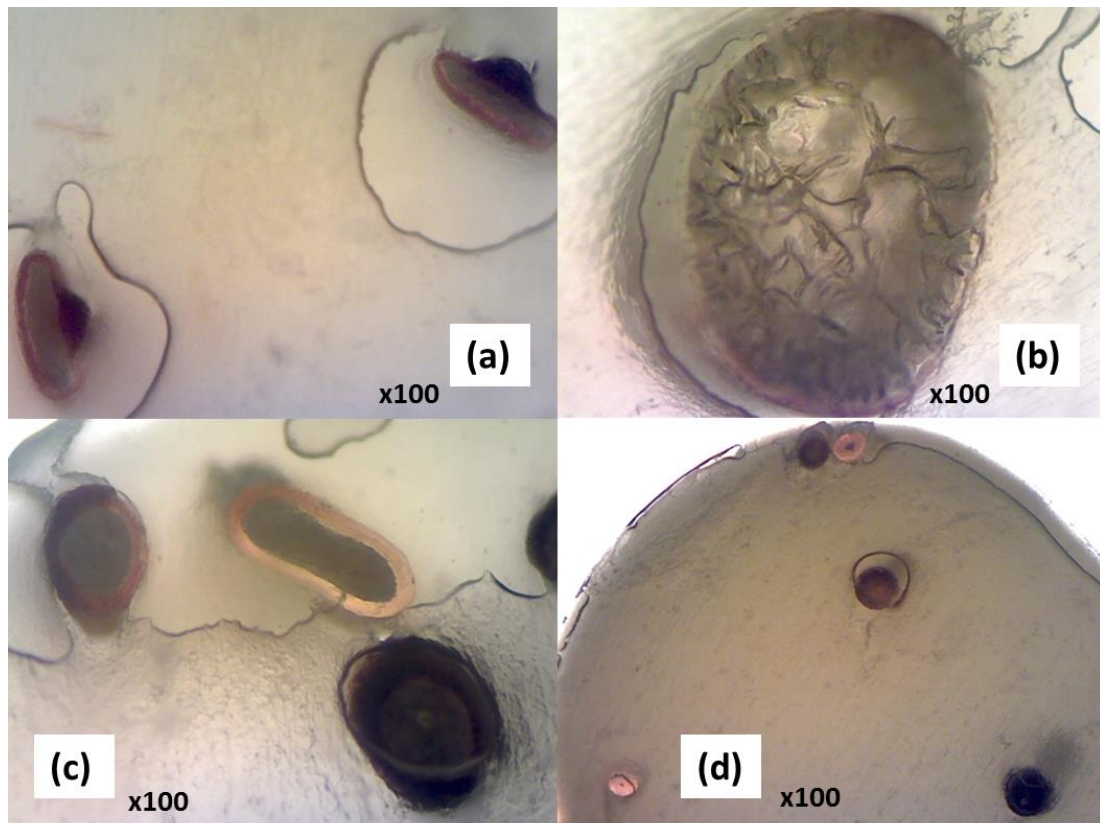
Figure 4.1: Cross sections of four different species; (a) impala, (b) klipspringer, (c) giraffe, (d) baboon (images taken during assemblage of reference slides for this study).

In order to get a reasonable overall and unbiased view of the prey species contained in each scat in this study, 20 hairs were selected at random from each individual scat. Previous studies on leopard diet on the Soutpansberg have analysed just 10 hairs per scat (Schwarz and Fischer, 2006; Chase Grey, 2011). However, Mukherjee et al. (1994) determined that for leopard scats containing more than one prey species, all species present are detected by examining a minimum of 15 hairs per scat, but to be more statistically confident, 20 hairs per scat were recommended to enable the detection of multiple prey species. The first stage of analysis involved identifying macroscopic features of each hair such as length, colour and thickness, as well as noting other items that were present in the scat sample such as bone

fragments, hooves or digits. Once any macroscopic features were identified, microscopic analysis was conducted.

To produce cross-sections, a method similar to that described by Douglas (1989) was used, which is fast, effective and inexpensive as it requires no highly specialised equipment. Approximately 4-5 hairs were inserted into a single plastic Pasteur pipette using tweezers. The bulb at the end of the pipette was pressed to expel any air, and then a small amount of melted beeswax was drawn into the pipette to set the hair in place. When the wax cooled, a scalpel was used to cut 10-12 thin-sections of hair, approximately 1mm thick, from each pipette. This type of cross-sectional profile, consisting of a series of cross-sections cut along the length of the hair, allows variations in medulla shape and size to be observed more easily (Douglas, 1989) which in turns makes species identification easier. Thin-sections were placed on glass slides, examined using the 100x magnification of a light microscope and compared to the reference library. The reference library consisted of a collection of cross-sections, prepared using the procedure described above, from hair samples of all potential prey species in the study site. Reference hair samples were collected from animals hunted in the region, carcasses found in the study area, and from local taxidermists and museums. Where possible, hair samples were taken from many different parts of the body, from adults and juveniles, and from both sexes. Known reference collections produced by Keogh (1983), Buys and Keogh (1984) and Kent (2004) were also used for comparison. The ring of plastic from the pipette surrounding the wax-embedded hair prevented the wax from cracking and meant both the samples and reference library could be used and stored without fear of deterioration.

The number of scats analysed is statistically important. The cross-sectioning process was conducted for a total of 162 scats in this study. Trites and Joy (2005) used simulations to determine that 94 scats were required as a conservative minimum to ensure that diets containing at least six prey species can be determined, assuming prey are independently and identically distributed. They suggest that larger sample sizes reduce the amount of total variability attributed to sampling error and, therefore, approximately 100 scats is an appropriate number to detect differences in diet across time or geographic area. Collecting too many scats may result in wasted resources. Mukherjee et al. (1994) recommend a minimum of 80 scats be analysed to reliably estimate leopard's diet. The number of samples used in leopard scat analysis varies greatly from just 50 samples used by Braczkowski et al. (2012) to 196 used in the study by Henschel et al. (2005). Previous studies on African

leopards in mountainous areas (Schwarz and Fischer, 2006; Chase Grey, 2011; Martins et al., 2011) analysed 179, 100 and 93 scats, respectively.

4.2.2 Scat Data Analysis

Traditionally, there are two main methods of reporting scat analysis results: one calculates the percentage of all scats in which a particular prey species is found, the other calculates the percentage of all occurrences in which a prey species is found (Baker et al., 1993). Often, both of these methods are given the same name: frequency of occurrence. This study follows Lyngdoh et al. (2014) who defined frequency of occurrence as the frequency at which a certain prey item is found in relation to the total number of prey items found in the scats (the number of occurrences of one species / total number of occurrences $\times$ 100).

Converting frequency of occurrence data into biomass consumed is considered the best approximation of true diet (Klare et al., 2011). This can be done using a model developed either for the same species or a closely related species. Biomass calculations were originally carried out by Floyd et al. (1978) studying wolves. They calculated an index that compensated for the discrepancy between the various prey sizes being represented in the wolves' diet. Similar to previous studies on leopard diets (Karanth and Sunquist, 1995; Henschel et al., 2005; Schwarz and Fisher, 2006; Andheria et al., 2007; Chase Grey, 2011; Braczkowski et al., 2012; Selvan et al., 2013), this study used a correction factor established by Ackerman et al. (1984) to calculate biomass consumption; i.e to determine the proportion of meat of a specific prey species in the leopard's overall diet (Andheria et al., 2007). This index was developed based on captive feeding trials of cougars (*Puma concolor*) using known prey of different sizes. Use of this index assumes that the digestive system and feeding habits of leopards and cougars are comparable. The Ackerman Index equation relates the average weight of a prey individual consumed (X) to the total weight of consumed prey represented by a scat in kg (Y):

$$Y = 1.98 + 0.035X$$

This equation can then be applied in the form of the correction factor (Y), to convert frequency of occurrence (F) to relative biomass consumed (D) in order to calculate the proportion of each prey species in leopard diets:

$$D = (F \times Y) / \sum (F \times Y) \times 100$$

Species less than 2 kg were simply multiplied by the average weight of the species to estimate biomass consumed (Ackerman et al., 1984). The average weight for each species was calculated by the PPP using the average weight from trapping data in addition to a number of reference studies conducted in the area.

The identified prey species can be arranged together into different groups depending on their size (weight in kg). By grouping species of similar sizes, it may be determined if leopards preferentially prey upon certain species based on their weight. The following four groups were used to distinguish between species size:

1) Greater than 60 kg (>60) = large,

2) 20-60 kg = medium,

3) 5-20 kg = small,

4) Less than 5 kg (<5) = very small.

The species will also be grouped together into their different taxonomic orders: Artiodactyla (containing Bovidae and Suidae), Primates, Rodentia and Hyracoidea. This will aid in determining which, if any, taxon is the biggest contributor to leopard diets and, hence, most important to them.

4.2.3 Analysis of Scat and Camera Trap Data

Camera images were tagged with their species identification and independent events were extracted using the definition that consecutive images of the same species that are captured more than one hour apart are deemed independent (see Chapter 3.4.1 for further details). These independent trap events were used as an indication of the relative frequency of encounters between leopards and prey species in the area, under the null model of random movement. This likelihood of encounter thus reflects the expected frequency of occurrence in the diet, if the predator has no preferences among prey (arising, for example, from dietary preferences, temporal separation, prey crypsis, etc.).

Selection for the main prey species was assessed using Manly's selectivity index (α) (Manly et al., 1972; Chesson 1983), simplified as:

$$\alpha = \frac{C_x / E_x}{\Sigma\, C / E}$$

C_x indicates species consumption and was calculated by dividing the relative biomass consumed of species x (determined during scat analysis) by the total biomass consumed of all species being investigated.

E_x indicates the encounter rate or availability of the prey and was calculated using both the relative encounter rate (RER) and relative biomass encounter rate (RBER). Both of these were calculated as separate Manly's indices in order to investigate the impact, if any, the inclusion of biomass made on the value attributed to each species.

$$RER = \frac{Photos_x}{\Sigma\, Photos} \qquad RBER = \frac{Photos_x * Weight_x}{\Sigma\, Photos * Weight}$$

whereas

In addition to Manly's selective index, the top five species that occurred in the scats most frequently were compared to the independent trap events for those species to determine if their availability had any impact on the probability of another species being eaten. To do this, bivariate linear interpolation (using the "interp" function in the R package *akima*, which is based on FORTRAN code by Akima (1996)) to determine, for each scat location, the smoothed IERs of the top five prey species, interpolated from the four nearest camera trapping stations.

In order to produce IERs that could be used to compare with presence or absence of a species in a scat, there needs to be enough data in both sets for accurate estimates to be made. To overcome this issue, the five species that occurred most often in scats but were also frequently captured on camera traps were chosen for this set of analyses. This meant excluding dassie as they were not well represented on the cameras and also excluding species such as porcupine, red duiker and warthog as they were not well represented in the diet.

In order to measure the IERs for each of these five species, a small proportion of scat locations (<10%) had to be removed from this part of the analysis as their coordinates were not situated within the vicinity of any camera trap stations (Figure 4.2).
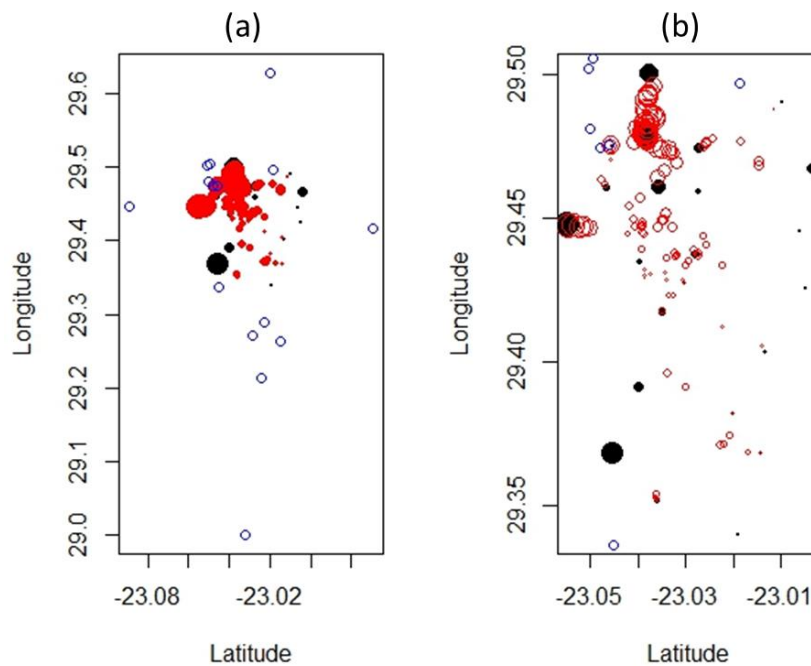
Figure 4.2: GPS positions of camera stations (black), scats within the camera grid (red) and scats outside of the camera grid (blue). (a) shows all outliers, (b) is a zoomed in image of the same data.

Once the IERs were calculated, a binary logistic regression was performed using the function "glm", with function family set to 'binomial'. This regression determines whether the IERs of any of five species helps to explain the presence or absence of a given species in the scat; for example, if the presence or absence of baboon remains in a scat can be explained by the availability of baboon and/or other commonly consumed prey species. The purpose of using more than one species IERs to predict occurrence in a scat is that the focal species' availability might be expected to increase occurrence but, equally, the availability of other common species in the area might be expected to reduce it.

4.3 Results

4.3.1 Dietary Analysis

A total of 162 leopard scats (3,240 hairs) were analysed and contents were identified to species level. Within that total, 112 scats (69.14%) contained a single prey species, 44 (27.16%) contained two prey species and 6 scats (3.7%) contained three. From these 162

scats, 22 different prey species were identified and a total of 217 prey items/occurrences were recorded (Table 4.1). Bushbuck occurred most frequently with a total of 66 occurrences, followed by bushpig with 21 occurrences. Baboon, common duiker, rock dassie, yellow-spotted dassie and vervet monkey all had similar number of occurrences of 12 to 16 scats. Most species were found in various combinations, either as the sole prey species in the scat or with a mixture of one or two other species. Giant rat, Namaqua rock mouse, rock elephant shrew and woodland dormouse never occurred as the only item in a scat. No remains of any other carnivore species were found in the scats, nor were there any livestock or expensive game species present.

Table 4.1: The number of times each of the 22 species was identified in scats containing 1, 2 and 3 items, as well as the total number of occurrences of each species.

Species	1 Item	2 Items	3 Items	Total
Baboon	6	5	3	**14**
Bushbuck	47	17	2	**66**
Bushpig	13	6	2	**21**
Common duiker	6	6	3	**15**
Dassie (rock)	2	13	1	**16**
Dassie (yellow-spot)	6	6	0	**12**
Four striped mouse	1	0	0	**1**
Giant rat	0	1	0	**1**
Grey rhebok	1	0	0	**1**
Impala	2	2	1	**5**
Klipspringer	2	6	2	**10**
Kudu	4	2	0	**6**
Mountain reedbuck	1	1	0	**2**
Porcupine	3	1	2	**6**
Red duiker	5	3	1	**9**
Rock elephant shrew	0	2	0	**2**
Namaqua rock mouse	0	1	0	**1**
Samango	3	1	0	**4**
Vervet monkey	8	6	1	**15**
Warthog	1	5	0	**6**
Waterbuck	1	2	0	**3**
Woodland dormouse	0	1	0	**1**
Total no. of occurrences	**112**	**87**	**18**	**217**

Frequency of occurrence and relative biomass consumption calculations were performed for each of the identified species using Ackerman's (1984) correction factor (Table 4.2). Both

methods rated bushbuck as the most common prey; they were the most frequently eaten prey item (30.4%) and also accounted for the largest proportion of prey items consumed by leopards (31.1%). Dassie species, when combined, were the second most frequent species (12.9%), although they contribute 8.4% of the relative biomass consumed ranking them third after bushbuck and bushpig (13.4%).

Table 4.2: Frequency of occurrence (%), average weight (kg), correction factor and relative biomass consumed (%) for each species identified in the scats, ordered by decreasing frequency of occurrence estimates.

Species	Frequency of Occurrence (%)	Average Weight (kg)	Correction Factor	Relative Biomass Consumed (%)
Bushbuck	30.4	37.5	3.29	31.1
Bushpig	9.7	70.6	4.45	13.4
Dassie (rock)	7.4	3.6	2.10	4.8
Common duiker	6.9	16.1	2.54	5.5
Vervet monkey	6.9	4.8	2.15	4.6
Baboon	6.5	21.3	2.73	5.5
Dassie (yellow-spot)	5.5	3.6	2.10	3.6
Klipspringer	4.6	11.9	2.40	3.4
Red duiker	4.2	11.8	2.39	3.1
Kudu	2.8	199.5	8.96	7.7
Warthog	2.8	68.1	4.36	3.7
Porcupine	2.8	12.2	2.41	2.1
Impala	2.3	47.7	3.65	2.6
Samango	1.8	5.1	2.16	1.2
Waterbuck	1.4	260	11.08	4.8
Mountain reedbuck	0.9	29.2	3.00	0.9
Rock elephant shrew	0.9	0.7	N/A	0.7
Grey rhebok	0.5	21.5	2.73	0.4
Giant rat	0.5	2.9	2.08	0.3
Namaqua rock mouse	0.5	0.2	N/A	0.2
Four striped mouse	0.5	0.1	N/A	0.1
Woodland dormouse	0.5	0.1	N/A	0.1

It is clear from Table 4.2 that Ackerman's correction factor changes the estimates associated with each species; larger and heavier species such as bushpig and waterbuck have higher relative biomass consumed proportions than the frequency of occurrence calculations. Smaller species such as the rodent and dassie species were apportioned lower values for

relative biomass consumed than they would have been without the correction factor. Incorporating body size can change the importance of each estimate (Figure 4.3).
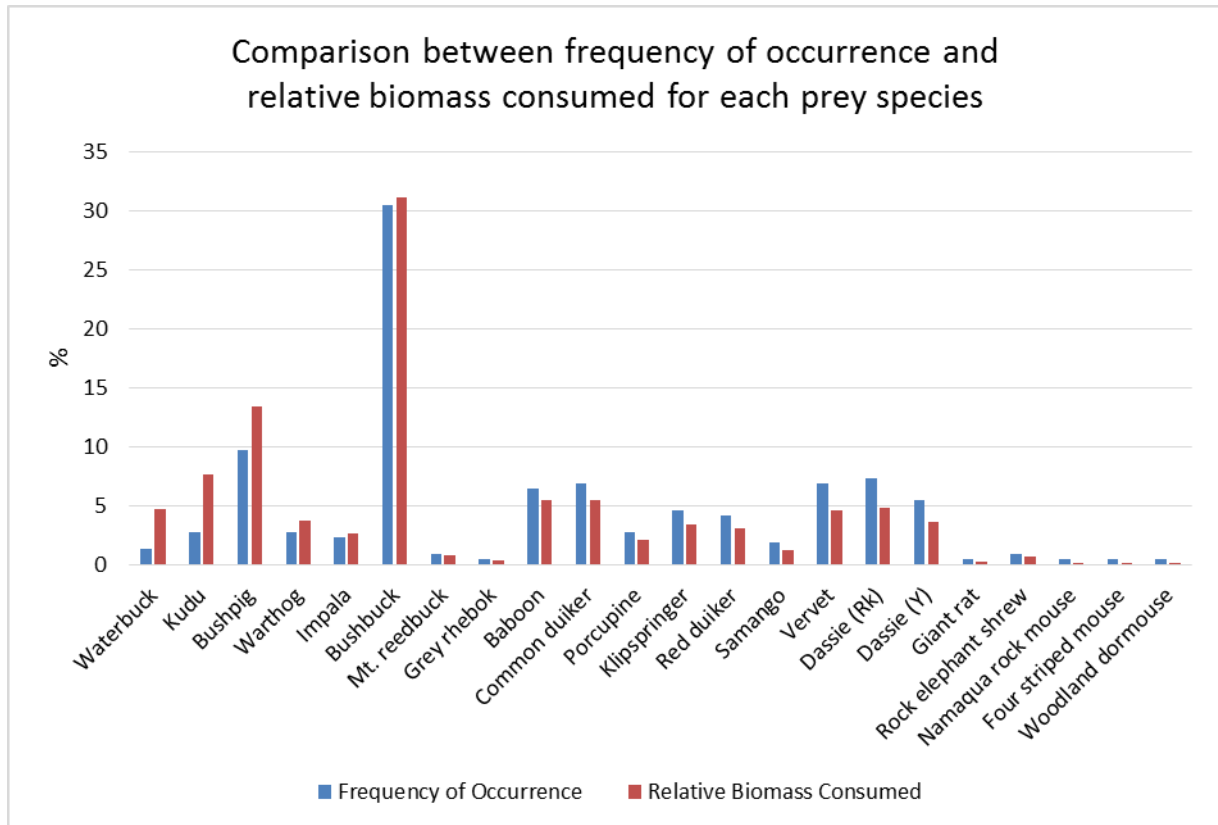
Figure 4.3: Comparison between frequency of occurrence estimates (blue) and relative biomass consumed estimates (red) for each species in order of decreasing weight.

The medium sized 20-60 kg group contributes the highest proportion to both estimates of frequency of occurrence and relative biomass consumed, and the small 5-20 kg group contributes the least (Figure 4.4). However, in terms of frequency of occurrence, the second most frequently preyed upon group is the very small <5 kg group, whereas the group with the second highest biomass consumption is the large >60 kg group.
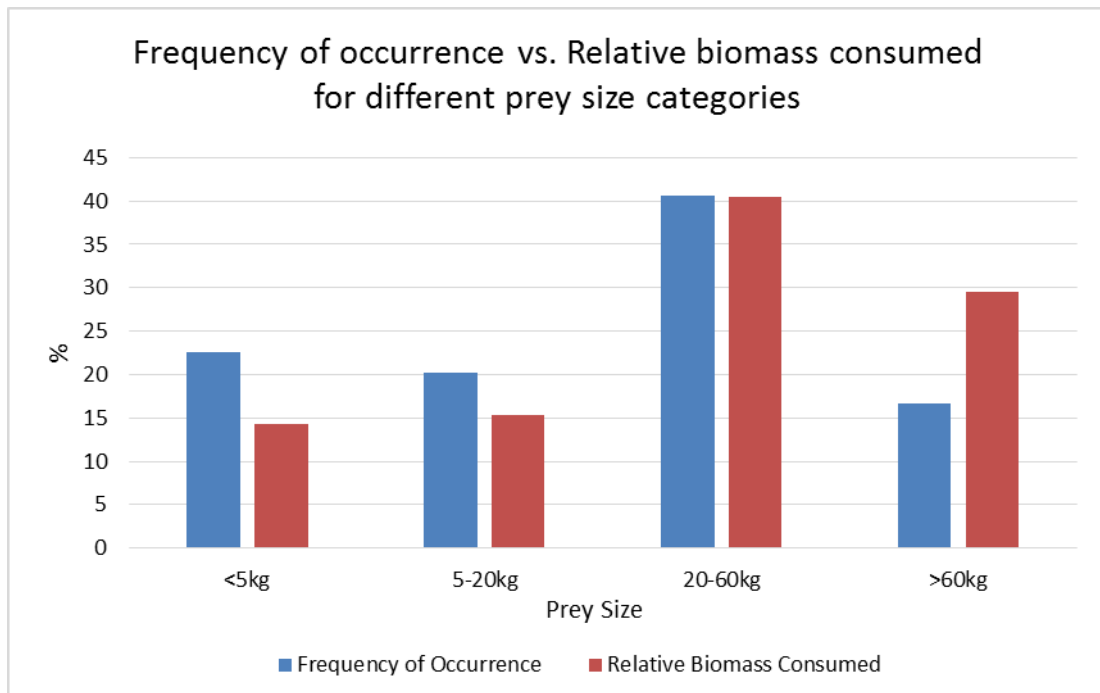
Figure 4.4: Percentage frequency of occurrence (blue) and relative biomass consumed (red) for each of the 4 prey size categories; <5 kg, 5-20 kg, 20-60 kg and >60 kg.

Artiodactyla, represented by Bovidae and Suidae, contribute the most to leopard diets, with 76% of consumed prey biomass being within this Order. Each of these families contribute 59% and 17%, respectively, to the relative biomass consumed by leopards. The Primate Order accounts for the third highest percentage of relative biomass consumed at 11%, Hyracoidea have similar proportions consumed at 9% and Rodentia only made up 4%.
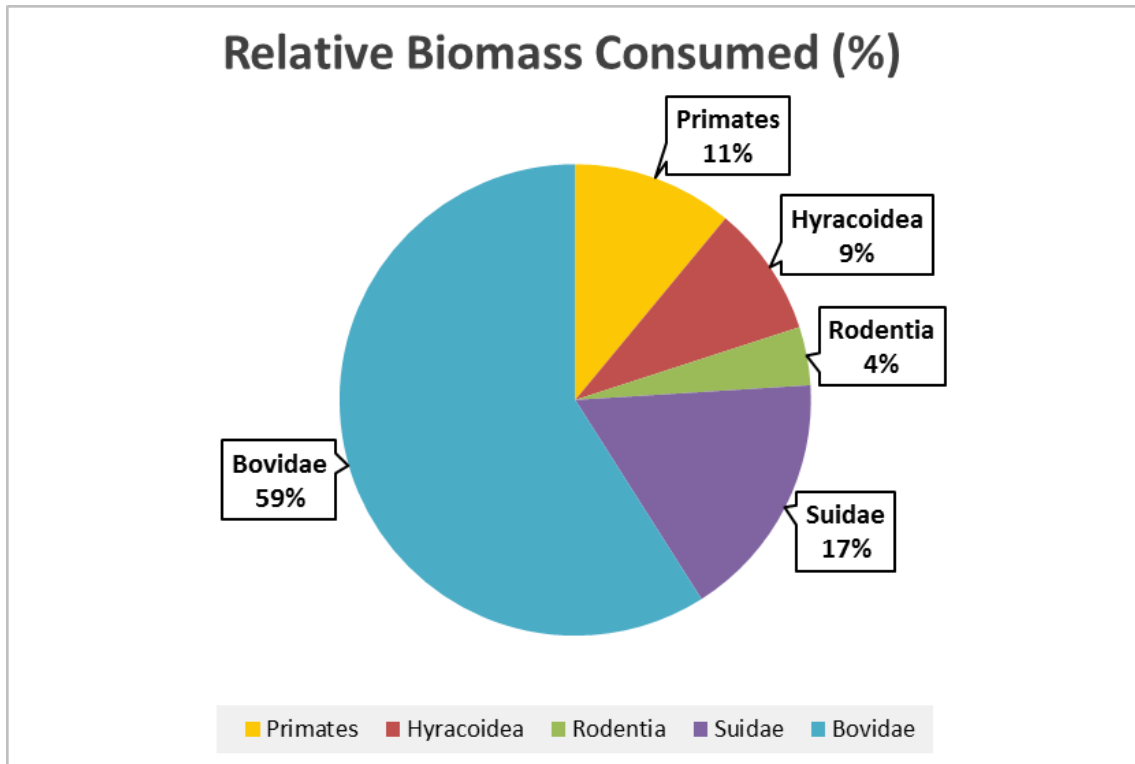
Figure 4.5: The relative biomass consumed of each of the four Orders; Artiodactyla (represented by Bovidae and Suidae), Hyracoidea, Primates and Rodentia.

4.3.2 Comparison with Camera Trap Data

A total of 32 potential mammalian prey species were recorded by the camera traps in this study. Most rodent species such as rats, mice and shrews, as well as hares and mountain reedbuck were all recorded less than 10 times. Bushbuck were the most abundant species in terms of camera trap events, with a total of 1936 events recorded during the study. Porcupine and baboon also had camera events numbering over 1,000 (Table 4.3). Individual dassie species were combined under the label of "Dassie".

Table 4.3: Prey species with over 100 independent trap events.

Species	Total no. of independent photos
Bushbuck	1936
Porcupine	1519
Baboon	1193
Red duiker	500
Warthog	438
Bushpig	361
Domestic animal	311
Kudu	227
Vervet monkey	225
Aardvark	152
Common duiker	143
Dassie	122

Manly's selectivity index values were assessed for the most commonly occurring species in both leopard diet and on camera. Although dassie fit into these criteria, their capture rate on camera traps is likely to be inaccurate due to the bias in camera location and so they were not included. Therefore, the nine species investigated were baboon, bushbuck, bushpig, common duiker, kudu, porcupine, red duiker, vervet monkey and warthog (n=9). As n=9, a value of $\alpha<0.11$ indicates the species is eaten less than expected and $\alpha>0.11$ indicates the species is eaten more than expected. Table 4.4 gives the consumption rate and encounter rates for each species, as well as the corresponding Manly's α value for both variations (biomass of prey included and biomass not included). It is clear from this table that the inclusion of biomass results in a difference to the α values of the larger species such as bushpig and kudu, changing their consumption from being eaten more than expected to less (0.228-0.060 and 0.186-0.017 respectively), but the other species remain within the same selectivity range. However, it could be argued that biomass was already included when calculating consumption rate and therefore does not need to be accounted for again in the encounter rate. Also, a proportion of the species that occurred in scats may have been juveniles and so inclusion of biomass when calculating the encounter rate may cause distortions. For these reasons the results of the standard α value, without biomass, will be used for interpretation of this study.

Table 4.4: Consumption rate (C), relative encounter rate (RER) and corresponding α index, and relative biomass encounter rate (RBER) and corresponding α index for each of the nine species.

Species	C	RER	α	RBER	α (Biomass)
Baboon	0.071	0.182	**0.028**	0.110	**0.025**
Bushbuck	0.406	0.295	**0.099**	0.313	**0.049**
Bushpig	0.175	0.055	**0.228**	0.110	**0.060**
Common duiker	0.071	0.022	**0.235**	0.010	**0.272**
Kudu	0.100	0.039	**0.186**	0.219	**0.017**
Porcupine	0.027	0.231	**0.008**	0.080	**0.013**
Red duiker	0.040	0.076	**0.038**	0.025	**0.060**
Vervet monkey	0.060	0.034	**0.126**	0.005	**0.490**
Warthog	0.049	0.067	**0.053**	0.129	**0.014**

These α results (Table 4.4) indicate that bushbuck and vervet monkeys are the only species that are eaten about as much as is expected based on their encounter rates in the area (α=0.099 and 0.126, respectively). Baboon, porcupine, red duiker and warthog are all eaten less than expected and bushpig, common duiker and kudu are eaten more than would be expected.

The five prey species chosen for the IER analyses that occurred frequently in scats and also had a high number of capture events were baboon, bushbuck, bushpig, common duiker and vervet monkey. Domestic animals were also included as a variable in the regressions to determine if their presence caused the frequency of any natural species in a scat to decline. As no domestic animal remains were found in scats, this variable could only be used in terms of investigating the effect they may have on natural prey, and not the other way around.

Table 4.5: Main results of the IER regression analysis including the best model and corresponding p-value significance

Species	Best Model Variables	p-value
Baboon	Bushbuck (-0.012)	0.034
Bushbuck	Null Model	0.032
Bushpig	Common duiker (-0.057)	0.109
	Vervet monkey (0.063)	0.093
Common duiker	Bushbuck (0.008)	0.087
Vervet monkey	Bushbuck (0.013)	0.006

No species had an effect on the presence of bushbuck in a scat with the null model being the best model (Table 4.5). The IERs of bushbuck had effects on the probability of baboon, common duiker and vervet monkey being present in a scat. Bushbuck had a significant negative effect on the probability of baboon being in a scat, meaning the more bushbuck events in an area, the less likely it is to find baboon in a scat there. Bushbuck event rates had a positive relationship with both common duiker and vervet monkey, although only the latter was significant. For bushpig, both vervet monkey and common duiker event rates had an effect on the probability of bushpig occurring in a scat, although neither were significant.

4.4 Discussion

A total of 22 mammalian prey species were found in this analysis of leopard scats. This is similar to a study of leopard diets in the Cederberg Mountains (Martins et al., 2011) where 23 species were recorded, but almost double the number recorded by previous studies in the Soutpansberg area by Schwarz and Fisher (2006) and Chase Grey (2011), who found 13 and 12 species respectively. Schwarz and Fisher (2006) hypothesised that the low number of prey species they recorded may be due to the extermination by man of typical prey species recorded in other regions. However, of the 22 species recorded in this study, 21 of them occur naturally in the Soutpansberg area; impala was the only species preyed upon that has been reintroduced by private reserves. To compose 95% of prey occurrences in the analysed samples, over half of the species (15 out of 22) need to be taken into account, indicating a broad diet in which no prey species majorly dominates. With that said, Artiodactyla species were most commonly consumed, with bushbuck in particular being the biggest contributor to leopard diet (approximately a third of species occurrences) indicating that these species are of high importance to leopards.

Medium sized species within the 20-60 kg range contributed most to the relative biomass consumed by leopards but species outside of this range were still frequently consumed, revealing the opportunistic hunting approach of leopards in this region. No evidence of any livestock species was found in any of the scats, indicating that livestock depredation is much lower than landowners perceive. Warthog, red duiker, baboon and porcupine were consumed less than expected based on their relative encounter rates, while common duiker, kudu and bushpig were eaten more than expected. These consumption rates could be a result of the

risks associated with hunting specific species, but temporal partitioning of activity between prey and leopards may also play a significant role.

The findings of the scat analysis are discussed in more detail in the following section, followed by a discussion of the comparison between camera trap and scat data. The implications of these results in terms of human-wildlife conflict are also outlined. Finally, the concluding section of this chapter brings together the major findings of this analysis in a summary of leopard diet in this study region.

4.4.1 Leopard Diet

This study found that bushbuck was represented most frequently in the scats, followed by bushpig, rock dassie, common duiker, vervet monkey and baboon. This result is similar to previous studies in the area (Schwarz and Fisher, 2006; Chase Grey, 2011) who found bushbuck to be the most commonly consumed prey, albeit at higher proportions, followed by dassie, vervet monkey and common duiker. Davies-Mostert et al. (2010) encountered issues with differentiating between bushbuck and kudu hair cross-sections, but these species were successfully identified in this study.

Bushbuck are considered one of the most important prey species for leopards in the Soutpansberg Mountains (this study) and globally (Hayward et al., 2006), so the results of this study are not surprising. Female bushbuck often leave their offspring alone in clumps of thicket or bush for long periods of time, only returning to feed them (Wronski et al., 2006a). This, combined with the evidence that there are a lot of bushbuck in the area, might account for the high predation rate by leopards. However, bushpig have not previously been recorded as a big contributor to leopard diet. Hayward et al. (2006) suggested two reasons for bushpig being hunted less frequently than expected based on their abundance: (i) bushpig exceed the preferred weight range of leopard prey (10-40 kg) and (ii) bushpig have an ability to inflict serious injury on any opponent. Bushpig have a reputation for being highly aggressive and unpredictable (Kennedy and Kennedy, 2014), particularly when they have piglets. Their tusks can cause serious injury which can have fatal implications for solitary hunters like leopards. It is possible, nonetheless, that some individual leopards adapt hunting strategies that allow them to prey upon these high risk species with minimum risk of injury. Prey specialization by individuals within a population is not uncommon in populations (Araújo et al., 2011), but

given the high occurrence of bushpig in the scats of this study, it is unlikely that a single specialised individual is responsible for all of the scats found.

It may be that the majority of bushpig killed in this study were juveniles, which would be smaller and present less risk for leopards. However, Henschel et al. (2005) found that red river hog, a close relative of bushpig, made up the largest proportion of biomass consumed by leopards in Central Africa, indicating that for some leopards at least, these large, dangerous prey are not a problem. While bushpig occurred quite frequently in leopard diet, warthog only occurred six times throughout the scat analysis despite similar body sizes and risks of danger for these prey species. Perhaps there are differences in the behaviour of these species that result in one being preyed upon more than the other, such as activity at different hours or in different habitat types. A possible explanation may be that previous studies have found bushpig are active late at night (Seydack, 1990), whereas warthog are diurnal (Somers, 1997). If similar patterns of activity are displayed by these species in the Soutpansberg then this may explain the difference in predation levels between the two species (chapter 5 will investigate this hypothesis further).

When prey were grouped into four different weight categories, the medium sized group 20-60 kg contributed most to the relative biomass consumed which is in agreement with previous studies (Schwarz and Fisher, 2006; Chase Grey, 2011; Selvan et al., 2013) who all found medium sized prey occurred in scats most often. The large >60 kg group were the next highest consumed group which was less expected based on results of previous studies who suggest that species weighing over 45 kg are avoided (Clements et al., 2014) or that species over 20 kg were rarely taken due to them being rarer, more dangerous or difficult to hunt and because there is a high profitability attached to consuming smaller prey (Ray and Sunquist, 2001). Very small species <5 kg were ranked as the lowest contributors to biomass consumed. While there are prey of varying sizes in this study area, results indicate that leopards may prefer to prey upon those species that are between 20-60 kg most often. However, they are also opportunistic hunters and will readily consume any species they come across, regardless of size, as indicated by the notable consumption of other species outside of this range. When looking at the groups in terms of frequency of occurrence, the ranking order changes. Many previous studies (Ray and Sunquist, 2001; Schwarz and Fisher, 2006; Chase Grey, 2011, Selvan et al, 2013) used frequency of occurrence estimates, which ranked the very small species quite high. However, if relative biomass consumed estimates had been

used their results would probably have been closer to those reported here. It is understandable that prey over 60 kg would contribute a larger proportion to prey biomass consumed by leopards than very small species, especially if eaten in similar quantities, as was the case here. Taking account of the conclusions of Henschel et al. (2011), that predation on species much lower than the preferred weight range is an early indicator that the population may be at risk of extinction, it is a good sign for leopard conservation that species over 20 kg make up the majority of the biomass consumed by them in the Soutpansberg.

When comparing the various taxonomic orders consumed, ungulates (Artiodactyla) made up the majority of relative prey biomass consumed, with primates and dassies (Hyracoidea) having lower proportions. This is similar to previous studies (Hart et al., 1996; Henschel et al., 2005; Hayward et al., 2006; Schwarz and Fisher, 2006) where ungulates were recorded as making up the largest proportion of biomass consumed, followed by primates. Some studies have also recorded rodents as contributing a substantial amount to leopard prey (Ray and Sunquist, 2001; Henschel et al., 2005; Selvan et al., 2013), however, this is not the case here, perhaps due to the high availability of larger prey that would be more beneficial for leopards to hunt. Larger prey contain more meat, and therefore, more energy than a smaller species would, thus the energy expended finding and killing prey is outweighed by the higher proportion of energy gained when a larger species is consumed.

4.4.2 Scat and Camera Trap Data

Based on camera trap images, bushbuck were the most available species at Lajuma with the highest encounter rate recorded at almost 2,000 camera events. This high availability of prey that not only lies within the preferred prey weight range for leopards but is also relatively easy to hunt, i.e. has no dangerous defence mechanisms, may explain why leopards consume bushbuck as often as they do.

Porcupine were the second most available species in this study. Kittle et al. (2014) found the Indian porcupine to be represented most frequently in their study of leopard scat. However, while there were a small number of porcupine occurrences in the scat of this study, they did not occur in scats as often as would be expected from their high abundance in the area. This is most likely due to them being dangerous prey to hunt, as their body of sharp quills could cause serious injury to a leopard.

Red duiker and warthog were among the top five most available species in the camera trap data but were not consumed as frequently as would be expected, based on the camera data. This is interesting as common duiker and bushpig, which are similar species respectively, are consumed much more often, even though they have lower numbers of camera recordings. Common duiker and red duiker are of a similar size, as are bushpig and warthog, so there is no obvious reason why the species that are encountered less often would be consumed more often. Investigation into the species activity patterns (Chapter 5) may provide explanations for these differences in consumption rates.

Baboons have long been considered preferred prey of leopards but in this study, baboons were preyed upon less than expected based on their encounter rates (availability). Baboons are known to defend themselves by cooperative mobbing and group vigilance during the day (Jooste et al., 2012), therefore leopards tend to hunt baboons during the night, when they try to escape by climbing to outer branches rather than actively defending themselves (Busse, 1980; Bailey, 1993). It would seem that, in Lajuma, while leopards may be the main predator of baboons, they do not preferentially prey on them. Adult male baboons are particularly aggressive, with retaliation often resulting in the death of the leopard (Jooste et al., 2012). Considering this potentially lethal risk, it has been suggested that leopards will only hunt baboons when other prey is scarce (Hayward et al., 2006). However, as with bushpig, there is evidence that leopards in this study have learnt to catch and kill dangerous prey resulting in these species forming a more noticeable part of their diet. That vervet monkeys were consumed in proportion to their expected availability may be explained by the fact that, though primarily arboreal species, vervet monkeys spend time on the ground, particularly during the day. However, being primarily arboreal, vervet monkeys may not be captured on the camera traps as often as they should be. This may have, potentially, led to a lower number of independent events for vervet monkeys which would in turn indicate that their selectivity value may deviate from reality.

Despite a strong presence of domestic animals in the study area, none were found in the scats analysed. This supports previous conclusions made (Selvan et al., 2013; Marker and Dickman, 2005) that if there is a high abundance of wild prey available, leopards will not hunt livestock. Kudu were eaten more than expected based on their availability in the area as recorded by the camera traps, however their actual frequency of occurrence in scats was still relatively low. This is possible due to their size. They weigh an average of 200 kg which is

way beyond the prey preference range estimated by Clements et al. (2014) of 15-45 kg, and even outside of the range 30-175 kg suggested by Karanth and Sunquist (1995) for leopards in tropical forest. It is possible that the kudu identified in the scats may have been calves or juveniles which would weigh less and be easier to hunt, or they could have been scavenged.

Of the species whose Independent Event Rates (IERs) were calculated, none had any effect on the probability of bushbuck occurring in a scat. These results were unexpected as they indicate that the occurrence of bushbuck themselves at a site had no effect on the probability of them being in a scat although, like leopard occupancy in the previous chapter, bushbuck occurrence may be relatively even throughout the study site making statistical relationships unlikely. Bushbuck event rates, and therefore abundance, had a negative effect on the probability of baboon occurring in a scat indicating that in areas where there were a lot of bushbuck, baboon were less likely to be consumed and therefore be present in a scat. One reason for this may be that, as previously discussed, baboons can be dangerous animals to prey upon and if bushbuck, who are easier to hunt, are in the area they may be preferred over baboon. Domestic animals were found to have no effect on the probability of any of the five tested species being in a scat indicating that their presence in an area has no influence on the selection of natural species by leopards. The relationships between all of these species are not fully understood from this study, but are interesting none the less. More research on this is needed in the future in order to determine more clearly the effect other species' abundance may have on a particular species being preyed upon. It is important to note that there is always the possibility of uncertainty with collected data, however the large scat sample size used in this study reduces this possibility.

Klipspringer and dassie were both consumed frequently by leopards but results of the camera trapping imply that they are not common in the study area. This is not a realistic conclusion, however: cameras were set up to capture images of leopards and so smaller animals or animals that occur in difficult-to-reach terrain would not be recorded as often as they might be. It may be that both klipspringer and dassie are more abundant in the area than camera traps would suggest, as they are both species known to live in mountainous and rugged regions, but the cameras were not set up in locations that were preferable to these species. Their frequency in leopard scat supports this idea. However, camera trap locations along trails and roads decreased the number of events captured for these species, making it difficult to compare their consumption by leopards to their abundance in this case.

If a species is killed relatively more frequently than it exists in then it is considered preferred, whereas if it is taken less frequently it is avoided (Hayward et al., 2006). Based on this statement, aardvark and domestic species seem to be avoided even though they were common in the area. The results of this study highlight the fact that while leopards consumed a large range of species, not all available prey was taken. Since the number of camera events provide an indication of the relative encounter rates of each prey species at the study site, it suggests that there is a strong and diverse range of prey species within the Soutpansberg Mountains. This high availability of prey species may directly affect the numbers of leopard in the area, supporting and enabling the high density of leopards that have been recorded here to survive.

4.4.3 Implications for Human Conflict

Leopards have been shown to have lower survival rates in non-protected areas than in protected areas (Swanepoel et al., 2014). This lower survival rate was mostly the result of human-related mortality driven either by carnivore conflict or demand for trophies and skins (Balme et al., 2012). This assessment of leopard diet may help to mitigate human conflict in the non-protected Soutpansberg Mountains, as many local farmers persecute leopards in the belief that they pose a threat to their livestock. A study in the Eastern Cape of South Africa showed that less than 5% of the leopard's diet was composed of domestic animals (Ott et al., 2007). Similarly, studies on leopard diet conducted in the Soutpansberg Mountain region in the past have found no evidence of domestic animal during scat analysis (Stuart and Stuart, 1993; Schwarz and Fischer, 2006; Chase Grey, 2011). Despite this, local livestock and game farmers still believe leopards are to blame for missing or dead animals.

Scat analysis in this study provided clear and unbiased evidence of no livestock being consumed by the leopards at Lajuma and the surrounding properties. This is despite the fact that three of the properties in the study area actively farm cattle on their land. This is in accordance with other studies on leopard diet in mountainous regions (Stuart and Stuart, 1993; Schwarz and Fisher, 2006; Chase Grey, 2011; Martins et al., 2011). However, while there were cattle on farms adjacent to the study site used by Schwarz and Fisher (2006), the actual study area did not include any cattle farms which may have contributed to the lack of livestock in their scat analysis. In contrast, many studies have found that domestic animals

make a significant contribution to leopard diet, particularly when they are outside of protected areas (Seidensticker et al., 1990; Edgaonkar, 1998; Thorn et al., 2012).

Despite the evidence that this study, and others, provide on the lack of livestock in leopard diets in the Soutpansberg, camera images from the PPP have recorded leopards preying on livestock in the area, albeit at very low levels. This indicates that local landowners' perception of leopards as a threat to their animals and the retaliatory killings recorded in the area (Chase Grey, 2011) are not without reason. It also indicates that analysis of 162 scats may be insufficient to pick up rare species in the diet of the leopards in this region. This low level of livestock predation does not justify the high level of leopard kills or injuries (e.g. from snares). Even though results of these studies should aid in combatting the perception of landowners, often facts are not enough to change people's beliefs. Rather than trying to convince local landowners that leopards are not as big a problem as they think, aid and advice could be given on how to improve livestock husbandry and engage in non-lethal techniques such as such as the use of shepherds, guard dogs and/or bomas (Ogada et al., 2003; Woodroffe et al., 2007) to prevent predation. This would not only give landowners peace of mind but would also help to reduce the number of livestock being taken by any carnivore species. Increasing the use of non-lethal techniques would also ensure that local people can continue to gain from the benefits associated with leopards and other predators, such as ecotourism.

The only game species found in this diet analysis of leopards were impala. There is one private game reserve used for ecotourism in the study site. These species would have been introduced to the private farm, as they no longer occur naturally in the region. Impala amounted to a small proportion of the relative prey biomass consumed by leopards, and much rarer and expensive game species such as sable were not present in the diet at all, suggesting that the wild, natural prey available throughout the region is sufficient to prevent leopards entering private game farms where they may be met with hostility from landowners.

Studies have suggested that if wild ungulate prey is abundant then predators such as leopards will not take livestock (Marker and Dickman, 2005; Selvan et al., 2013). However, their broad, flexible diet means that they can easily switch to hunting domestic animals when their natural prey has been depleted. Camera trap data in this study show that there was an abundance of domestic animals in the area that leopards could potentially prey upon. But similarly, there is also a plentiful and varied source of natural prey for the leopards in the

Soutpansberg, reducing their need to hunt livestock and private game species, as confirmed by scat analysis.

4.4.4 Conclusions

The main conclusions of this study are:

1) Baboon, porcupine, red duiker and warthog are all preyed upon less than expected based on their encounter rates,

2) Bushbuck are not only the most available species in the Soutpansberg in terms of their encounter rates, but also the top prey species for leopards,

3) Species belonging to the Artiodactyla taxa make up the majority of species consumed by leopards in the area,

4) Medium sized prey between 20-60 kg are the most commonly consumed prey,

5) There is no evidence of livestock consumption in any of the scat samples analysed.

This study provides vital information for future conservation work in the Soutpansberg as being able to identify which species leopards consume most frequently enables the availability of these key prey species be monitored and maintained; a crucial factor for the survival of any large predator (Clements et al., 2014; Lyngdoh et al., 2014). Thus, dietary analysis of this study will not only aid in conserving leopards but also their natural prey populations and, therefore, the ecosystems of the mountain as a whole. The availability and high encounter rates of various prey species in this study area, along with the evidence from scat analysis that leopards consume a wide range of these species, suggests that prey populations in the Soutpansberg are thriving, which enables a high density of leopards to survive in this region. Maintaining these prey populations will not only enable a growing density of leopards to survive here, they will also aid in keeping livestock consumption down, which in turn will reduce leopard conflict with humans. Scat analysis also suggests that while bushbuck are most commonly consumed, leopards will consume a variety of prey whenever the opportunity arises. Indeed, some leopards appear to have the skills necessary to hunt dangerous species. The fact that no occurrences of any livestock species were recorded in the scats of leopards in the area provides important data for mitigating the conflict between local farmers and leopards. With the support from landowners living in and around the area, the

Soutpansberg Mountains may truly become a significant non-protected area of conservation for leopards in South Africa.

Chapter 5 - Activity Patterns

5.1 Introduction

Predator-prey interactions affect virtually every animal on the planet and play important roles in shaping species' evolution. Predation is one of the most common causes of mortality (Penteriani et al., 2013) and predators depend on their hunting success to survive. Predator-prey interactions are extremely complex as they are determined by a number of elements such as individual characteristics (e.g. physiology, health), external factors (e.g. weather, seasons) and properties of both the predator and prey populations (e.g. spatial and temporal distribution of individuals) (Penteriani et al., 2013). Continuous arms races are ongoing between predators and their prey, resulting in predator and anti-predator adaptations (Eriksen et al., 2011) that have deeply influenced the evolution of such species. Successful anti-predator adaptations result in a selection for predator traits that can evade such prey defence behaviour (Vermeij, 1994). An example of such an adaptation is temporal partitioning, where prey may change their activity pattern in response to their main predator's activity in order to avoid predation. A predator may then alter their activity to coincide with the activity of their prey, in order to maximise their hunting efficiency. Put simply, predators seek to increase their access to prey by being active at the same times as their prey, while prey seek to minimise their chances of being eaten by reducing their activity overlap with predator activity patterns.

Prey availability and dietary specialisations are important factors structuring a predator's activity pattern (Monterroso et al., 2013). For example, a predator that specialises in hunting a specific prey species should try to synchronise its activity pattern with that of its main prey. On the other hand, a generalist predator that hunts a number of different species may only follow any particular species' activity to a certain level as there will be alternative prey options available. It has, therefore, been suggested that predators only track prey activity so far, until they reach a point where the trade-off between predation success and the energetic intake from consuming the prey is ample enough to fulfil its biological needs (Monterroso et al., 2013). Put simply, a predator can only afford to track and hunt a specific prey individual for a certain amount of time before the energy spent hunting will outweigh the energy gained from consuming the animal. When this threshold is reached, there is no benefit in continuing to track this individual. Prey species, too, have to balance between trading factors such as

optimal feeding opportunities and finding mates, with avoiding encounters with predators (Ross et al., 2013).

Many studies provide evidence to support the hypothesis that predators synchronise hunting activity with periods of activity of their principal prey species (Ramesh et al., 2012). Jenny and Zuberbühler (2005) found that leopards in West Africa mirrored the activity patterns of their main prey, which varied throughout different regions. Similarly, Kawanishi and Sunquist (2004) found that tigers in Malaysia were mainly diurnal and, therefore, in phase with the activity patterns of their principal prey species. However, not all predators synchronise their activity periods with those of their prey. Lions are mainly nocturnal hunters, but they depend on prey species that are diurnal, such as zebra and wildebeest (Mills and Shenk, 1992). As an example of prey shifting their activity patterns to avoid predators, Ross et al. (2013) discovered that bearded pigs were diurnal in areas where clouded leopards, their main predator, occurred but in the absence of clouded leopard, bearded pigs were almost exclusively nocturnal. This suggests that whilst it may be more efficient for bearded pigs to be active during the night, they change their patterns of activity to be active during the day to avoid the nocturnal clouded leopards, hence, it would seem that the expenditure of energy from moving and foraging during the high temperatures of the day is outweighed by the lower risk of predation. Furthermore, increased predation pressure exerted by diurnal weasels encouraged more nocturnal activity of the voles (Gliwicz and Dabrowski, 2008), while the usually nocturnal rats in a study by Fenn and Macdonald (1995) showed more diurnal activity to avoid nocturnal red foxes.

Chapter 4 used dietary analyses to identify that some species were preyed upon more or less than expected, based on their availability in the study area. To explore the extent to which these patterns arise as a result of temporal partitioning of activity, the activity patterns of leopards and their main prey will be investigated. By determining activity patterns of prey species in relation to leopard activity, it is hoped that they will provide an important insight into why leopards prey on one species rather than another, very similar, species. This, in turn, may aid in explaining the high density of leopards found at the study site and the role prey populations play in leopard conservation. In addition, understanding when, and why, leopards are active at particular times will add to the understanding of leopard ecology in the Soutpansberg Mountains and assist in possible future conservation initiatives involving leopards in this particular region.

5.1.1 Leopard Activity

Many animals follow cyclic patterns of activity that are regulated by external factors such as weather, seasons and day length (Nouvellet et al., 2012). In areas with multiple predators, it is common for subordinate predators to alter their activity patterns to avoid competition with the dominant species (Cozzi et al., 2012). Small carnivores may themselves become prey for the larger species, or may suffer harassment or injury that will affect their hunting abilities (Mukherjee et al., 2009). There is a general belief that leopards are mostly nocturnal predators (Sunquist and Sunquist, 2002), but various studies have reported conflicting results on leopard activity patterns which suggest that leopard activity can vary greatly depending on their location and the behaviour of their prey and competitiors. Sunquist and Sunquist (2002) noted that in areas that lack inter-specific competitors like lions, leopards tend to be more diurnal, while in areas with a strong human presence, leopards tend to be nocturnal. However, Martins and Harris (2013) contradict the findings of Sunquist and Sunquist (2002); they found that leopards in an area with no competing predators and low human impact were still nocturnal.

Leopards in the Kalahari spend the daytime hours resting and are active mainly at night (Bothma and Bothma, 2006), while forest leopards are diurnal and crepuscular, following the activity patterns of their prey (Jenny and Zuberbühler, 2005). In mountainous environments, Norton and Henley (1987) found that leopards in the Cederberg Mountains were diurnal with peaks of movement in the late morning and early evening, whereas Martins and Harris (2013) reported leopards in the same region as being predominantly nocturnal. Similar to Martins and Harris' (2013) findings, leopards in the Waterberg Mountains were also nocturnal (Pitman et al., 2013). It will be interesting to determine how the leopards of this study behave in the mountainous environment of the Soutpansberg, as they do not suffer from inter-specific competition or harassment from larger predators here, but there is a strong and persistent human presence in the area which they may be pressured to avoid.

5.1.2 Prey Activity

Many studies of leopards assume that they are active at a particular time of day based on the species of prey they consume most often, despite not having conducted any activity pattern analysis to confirm this (Norton and Henley, 1987; Stuart and Stuart, 1993; Schwarz and Fisher, 2006; Chase Grey, 2011). For example, a high frequency of diurnal species such as

dassie or small antelope in the diet of leopards in these studies was assumed to indicate that leopards must also be diurnal. However, the leopards in the Soutpansberg preyed upon a large range of species, 22 in total (Chapter 4.3.1), all of which have their own varying patterns of activity. Therefore, in order to gain a better understanding of why some species are preyed upon more often than others, their specific activity patterns need to be examined and compared to that of leopards to determine the degree to which the activity patterns overlap.

The results of leopard dietary analysis in Chapter 4 suggest some degree of prey selection, for example some species, such as bushpig and common duiker, were consumed more than expected, while others, such as warthog and red duiker, were consumed less than expected. Bushpig were found to be the second most frequent prey of leopards in this study, as well as contributing the second highest relative biomass consumed. Bushpig have been found to be active during both early morning and late at night in order to avoid extreme daytime temperatures (Seydack, 1990). Therefore, there is a high chance that leopards would encounter bushpig at some point during a 24-hour period. Warthogs belong in the pig family, Suidae, along with bushpig. They are of similar size and both species possess dangerous tusks. Warthog, however, were preyed upon much less frequently than bushpig in this study. A key reason for this could be that warthog have been recorded as crepuscular (Hayward and Slotow, 2009) or diurnal species (Somers, 1997). This difference in activity between the two species may explain the high levels of predation of bushpig but not warthog. Common duiker have been recorded as active during both day and night, whereas red duiker are considered to be diurnal (Estes, 1991). Like bushpig and warthog, this could be a reason for the more frequent consumption of common duiker than red duiker.

This analysis will look at the activity of abundant species in the area, some of which are consumed by leopards more or less than others, despite having similar characteristics (as outlined in above examples). By looking at the activity patterns of such species and comparing them to leopard activity, it will become clear how some prey species may avoid predation through temporal partitioning and, thus, shed some light on the reasons behind the suggested prey selection indicated in the dietary analysis.

5.1.3 Methods for Studying Activity

Previous studies on leopard activity largely use satellite tracking (Bothma and Bothma, 2006) radio transmitters (Karanth and Sunquist, 2000; Jenny and Zuberbühler, 2005; Odden and Wegge, 2005) or GPS collars (Pitman et al., 2013) as the sole method for determining the activity pattern of the species. Due to the expense and effort required to use these devices, the number of individual leopards actually investigated in each of these studies was often quite low. Few studies to date have used camera trapping as a means to determine leopard activity patterns (Azlan and Sharma, 2006; Martins and Harris, 2013). Though they are still expensive, camera traps have the potential to become a popular method for studying activity patterns of various species (O'Connell et al., 2011), as they are not solely associated with one particular individual like, for example, GPS collars are. Camera traps can uncover patterns arising from predator-prey interactions by detecting species that are active in the same areas and recording their behaviours and times of activity (Lazenby and Dickman, 2013). With camera traps, an entire animal population can be captured photographically, rather than a limited number of individuals that may be captured physically, leading researchers to come closer to population level assessment of activity (Bridges et al., 2004). Camera traps can record multiple species, at a number of sites simultaneously over a long period and provide the opportunity to study temporal patterns at camera sites by stamping photos with the date and time that the image was taken. It has been said that recording behavioural data using the time given by a clock may generate errors compared with the real time of events, as given by the position of the sun in the sky (Nouvellet et al., 2012). However, studies that use data grouped into periods, such as seasons, avoid this timing problem.

Based on the advantages of the use of camera traps for studying activity patterns, this study will determine the activity pattern of leopards and various prey species using camera trap data.

5.2 Methods and Analysis

The data used for this analysis came from the forty-eight cameras set up at 24 stations around Lajuma and neighbouring properties over an area of 60 km^2 (Chapter 2.3). Using the date and time of independent photographs in this study, defined as images of the same species captured more than one hour apart, or consecutive images of different species (see Chapter 3.4.1 for further details of camera trap data analysis), the activity patterns of leopards, prey

species and humans were determined using techniques developed for circular data. Since this analysis aims to understand the consumption by leopards of some prey species more than others, both species that were preyed upon frequently and those that were preyed upon less than expected were included. Prey species were chosen from among the most common species occurring in either leopard diet or on the camera traps. Therefore, the activity patterns of leopards and nine prey species were investigated. These species were bushbuck, bushpig, baboon, common duiker, dassie (combining both rock dassie and yellow-spotted dassie), kudu, red duiker, vervet monkey and warthog. The activity pattern of humans was also investigated to understand the effect human presence may have on leopards in the area. Camera traps in this study recorded data from four 60-day periods, representing two consecutive winter and summer seasons. The dates of the two summer seasons were 21/01/12 - 20/03/12 and 19/01/13 - 19/03/13 and the winter seasons were 24/06/12 - 22/08/12 and 18/05/13 - 16/07/13. Data for each season were pooled in order to obtain a single data set for both winter and summer.

The data analysis in this study is based on the statistical technique developed by Ridout & Linkie (2009) which estimates activity pattern overlap between species using camera trap data and also includes a measure of precision of the estimated overlap value in the form of confidence intervals. Analysis was conducted using the R packages *overlap* (Meredith and Ridout, 2014), *circular* (Agostinelli and Lund, 2013), and *boot* (Canty and Ripley, 2014). *overlap* provides functions to fit kernel densities to data on temporal activity patterns of species, estimates coefficients of overlapping of densities for two species and calculates bootstrap estimates of confidence intervals. The *circular* package allows the analysis of circular data (e.g. time of day data) and *boot* provides functions for bootstrapping. Statistical code for use in R was provided by Linkie and Ridout (2011).

The measure of overlap used is the coefficient of overlapping (Δ), which can be estimated non-parametrically using kernel density estimates, similar to the approach of Schmid and Schmidt (2006). Δ is defined as the area under the curve that is formed by taking the minimum of the two activity patterns at each time point (Linkie and Ridout, 2011). The coefficient of overlapping lies between 0 and 1, with 0 indicating no overlap, i.e. one species may be strictly diurnal and the other strictly nocturnal, and 1 indicating complete overlap, i.e. both species have identical patterns of activity. There are a number of ways to estimate the coefficient of overlapping. The most reliable estimator for use with larger sample sizes

typically greater than 75 is Δ_4 (Ridout and Linkie, 2009), hence this was the estimator used for this analysis. An alternative to using kernel density estimates would be to fit parametric distributions such as trigonometric sum distributions. Both of these methods produce highly similar estimates of overlap, but kernel density estimation requires much less computing time (Linkie and Ridout, 2011). This is an important consideration for calculating bootstrap intervals which is why kernel density estimates were chosen for estimation in this study. Confidence intervals were produced as percentile intervals from 500 bootstrap samples to compute the precision of the estimates.

Initially, the activity pattern of each of the nine species plus humans was estimated separately for the entire duration of the study, using non-parametric kernel density estimation. Next, a measure of the overlap between the kernel density estimates for each species and leopard was calculated to quantify the extent of overlap between species. This calculation was performed for prey species during both summer and winter seasons in order to allow a comparison between seasons to determine any possible activity differences.

To examine the strength of the relationship between Manly's selectivity index (Chapter 4.3.2) and the coefficient of overlap calculated in this chapter, a Pearson's correlation test was used. This also helped to identify outlier species that were selected more or less than expected, given their encounter rates. The correlation was calculated for the eight prey species that had both selectivity and overlap values: baboon, bushbuck, bushpig, common duiker, kudu, red duiker, vervet monkey and warthog.

5.3 Results

A total of 8,970 independent camera images were recorded for the species in this analysis. These images were taken over a period of 5,460 trap nights, 2,700 in summer and 2,760 in winter. Humans had the highest number of independent camera events. Of the remaining species, bushbuck had the highest number of events while dassie had the lowest (Table 5.1). All species had a total of over 100 events each. Bushbuck had the biggest difference between seasons, with nearly double the number of events in winter as opposed to summer. Other species number of events increased or decreased slightly between seasons but not to the same extent as bushbuck, indicating little seasonal variation.

Table 5.1: The number of independent camera events for each species during the summer and winter, and in total.

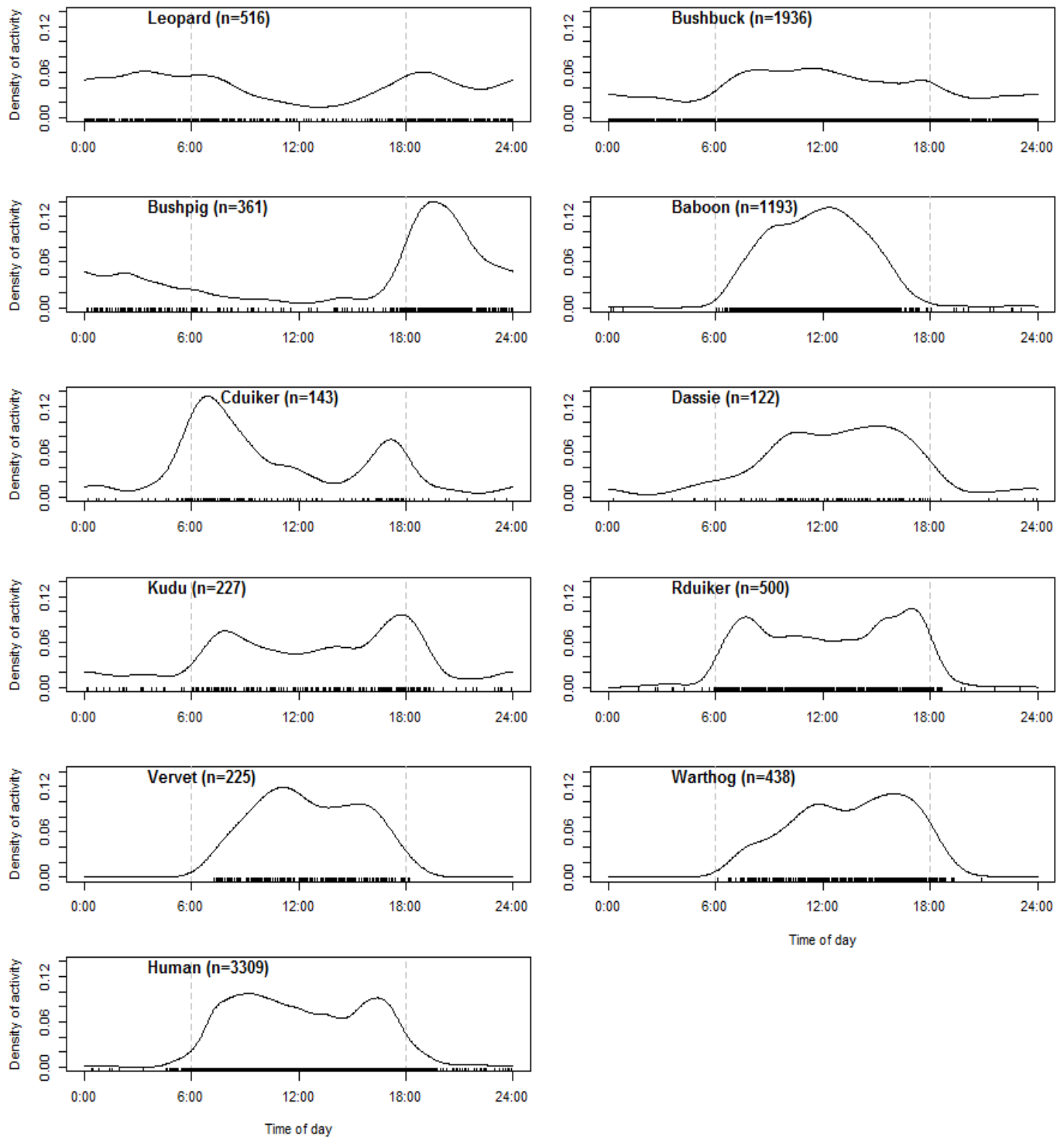| Species	Summer	Winter	Total
Leopard	235	281	516
Bushbuck	658	1278	1936
Bushpig	200	161	361
Baboon	652	541	1193
Common duiker	72	71	143
Dassie	56	66	122
Kudu	107	120	127
Red duiker	196	304	500
Vervet monkey	86	139	225
Warthog	227	211	438
Human	1507	1802	3309

Figure 5.1: Average daily activity patterns of leopard, nine prey species and humans using their kernel density estimates. The two vertical dashed lines in each plot indicate the approximate time of sunrise and sunset. The short vertical lines along the x-axes indicate the times each individual photo was captured.

Table 5.2: The percentage that each species was active diurnally between 06:00-18:00, as well as the overall kernel density estimate of overlap of each species with leopards and 95% bootstrap confidence intervals.

Species	% Diurnal	Kernal Density Estimation of Overlap Δ_4	95% Bootstrap Confidence Intervals
Leopard	36	-	-
Bushbuck	67	0.70	(0.66-0.74)
Bushpig	18	0.69	(0.63-0.73)
Baboon	99	0.31	(0.28-0.34)
Common duiker	78	0.59	(0.51-0.65)
Dassie	90	0.46	(0.37-0.52)
Kudu	74	0.63	(0.57-0.69)
Red duiker	94	0.46	(0.42-0.50)
Vervet monkey	99	0.34	(0.30-0.38)
Warthog	94	0.40	(0.35-0.43)
Human	93	0.43	(0.39-0.46)

While leopards were active throughout the day and night, they were active for a larger proportion of time during the night, with their lowest levels of activity around midday (Figure 5.1). Bushbuck were also active throughout both the day and night but the majority of their activity was during the day (67%) (Figure 5.1 and Table 5.2). Human activity was strongly diurnal with a high and relatively constant level of activity throughout the day, with the exception of a small dip in activity in the early afternoon. Bushbuck and bushpig had the highest degree of overlap with leopards (Δ_4 = approximately 0.7 for both) (Table 5.2), followed by kudu and common duiker (Δ_4 = 0.63 and 0.59 respectively). The other species had notably lower levels of overlap with leopards, Δ_4 = <0.50 for each, with baboon having the lowest degree of overlap (Δ_4 = 0.31). Confidence intervals were narrow due to the large sample sizes collected for each species. The wider confidence interval for dassie compared to red duiker, both of which were calculated to have an overlap estimation of 0.46, is due to the sample size of dassie being less than a quarter of that for red duiker.

The next set of analyses does not include humans as they are focused particularly on leopards and their prey in order to investigate the prey preferences suggested by dietary analysis.
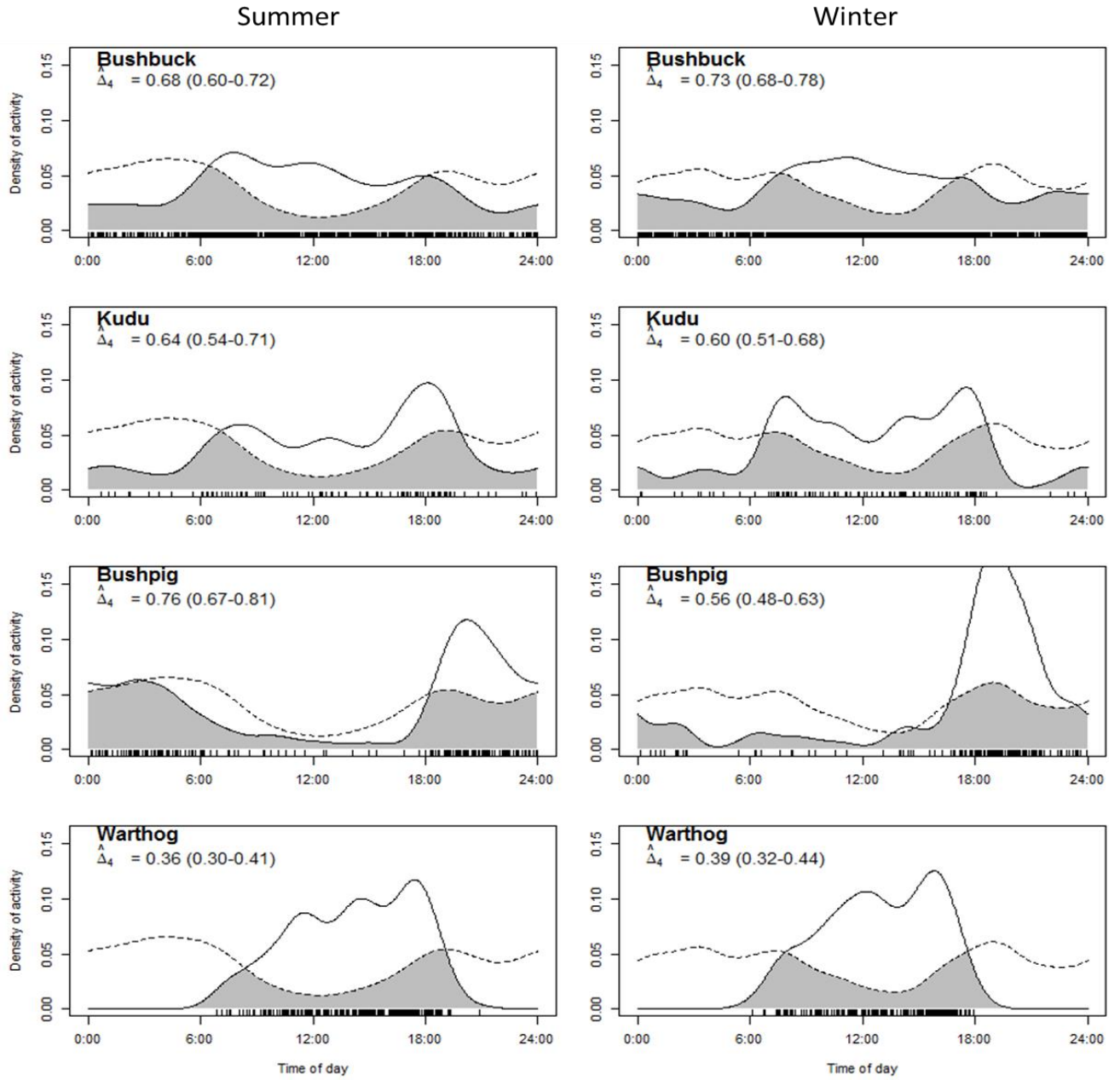
Figure 5.2 continued…

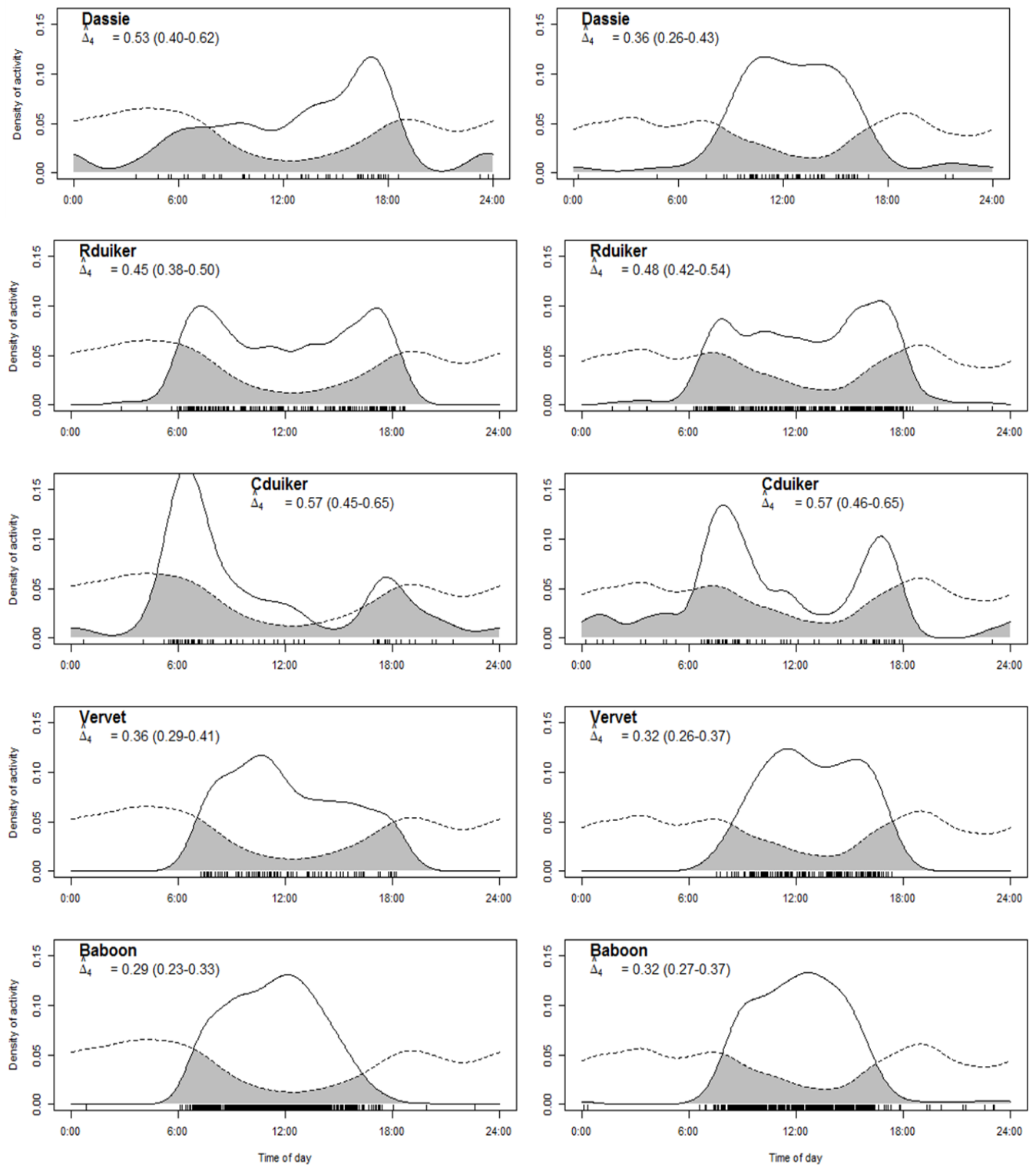**Figure 5.2:** Daily activity patterns of leopard and nine prey species during both summer and winter seasons. Leopard activity is illustrated by the dashed lines, the activity patterns of the indicated prey species are illustrated by the solid lines. The overlap coefficient (Δ_4) is indicated by the shaded area. These estimates of overlap are provided in each plot along with their 95% confidence intervals in brackets.

Bushbuck had a high overlap estimate with leopards during both seasons and their activity patterns for each season were quite similar (Figure 5.2). The activity patterns of warthog, red duiker, vervet monkey and baboon remained diurnal during both summer and winter, with the only difference being that the period of activity during summer was longer due to the longer days in this season. The overlap estimate of each of these species with leopard also remained similar between seasons and was always less than 0.50. Of all the species during both seasons, bushpig had the strongest estimate of overlapping with leopards which occurred during the summer ($\Delta_4 = 0.76$). Dassie had a noticeable difference in their overlap estimate, with their overlap with leopards being higher during summer than during winter. Common duiker had the exact same estimate of overlapping with leopards during both seasons.
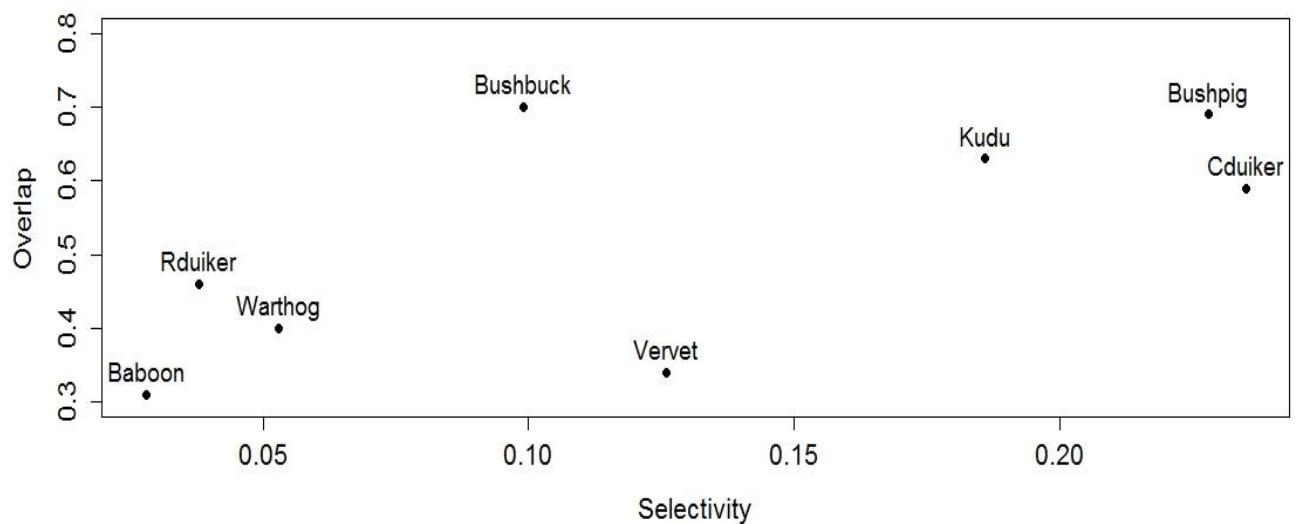
Figure 5.3: The positive correlation between selectivity and overlap for eight prey species.

A Pearson's correlation test between Manly's selectivity index (selectivity) and the overall coefficient of overlap (overlap) indicated a strong, near-significant, positive relationship between the two, with a correlation coefficient of 0.66 (p-value = 0.07). This implies that as the overlap of a species with leopard increased, its selectivity to be consumed by leopards also increased. There are two main outliers in this correlation, vervet monkeys and bushbuck (Figure 5.3). Vervet monkeys were taken more than would be expected by chance based on their encounter rates, whereas bushbuck were taken less than expected. The selection by

leopards of the remaining prey species may all be explained by their overlap with leopards, as indicated by their resemblance of a straight line.

5.4 Discussion

This study is one of few to use camera traps to study the activity patterns of leopards (Azlan and Sharma, 2006; Martins & Harris, 2013) and is the first study to investigate the activity patterns of these species and their prey in the Soutpansberg Mountains. This study provides evidence that the selectivity of many prey species by leopards can be explained by the temporal overlap between them. For example, Chapter 4 found that bushpig were preyed upon more than expected but warthog were preyed upon less than expected, despite having similar characteristics. This activity study illustrated that this selection by leopards may largely be explained by the degree of overlap between each species and leopard. While it is possible that leopards are able to prey upon many species when they are inactive, indicating that activity does not necessarily lead to predation, the results of this study provide strong evidence that activity of prey has an important role in determining whether they are predated upon or not. The results indicate that leopards in the region are active throughout the 24-hour period, however, the largest portion of their active time occurs during the night. This supports the findings of previous studies that leopards in other mountainous regions are largely nocturnal (Martin & Harris, 2013; Pitman et al., 2013), but contradicts the conclusions of Norton & Henley (1987) that leopards were diurnal. Human activity, as expected, was predominantly diurnal. This may be a reason for the gradual decrease in activity pattern of leopards leading to midday before increasing again towards the evening. Both tigers (Carter et al., 2012) and leopards (Kittle et al., 2014) engage in temporal partitioning with humans, typically avoiding daytime activity when humans are most active. This seems to be the case for this study, but more research is needed to be certain that human avoidance is the main cause for leopards' more nocturnal patterns.

Activity of each prey species is discussed in more detail in the next section along with a discussion of their specific overlaps with leopard activity and the implications of these overlaps. Study limitations specific to this study of activity, along with suggestions for future research are provided, before the final conclusion draws together the major findings of this chapter on leopard activity in relation to their prey.

5.4.1 Prey Activity & Overlap with Leopards

Bushbuck were found to be active throughout the day and night, but with the majority of their activity occurring during the day. Overall, bushbuck had the strongest estimate of overlap with leopards. Overlap remained relatively consistent regardless of the season, with no periods of no-overlap occurring between bushbuck activity and that of leopards throughout the 24-hour cycle. This consistently high co-efficient of overlap between the activity of bushbuck and leopards has no doubt contributed to bushbuck being the most frequently consumed species by leopards in this region. Despite being the most commonly consumed species and the species with the highest encounter rate, bushbuck appear to be preyed upon much less than expected based on the correlation between bushbuck selectivity and their overlap with leopards. This study recorded a lower frequency of occurrence of bushbuck in scats than previous studies (Schwarz and Fisher, 2006; Chase Grey, 2011), however, the reasons for them being eaten less than expected based on their encounter rates in this study are unknown and further analysis is needed.

There is little consistency in the reported activity of bushbuck to date (Waser, 1975; Elder and Elder, 1970; Wronski et al., 2006b; Yazezew et al., 2011), and no clear data on that activity in this study area. The results of this study agree most closely to those of Waser (1975) who found bushbuck to be active during the day and night, but bushbuck in the Soutpansberg do not show any crepuscular peaks of activity as those in Waser's (1975) study did, indicating that bushbuck may subtly alter their patterns of activity based on their surrounding environment.

Kudu had peaks of activity in the late morning and early evening, however they also showed low levels of activity occurring at night, resulting in them having the third highest overlap with leopards overall. This agrees with previous studies (Owen-Smith, 1998; Annighöfer and Schütz, 2011) who found kudu to show peaks of activity during the morning and afternoon but also during the night. Despite this high overlap with leopards, kudu were not preyed upon that often. As suggested in Chapter 4.4.2, this may be due to their large size which is way beyond the prey preference range of leopards, estimated as 10-40 kg (Hayward et al., 2006).

Dassies were found to be strongly diurnal overall. As a result of extra activity during the summer season, dassie activity overlapped with that of leopards considerably more than during winter, although overlap was not particularly high in either season. Rock dassies in particular are known to spend the majority of their time basking in the sun to avoid nocturnal

hypothermia (Brown and Downs, 2005). Considering that dassie species were one of the most frequently consumed prey species by leopards in this study, leopards may prey upon them during the hours that their activities are overlapping, or they may take advantage of dassies' extra period of activity during summer nights to hunt them in larger proportions. However, as an aside, scat data were investigated to test this idea and it was found that more scats containing dassie were actually collected in winter than in summer. As an alternative explanation, Martins and Harris (2013) suggest that leopards may hunt dassie during the night in general, using their forepaws to extract them from their nocturnal refuges in rock crevices (Sale, 1970). It has also been suggested that dassie activity is actually associated with illumination rather than temperature (Coe, 1962), as they have been recorded foraging on moonlit nights, making their diurnal status less solid. This explanation may be an important one for leopards in the Soutpansberg. The degree of overlap between leopard and dassie activity is not high, which indicates that leopards must have some alternative method that allows them to hunt dassie so successfully.

Bushpig in this study were strongly nocturnal. Their nocturnal behaviour coincides with the more nocturnal behaviour of leopards and most likely results, as evidenced by scat analysis, in greater consumption by leopards of bushpig over most other available species. In contrast to bushpig, warthog were found to be strictly diurnal. Due to this diurnal behaviour, overlap of activity with leopards was low, therefore reducing their risk of predation. Indeed, warthog were not consumed as frequently as expected by leopards given their availability, and the results of this activity analysis provide reasonable explanations for this.

Red duiker were also strictly diurnal. Patterns of activity remained similar regardless of season, as did their estimated overlap with leopards. Common duiker have a relatively bimodal pattern of activity, tending towards being crepuscular, with their peaks of activity around the hours of sunrise and sunset. The overlap estimate between common duiker and leopards was the same in both seasons and was relatively high, despite differences in seasonal activity. As with bushpig and warthog, this difference between the activity patterns of red and common duiker may explain why common duiker are preyed upon much more often by leopards than red duiker, despite the higher availability of red duiker. Common duiker are active later into the evening and night and earlier in the mornings than red duiker, which coincides with greater leopard activity.

As expected from previous studies (Baldellou and Adan, 1998; Hill, 2006), baboons and vervet monkeys were strictly diurnal. These species had the lowest estimates of overlap with leopards of all nine prey species studied. Despite this, both vervet monkey and baboon were frequently found in the scats of leopards in the area, indicating that they are commonly hunted and eaten by leopards here. There are different explanations for this frequency in scats. While leopards in this study tended to be more nocturnal, they were still active during the day, albeit at lower levels. Therefore, leopards may simply prey upon these species during the occasions when their activity patterns overlap. Leopards are known to hunt vervet monkeys foraging on or near the ground during the day, as at night they sleep among the higher branches of trees that are inaccessible to leopards (Seyfarth and Cheney, 1986). A second, more likely, explanation however, may be that leopards actually hunt these species during the night when they may be easier to catch. Indeed, Busse (1980) recorded that leopards specifically hunted baboons at night, despite the fact that they often sleep in difficult to access areas such as cliff faces, caves or tall trees (Hamilton, 1982). Busse (1980) also noted that during the night baboons don't actively defend themselves by harassing leopards like they do during the day, which would make them a lot easier and less dangerous to hunt. That the correlation between selectivity and overlap of vervet monkeys suggest they are preyed upon more than expected, based on their encounter rates, may be explained by vervets being typically arboreal resulting in lower capture rates by the camera traps (as outlined in Chapter 4.4.2) which may distort the selectivity value.

Leopards have access and scope to take advantage of the large range of prey species available to hunt in the area with no competition from other large predators, while also reducing the risk of human conflict by avoiding, to some extent, their period of activity. Martins and Harris (2013) found leopards in the Cederberg Mountains to be predominantly nocturnal, but they hunted diurnal prey. This seems to be mostly the case for leopards in the Soutpansberg too. The only nocturnal prey species in this study were bushpig, the other species were either strictly diurnal, predominantly diurnal or crepuscular. It is unclear whether these diurnal species are hunted during the day or night, however it is hypothesised that they may be hunted at night due to the more nocturnal activity of leopards and the reduced risk for leopards associated with hunting some species during this time.

5.4.2 Study Limitations and Future Studies

The fact that camera traps were set predominantly to capture images of leopards could be seen as a limitation on this study. However, the species chosen for this analysis all had a number of independent capture events greater than 100, ranking them among the highest photographed species. While species such as dassie and vervet monkey may have been photographed more if cameras were placed in more suitable locations, the photos that were captured of them still provide a good indication of the timings of their activity.

Future studies might consider including moonlight as a variable in their study of activity patterns. Lunar cycles have recently been shown to affect both predator and prey strategies and behaviour (Penteriani et al., 2013). On one hand, the potential for nocturnal predators to visually detect prey increases with increasing moonlight. On the other hand, prey may be harder to find as activity is riskier during bright nights. It would be interesting to investigate the activity of dassie during various stages of moonlight to determine if activity increases with brighter nights and if this in turn leads to higher predation rates by leopards. Both this study and that by Martins and Harris (2013) found that leopards were largely nocturnal predators, hunting diurnal species, in mountainous areas that lacked interspecific competition. Thus, another aspect that may be interesting for future research would be to study leopards in a similar environment and with similar prey species available, but with other large predators competing for this prey. This would determine how competition impacts not only on leopards' activity pattern, but also the activity patterns of the prey species in a mountainous habitat.

5.4.3 Conclusions

This study set out to determine when leopards were active in the Soutpansberg Mountains. It also aimed to determine the reasons behind why some less available species were consumed more frequently than similar, more available, species in the area. This study provides accurate and unbiased patterns of activity for leopards, nine prey species and humans, as well as the estimate of overlapping of each species with leopard by using camera traps, which has enabled the following main conclusions to be made:

1) Leopards are active during both the day and night with no regular periods of inactivity, but a slightly larger proportion of activity is nocturnal,

2) The most frequently consumed prey species, bushbuck, are also active throughout the day and night, but are predominantly diurnal,

3) Warthog and red duiker are strictly diurnal and this temporal separation may explain why they are consumed less than expected compared to species with similar characteristics.

This study provides evidence that temporal overlap greatly aids in explaining patterns of diet selection. Leopards' patterns of activity overlap the most with those of both bushbuck and bushpig, their most frequently consumed prey species, and overlap is low with species that were consumed less frequently. Based on these results, it seems likely that leopards in the Soutpansberg may hunt at night. Their most commonly consumed prey species are active during this time, and it is also easier to hunt many diurnal species at night. Night-time hunting also explains why warthog and red duiker were consumed less than expected. If leopards hunted during the day there would be no reason why these species should be consumed any less than others. The high availability of prey determined from numbers of camera trap events, with patterns of activity suitable for efficient leopard predation, enables and provides support for a high density of leopards to thrive in this region.

Chapter 6 - Final Discussion

6.1 Study Summary

The importance of mountainous regions for species conservation is growing with the continued degradation by humans of lower-lying habitats, climate change and the upwards migration of many species. This study focused on the unprotected area of the Soutpansberg Mountains, South Africa, with the aim of gaining an understanding of the ecology of a predator and its prey in this environment. The top predator, leopard, was the focal species and their behaviour and ecology was investigated in relation to various prey species, using camera trapping as a common method for studying each aspect.

The main chapters of this study discussed three elements of leopard ecology under investigation: occupancy, diet and activity. Chapter 3 introduced the method of occupancy modelling as a technique for determining which variables, if any, dictate where a species occurs. This study looked at a variety of different variables that may have an effect on which areas leopards choose to occupy, such as habitat type, altitude, being situated on a road (or not) as well as the independent capture rates from various prey species, humans, vehicles and domestic animal. Ultimately, none of the variables investigated were found to influence where leopards occupy, which highlights the challenges in modelling occupancy in areas where occupancy is very high. Future research would need to study similar areas where leopards definitely do not occur, in order to provide a contrast by which critical predictors of occupancy could be discerned. As an important additional component of this study, I determined whether the number of sessions into which camera trap data were split had any effect on analyses of occupancy. No previous study had attempted to either investigate or provide support for decisions of this type. I found that, provided there is sufficient data in each session, there were no consequences of splitting data into any number of sessions. This is new and valuable information for future studies wishing to study occupancy using camera traps as these studies now have evidence to support that, on a whole, their choice does not matter.

Chapter 4 investigated the diet of leopards using scat analysis and compared these results with prey availability based on camera trap data. I aimed at producing a diet profile for leopards in the Soutpansberg in order to determine which prey species are most important to them, and also whether or not they are consuming livestock. Diet analysis was conducted using cross-sections of undigested hair from leopard scats collected in the study site and was

recorded as both frequency of occurrence and relative biomass consumed. Prey species that occurred in scats were compared to camera trap data to determine if the species were preferred, avoided or consumed as much as expected based on their availability. A total of 22 species were identified in the scats. Artiodactyla species were the taxa most consumed by leopards, with bushbuck being the most frequently consumed species, followed by bushpig. I found that leopards have a broad diet with prey of varying sizes, but consume species within the range of 20-60 kg most often. Manly's alpha selectivity results indicated that some species such as baboon, red duiker and warthog were eaten less than expected based on their relative encounter rate, whereas species such as common duiker and bushpig were eaten more than expected. None of the analysed scats contained evidence of livestock being eaten. This result is important for helping to reduce human-leopard conflict by proving that leopards are less at fault for the loss of livestock in the area than landowners may think.

The results of the selectivity index were investigated in more detail in Chapter 5. This chapter determined the activity pattern of leopards, nine prey species and humans, as well as estimating the overlap these species' activity patterns had with that of leopards in order to determine why some species were preyed upon more or less than expected based on their camera trap availability. Investigating activity patterns using camera traps is relatively new. The advantage of camera traps is that they can collect data on multiple species in the same location over a long period. Data were grouped into summer and single winter seasons for analysis. Leopards were found to be active throughout the day and night, although a larger portion of this activity was during the night. Activity patterns, combined with diet analysis, indicate that leopards may hunt predominantly at night when they have access to nocturnal prey and also less dangerous diurnal prey. The diurnal activity patterns of some prey species may be the reason that they were preyed upon less than expected. This study indicates that temporal separation provides a reasonable explanation for many apparent prey selections. It would seem that, in the absence of interspecific competition, leopards may have adapted their activity pattern to gain access to the broad range of prey species available to hunt at night, while also allowing them to reduce their overlap with humans during the day to avoid conflict.

6.2 Study Limitations & Future Work

The main issue with using data from a camera trap array was that cameras were set by the PPP to capture images of large carnivores like leopard and hyena. This resulted in a limitation of the data which was particularly noticeable in the analysis of occupancy and diet, although in different ways. While camera traps are often used to detect multiple species, no device can detect all species with equal efficiency. Cameras that are set at the optimum height and angle for leopards may not detect smaller animals such as rodents that pass through the site. Indeed, Henschel et al. (2011) confirm that camera traps do not effectively detect small animals. In addition, cameras were mostly placed along roads and trails meaning that animals that do not travel along these types of routes are less likely to be captured on the cameras. Species that inhabit very rocky and rough terrain, such as klipspringer, are also excluded as it may not be fruitful to position camera traps in those areas. Due to the set-up of the camera array in this study, species such as dassie, which are frequently sighted in the area (Primate & Predator Project, *pers. comms.*), are rarely detected by the camera traps and therefore their number of independent trap events is most likely an inaccurate measure of their actual occurrence in the area.. The potential abundance of dassie in particular is represented in the scat analysis of leopards which showed that they are among the most frequently eaten species. Due to their small size, it is unlikely that these species would be eaten as often by leopards if they were rare, as the energy and time taken to find and catch these prey would not be worth it. This limitation of camera data resulted in these species, and species such as rodents and klipspringer, being given an inaccurate value in terms of their possible influence on leopard occupancy. Likewise, these species could not be used for comparison with scat data due to their data being unreliable. Had these flawed data been used, results would have been misleading and inaccurate conclusions would have been made.

Future studies with similar aims to this one need to ensure that camera traps are set up appropriately to capture images of all species passing by. Camera traps that are set up to capture images of leopards may not capture other species that are present in the area in as reliable a manner. In order to combat this, a number of trap arrays could be set up at various heights in the same locations, providing a more rigorous data set with images of animals of various sizes. Of course, this may not be feasible due to costs of cameras but it is something that should be considered for studies that want to collect data on multiple species in an area. Likewise, cameras need to be placed in a variety of different locations such as roads, trails,

streams and rock crevices, as well as in habitats with varying vegetation density and cover, in order to encompass the natural habitats of all species being studied, not just a select few.

6.3 Final Conclusions

This study is the first of its kind to study both leopard occupancy and activity patterns in the Soutpansberg Mountains. It is also the first to combine scat analysis data with camera trap data to gain a better understanding of whether availability plays a role in selecting prey.

This novel study has provided valuable information for future occupancy studies using camera trap data. Based on the results of this study, researchers now have a reference to support their choice of session number and can be confident that the number of sessions they split their data into will not affect the resulting occupancy estimates. A solution to this issue has never been attempted before, with most studies splitting their data without providing reasons behind the session number.

Dietary analysis showed that the prey range for leopards in this region is much broader than previously recorded, indicating that leopards have the ability to prey on a wide range of species of various sizes and risks. Ready availability of prey in the area does not necessarily indicate that they will be preyed upon more frequently. Leopards in this region are active during the day and night, but a larger portion of activity is at night. The activity patterns of prey species play a role in determining how often they are hunted, with temporal partitioning providing viable explanations for many leopard prey selections.

Overall, this study provides in depth knowledge of leopard ecology in the Soutpansberg, as well as additional knowledge of various aspects of the ecology of different prey species. Through examination of diet and activity patterns in particular, insights into how the Soutpansberg's can support such a high density of leopards have been gained. This information can be used for future conservation and management planning in the Soutpansberg and other unprotected mountainous regions worldwide that require information about the relationship between leopards and their prey.

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Appendices

Appendix A: Simulation Data

Simulation 1			
Session Length	**Top Models**	**delta AICs**	**Weights**
2	Species A, Species A & B	0.0, 0.83	0.284, 0.187
3	Species A, Species A & B	0.0, 0.78	0.283, 0.192
4	Species A, Species A & B	0.0, 0.89	0.284, 0.182
5	Species A, Species A & B	0.0, 0.85	0.284, 0.185
6	Species A, Species A & B	0.0, 0.94	0.284, 0.177
10	Species A, Species A & B	0.0, 0.93	0.284, 0.178
12	Species A, Species A & B	0.0, 0.97	0.284, 0.174
15	Species A, Species A & B	0.0, 0.89	0.284, 0.182
20	Species A, Species A & B	0.0, 0.93	0.284, 0.178
30	Species A, Species A & B	0.0, 0.95	0.284, 0.177
60	Errors	-	-

Simulation 2			
Session Length	**Top Models**	**delta AICs**	**Weights**
2	Species A & B, Species A B &	0.0, 1.48	0.426, 0.203
3	Species A & B, Species A B &	0.0, 1.46	0.412, 0.199
4	Species A & B, Species A B &	0.0, 1.48	0.422, 0.202
5	Species A & B, Species A B &	0.0, 1.46	0.411, 0.199
6	Species A & B, Species A B &	0.0, 1.47	0.419, 0.201
10	Species A & B, Species A B &	0.0, 1.47	0.420, 0.201
12	Species A & B, Species A B &	0.0, 1.48	0.424, 0.203
15	Species A & B, Species A B &	0.0, 1.48	0.425, 0.203
20	Species A & B, Species A B &	0.0, 1.48	0.426, 0.203
30	Species A & B, Species A B &	0.0, 1.48	0.427, 0.203
60	Errors	-	-

Simulation 3

Session Length	Top Models	delta AICs	Weights
2	Species A & B, Species A B &	0.0, 0.96	0.411, 0.255
3	Species A & B, Species A B &	0.0, 0.97	0.412, 0.253
4	Species A & B, Species A B &	0.0, 1.04	0.414, 0.246
5	Species A & B, Species A B &	0.0, 1.03	0.414, 0.247
6	Species A & B, Species A B &	0.0, 1.03	0.414, 0.247
10	Species A & B, Species A B &	0.0, 1.04	0.414, 0.246
12	Species A & B, Species A B &	0.0, 1.02	0.413, 0.248
15	Species A & B, Species A B &	0.0, 1.03	0.414, 0.247
20	Species A & B, Species A B &	0.0, 1.01	0.413, 0.249
30	Species A & B, Species A B &	0.0, 1.02	0.413, 0.248
60	Errors	-	-

Simulation 4

Session Length	Top Models	delta AICs	Weights
2	Species A, Species A & B	0.0, 0.22	0.192, 0.172
3	Species A, Species A & B	0.0, 0.22	0.193, 0.173
4	Species A, Species A & B	0.0, 0.22	0.193, 0.173
5	Species A, Species A & B	0.0, 0.22	0.192, 0.172
6	Species A, Species A & B	0.0, 0.22	0.192, 0.172
10	Species A, Species A & B	0.0, 0.22	0.192, 0.172
12	Species A, Species A & B	0.0, 0.23	0.192, 0.171
15	Species A, Species A & B	0.0, 0.22	0.192, 0.173
20	Species A, Species A & B	0.0, 0.22	0.193, 0.172
30	Species A, Species A & B	0.0, 0.22	0.201, 0.180
60	Errors	-	-