The role of small private game reserves in leopard *Panthera pardus* and other carnivore conservation in South Africa

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I confirm that this is my own work and the use of all materials from other sources has been properly and fully acknowledged.

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Abstract

Many large carnivores are declining globally; most threatened or risk extinction due to a loss of habitat, resources, and direct removal; often the later as a result of conflict with humans. Although leopards and many meso-carnivore species are still free roaming in South Africa, few data are available on these species outside large protected areas as they are often elusive, wide ranging and found at low densities. More data are needed on the population dynamics, ecology and biology of species such as leopard, if we are to implement evidence-based approaches to their conservation within small reserves and surrounding unprotected areas.

Camera traps are being increasingly utilized in research, as they can record data on a species or a whole community at relatively low cost. Here we used a network of camera traps to monitor species presence at Thaba Tholo Wilderness Reserve, Mpumalanga, South Africa. We found that camera trap efficacy varied between species, with smaller carnivores significantly under-recorded more frequently than larger predators. However, leopards were successfully captured by camera trap when compared with more traditional monitoring methods (i.e. spoor).

Small reserves may play an important role in the conservation of carnivores, but often these reserves are surrounded by farmland and the successful separation of livestock and game using a fence can affect vegetation composition, fragmenting the land further. However, these effects may be limited by the free movement of wild browsers and grazers through holes in the fence which may also decrease the negative effects of fencing while supporting endangered and highly mobile species such as the leopard *Panthera pardus*.

Leopard densities were found to be 3.04 (S.E. +/-1.55) to 4.97 (S.E. +/-2.14) leopards per 100km^2, which was lower than other estimates from South Africa, however the population was stable throughout the study suggesting the reserve was a source for leopard and offspring were dispersing. Although there was no evidence of habitat preference by the leopard, habitat was found to be more significant in influencing relative local abundances of meso-carnivores than potential associations with leopard and other larger carnivores. However abundance may have been affected by factors outside the reserve as conflict with humans was evident.

Negative actions towards leopard and other carnivores in retaliation to the predation of animal stock occurred in the farmland surrounding the study site, with a significantly higher percentage of commercial game farmers responding that they would take action against one or more species of carnivore compared to livestock owners. The financial loss sustained with increasing game prices in South Africa could therefore increase the conflict between humans and carnivores across the country, which in turn could have detrimental effects on local leopard and other carnivore populations.

The relatively high numbers of the extremely rare erythristic leopard occurring within the relatively low density leopard population is likely to be the result of genetic drift, which may have been a result of this conflict; highlighting that although small reserves may play an important role in the protection and propagation of threatened species it is human acceptance of carnivores which is likely to be vital in the successful conservation and long term survival of predators outside protected areas.

Chapter 1

Introduction: The impact of humans on leopards and other carnivores.

1.1. Global threats to carnivores

Many of the world's large mammalian carnivores are under threat with populations declining despite conservation efforts (see Table 1; Winterbach *et al.* 2013; IUCN 2016). Although predators live in a variety of habitats and landscapes globally, the main drivers for decline are shared; loss of habitat, loss of food sources and direct removal (Woodroffe 2000; Vanak *et al.* 2013; Ripple *et al.* 2014). As a consequence of increasing pressure from the expanding human population species may be restricted to isolated pockets of protected land (e.g. Asiatic lion *Panthera leo persica* in Gir forest, Sunquist & Sunquist 2002). As human populations increase, it is becoming ever more important to understand the subtle interactions between habitats, species and humans in order to manage remaining populations more effectively (Woodroffe 2000), particularly in light of suggestions that 58% of land cover falls below a safe biodiversity level, which may affect the resilience of ecosystems to environmental change (Newbold *et al.* 2016). Apex predators are not only critical trophic regulators which maintain biodiversity and healthy ecosystems (Dalerum *et al.* 2008; Sergio *et al.* 2008) they are also economically valuable in terms of global wide tourism (Welch *et al.* 2016). Therefore carnivore conservation is essential for both financial and environmental motives.

1.2. Main factors for carnivore decline

The rapid increase in urbanisation and other anthropogenic changes have directly contributed to the reduction of wilderness areas and increases in habitat fragmentation, both of which have major implications for carnivores (Treves & Karanth 2003; Crooks 2002; Riley *et al.* 2003). Predators often have large home ranges in order to obtain enough food to meet metabolic needs (Gittleman & Harvey 1982) and subsequently live at relatively low densities (Karanth & Chellam 2009). Habitat destruction or fragmentation can lower carnivore densities further due to diminished resources which can reduce genetic variation if carnivore movement is inhibited between fragmented or isolated areas. In extreme cases this may lead to local extinction (Pullin 2002). Alternatively as prey numbers decrease with habitat loss through bottom-up processes or direct removal by humans (Graham *et al*. 2005), predators are likely to leave protected areas in search of prey which can cause conflict with humans (Polisar *et al.* 2003; Kolowski & Holekamp 2006; Dar *et al.* 2009).

Human-carnivore conflict can become more intense where habitat is fragmented, as carnivores move between areas of suitable and unsuitable habitat searching for food or mates. Where mobility is restricted due to fencing (Williamson & Williamson 2009; Woodroffe *et al.* 2014), unsuitable habitat (Trombulak & Frissell 2000; Jaeger *et al.* 2004; Ng *et al.* 2004; Shepherd *et al.* 2008; Kerth & Melber 2009; Farig *&* Rytwinski 2009; Abbott *et al.* 2012), or even a "landscape of fear" from anticipated human activity (Laundré *et al.* 2010; Ciuti *et al.* 2012), it can increase the risk of species losing genetic diversity, both within and among populations (Hayward & Kerley 2009) which can become detrimental to the local population (Pullin 2002).

Table 1: The IUCN status of large carnivores, population estimates and general trend (downloaded from the IUCN red data list 29/07/2016).

Species	**Binomial**	**Status**	**Population estimates**	**Extinction and trend**
Cheetah	*Acinonyx jubatus*	vulnerable	6,700	decreasing
Wild dog	*Lycon pictus*	endangered	6,600	decreasing
Ethiopian wolf	*Canis simensis*	endangered	360-440	decreasing
Manned wolf	*Chrysocyon brachyurus*	near threatened	17,000	unknown
Spotted hyena	*Crocuta crocutta*	Least concern	27,000 -47,000	decreasing
Iberian lynx	*Lynx pardinus*	endangered	152	increasing
Clouded leopard	*Neofelis nebulosa*	vulnerable	<10,000	decreasing
Lion	*Panthera leo*	vulnerable	7,500	decreasing
Jaguar	*Panthera onca*	near threatened	Not given	decreasing
Leopard	*Panthera pardus*	vulnerable	unknown	decreasing
Tiger	*Panthera tigris*	endangered	5,000-7,000	3 sub-species extinct decreasing
Snow leopard	*Panthera uncia*	endangered	4,080-6,590	decreasing
Brown hyena	*Hyaena brunnea*	near threatened	5,000-8,000	stable
Polar bear	*Ursus maritimus*	vulnerable	26,000	unknown

1.3. Conflict and Persecution

Direct removal of carnivores can be accidental (e.g. road kills) or deliberate through legal and illegal hunting (Swanepoel *et al.* 2014). Of the 285 mammalian carnivores assessed by the IUCN, 26.7% are listed as threatened or endangered on the IUCN (International Union for the Conservation of Nature) red data list. Five are extinct in the wild, eight are critically endangered, 24 endangered, 39 are vulnerable, 27 near threatened and 163 are least concern (IUCN 2016). The regulated number of permits to trade these species is controlled by the CITES NDF (Convention on International Trade in Endangered Species of Wild Flora and Fauna, Non-Detrimental Finding process; Lindsey *et al.* 2011). Permit allocations are issued to each country based on the assessment outcome by a team of experts within the country for each species in question, taking into consideration their management, biology, status and control (Lindsey *et al.* 2011).

The poaching of carnivores for live sales as pets (Lee *et al.* 2005) or the sale of body parts for aphrodisiacs (e.g. tiger and leopard penis; Oswell 2010), medicines (e.g. lion and hyena fats; Costa-Neto 2005), ornaments (e.g. lion teeth; Packer *et al.* 2011) and skins (e.g. tiger and leopard; Adeola 1992; Costa-Neto 2005; Oswell 2010) occurs throughout the world (Costa-Neto 2005; Doughty *et al.* 2015). In addition illegal killings can be retaliatory or fear-driven in areas where direct attacks on livestock (by e.g. tiger, Himalayan black bear *Ursus thibetanus*, snow leopards, leopard: Sangay & Vernes 2008; grey wolf *Canis lupus,* lynx *Lynx lynx* Jackson & Wangchuk 2001*;* brown bears *Ursus arctos*: Kaczensky 1999) or humans (e.g. lions and leopards, Treves & Naughton-Treves 1999; Woodroffe *et al.* 2007; jaguar, Neto 2011; Löe & Röskaft 2004) can occur. Carnivores can often be wrongfully blamed for a death which may have been caused by disease, injury or even a snake bite (Poliser *et al.* 2003). Removal methods include shooting, but may also include trapping and poisoning (Stahl 2001; Allen *et al.* 2014) which do not target a single animal and can have repercussions for many species (Glen & Dickman 2003).

1.4. Removal methods

Many methods have been used in an attempt to reduce human-carnivore conflict. Early practices included relocation (Linnell *et al.* 1997; Athreya 2007) and lethal removal (Wagner & Conover 1999; Treves & Naughton-Treves 2005), which can create other potential issues. Relocated individuals may not always find suitable habitat within the release area so may be forced to search out of the area (Weilenmann *et al.* 2010), or they may compete with other residents, resulting in displacement (Rabinowitz 1986; Karanth & Sunquist 1995) or possibly death. Leopard relocation in Maharashtra, India resulted in an increase in attacks on humans. This may have transpired either because of an increase in familiarity of humans during captivity and therefore fear was lost, or there was an increase in aggression from resulting stress, or there was simply an increase in movement through human dominate landscapes after release (Athreya 2011). Evidence also suggests that removing an individual predator may just lead to another individual occupying the newly opened territory (Linnell *et al.* 1997; Stahl *et al.* 2001). Where apex predators have been removed completely, meso-predator release has been documented, leading to damaging effects for other wild populations (Letnic & Kock 2010) and livestock (Treves & Naughton-Treves 2005).

1.5. Prevention methods

More recently preventative methods have been trialled to deter carnivores from attacking livestock. Dogs *Canis familiaris*, donkeys *Equus africanus asinus* (Ogada *et al.* 2003; Gehring *et al.* 2010) and people (Svengren & Björklund 2010) have been used across the world to protect cattle *Bos taurus*, sheep *Ovis aries,* and goats *Capra aegagrus*. Other methods include retaining horns on cattle or corralling herds at night (Woodroffe *et al.* 2007; Reinhardt *et al.* 2012), particularly when livestock have young or are birthing which makes them more susceptible to predators (Yom-Tov *et al.* 1995; Rosas-Rosas *et al.* 2008). Farming prey such as antelope with livestock has also been suggested as a method to reduce attacks (Winterbach *et al*. 2015) and promote conservation while generating income through tourism (Lindsey *et al.* 2013).

1.6. Compensation

Compensation schemes have been used in America, India (Agarwala *et al.* 2010) South Africa (Anthony *et al.* 2010) and Europe (Boitani *et al.* 2011; Rigg *et al.* 2011), where farmers are reimbursed for livestock losses, although it remains unclear how effective this approach is in terms of changing attitudes towards carnivores. Despite this, an increase in grey wolf numbers was observed in Wisconsin, USA over 30 years following the implementation of a compensation scheme (Treves *et al.* 2009). However numbers did not amount to those expected which was considered to be caused by illegal killings (Chapron & Treves 2016). Difficulties in locating dead animals and proving death was caused by a carnivore, as well as delays in receiving compensation payments may account for a lack of significant change in attitude towards carnivores where the scheme has been unsuccessful elsewhere (Nyhus *et al.* 2005; Anthony *et al.* 2010). A modified version of this has shown potential in Sweden whereby reindeer *Rangifer tarandus* herders are rewarded when carnivores successfully breed in an area. Potential damage caused by the predators is calculated and compensation is given accordingly (Zabel & Holm-Müller 2008). Where the scheme was implemented, wolverine *Gulo gulo* numbers have significantly increased over the last decade (Zabel *et al.* 2014).

1.7. Consequences of removal

Over harvesting of animals through trophy hunting can potentially reduce population densities (Loveridge *et al*. 2007; Croes *et al.* 2011; Packer *et al*. 2011) and negatively affect reproductive success through the elimination of the large dominant individuals who are more likely to produce strong offspring (Loveridge *et al*. 2007). This artificial selection within a population has also been attributed to the rise of tusk-less elephants *Loxodonta africana*, where large tuskers have been overharvested (Jachmann *et al*. 1995). Swanepoel *et al.* (2011) demonstrated that indiscriminate killings could potentially be even more detrimental to a population than trophy hunting due to the removal of females and offspring rather than older males; although the removal of dominant males can lead to infanticide as well as female mortality in some species (e.g. leopards, Balme *et al.* 2013; lions, Greene & Mangel 1998). The removal of too many animals could reduce the genetic viability of a population which may be intensified further if replacement is limited and subsequently may lead to genetic drift (Haag *et al.* 2010) and recessively inherited traits, such as colour variation, to occur in high frequency (e.g. melanism in leopards in the Malaysian peninsula, Kawanishi *et al*. 2010).

1.8. Ecological factors limiting carnivore distribution

Generally vegetation diversity and climate are regarded as key factors in terms of mammal distribution (Andrews & O'Brien 2000) and diversity (Avery 1993). Although prey abundance is an important factor influencing predator abundance (Stander *et al.* 1997a; Fuller & Sievert 2001), predator abundance and interactions through a top down regulatory process can also influence other predator distribution and abundance (Gommper *et al.* 2016). Apex predators can directly or indirectly affect other members of the carnivore guild, either by killing smaller carnivores or through competition for prey (Durant 2000; Caro & Stoner 2003; Vanak *et al.* 2013). Lions have been known to attack cheetah and wild dog, which were both found to avoid lions where they overlap (Durant 2000; Hayward *et al*. 2009). Caracal *Caracal caracal* and black backed jackal *Canis mesomelas* numbers rapidly increased after the removal of lions and other large predators in the Cape province of South Africa in 1900's (Beinart 1998; Stadler 2006), suggesting that they limited these meso-predator numbers prior to their removal. Similar patterns have been recorded in Australia with the increase in red foxes *Vulpes vulpes* and cats *Felis catus* where dingos *Canis lupus dingo* have been excluded (Letnic & Kock 2010), and in the USA where coyote, *Canis latrans* (Crooks & Soulé 1999) have been removed. Where cougar, *Puma concolor* densities were significantly reduced, mule deer numbers increased to the extent that vegetation was over-utilized and soil erosion occurred (Ripple & Beschta 2006). In some cases even just the scent of a larger carnivore can affect the behaviour of a meso-carnivore, which can exhibit more alert behaviour or alter their movements in response to the odour (Leo *et al.* 2015).

1.9. South Africa

1.9.1. Biomes of South Africa

South Africa contains a wide range of habitats, with nine described biomes ranging from desert and forest which cover the smallest areas, to savannah and mountainous grassland, which together cover almost two thirds of the country and are both considered to be important in terms of species diversity (Mucina *et al.* 2008). The country itself is ranked as the third most biologically diverse in the world (IUCN 2012). The smallest of the six world Floral Kingdoms, the Cape Floristic Region is located in the south eastern part of the country, which incorporates the fynbos biome and surrounding areas (Cowling *et al.* 2004). The central high plateau spans the interior of the country, with average heights of 1,500m above sea level (ASL) (Anon 2015a). It experiences rainfall in the summer (Harrison 1984) with high temperatures (Rutherford *et al.* 2006) compared to dry and cooler winters. In contrast, the south coast has most rainfall during the winter (Harrison 1984). On the west coast, summers are humid and hot with warm winters (Rutherford *et al.* 2006). Biomes are further divided into eco-regions which are based on biotic and physical features within a biome and transitional zones can span meters to a few kilometres. Grassland and savannah share the longest boundary of any two biomes, stretching some 18,800km (Rutherford *et al.* 2006; Mucina *et al.* 2008). Mining of various minerals including platinum, gold, silver and copper occurs mainly in the north east of the country within the savannah and grassland biomes (Anon 2015b). Much of the farming of livestock and crops, such as maize, wheat and citrus occurs in Mpumalanga and Free State provinces which cover the central part of the country within the grassland biome (Anon 2008).

1.9.2. Mammal distribution in South Africa

Of the approximate 4,700 known mammal species, South Africa is home to around 8.5%, 35 of which are terrestrial carnivores (Stuart & Stuart 2015). Species richness is higher in the north east, which is mainly where savannah biome occurs and decreases westwards with fewer species found in the succulent and nama karoos (Gelderblom *et al.* 1995; Andrews & O'Brien 2000, Mucina *et al.* 2008). Generally species richness is higher at the interface between two habitats (Leopold 1933). Historically it was believed to be beneficial to have a high degree of heterogeneity in an area, however more recently it is understood generalist species may benefit, but specialists that prefer a homogenous environment may suffer (Yahner 1988). Some mammal species are endemic to a particular biome within South Africa, such as the critically endangered riverine rabbit *Bunolagus monticularis*, which is restricted to the nama karoo; however others, such as the Chacma baboon *Papio ursinus,* are more tolerant of a wider range of environments (App 2000, Stuart & Stuart 2015).

1.9.3. Conservation in South Africa

Within South Africa, endangered and vulnerable species such as wild dog and cheetah (IUCN 2016) as well as mega-fauna such as elephant, buffalo *Syncerus caffer* and lion, which can pose a significant threat to humans, are mainly confined to reserves (Hayward & Kerley 2009; Stuart & Stuart 2015). Large government protected areas cover roughly 9.3% of the country and there are some 9,000 private game reserves which provide a further 16% of protected land in South Africa (Swanepoel *et al.* 2013). Kruger National Park is the largest of the government owned reserves covering almost 20,000 km^2 (Anon 2016a). In 2000, fences were dropped between the Limpopo National Park in Mozambique and Gonarezhou National Park in Zimbabwe to promote greater connectivity and movement for species while remaining within a protected area of 99,800km^2 (Spencely 2006).

1.9.4. Private reserves in South Africa

Private reserves in general are relatively smaller than the government owned reserves, and can be used as commercial tourist reserves, providing game drives and other game viewing activities, while others are utilized for private use, or for the purposes of trophy hunting (Taylor *et al.* 2016) which is prohibited in large government protected reserves. While reserves often contain wild, naturally occurring fauna, some introduce game previously extinct from the area or species which tourists or hunters expect during their trip (Hayward *et al*. 2007a; Cousins *et al.* 2008). Game species are bought and sold privately or through auction houses (Taylor *et al.* 2016) and game capture professionals are used to capture and transport game to and from reserves (Ebedes 1994; Cousins *et al.* 2008). Regulations do apply, with permits granted by the Department of Environmental Affairs (DEA) authorities for the transportation, capture and release of game species (Anon 2015c). Over the past 30 years there has been an increase in the breeding of valuable animals displaying colour variation, most often black, white, golden, and red (Erasmus 2016) for trophy hunting (Taylor *et al.* 2016). Demand for these colour variants has triggered game prices to rapidly increase (e.g. normal coloured impala were R1,106 (US$ 76) in 2011 rising to R2,568 (US$ 176) in 2015 (Erasmus 2016). Colour variants of some species can command prices >500% (Erasmus 2016) that of wild-type animals of the same species [e.g. a single black impala *Aepyceros melampus* ram reached R3.2 million (US$ 219,530) at auction in 2015 (Weavind 2015d)].

1.10. Fencing issues

Primarily property demarcation and animal movement is restricted by fencing in South Africa (Anon 2014a). The most common forms of fencing used in the country are either a simple 5 stranded cattle fence which stands 1.3m high, barbed or un-barbed (Hoare 1992), or a standard 18 to 22-stranded game fence over

1.8m tall. The latter can have electric fencing strands attached; a criteria which must be present when containing species such as lion or elephant on the reserve (Anon 2014a). Although various forms of fences have been utilized throughout the world (Williamson & Williamson 2009; Woodroffe *et al.* 2014) for other purposes including preventing the spread of disease (Andrews 1990; Vanak *et al*. 2010), protecting wildlife from poachers or roads (Putman 1997), or to reduce conflict with humans (Thouless & Sakwa 1995; Treves & Karanth 2003; Hayward & Kerley 2009), there is some debate over the true conservation value of fences (Woodroffe *et al.* 2014). Indeed where fences span large distances, migratory animals have been inhibited from accessing seasonal water and food causing significant mortality (Mbaiwa & Mbaiwa 2006; Williamson & Williamson 2009; Hayward & Kerley 2009). In addition, large numbers of animal fatalities have been documented from failed attempts to cross these fences (Caughley *et al.* 1987; Hayward & Kerley 2009). Fences may even enhance the hunting success in predators (e.g wild dog; Davies-Mostert *et al*. 2013) or promote over utilisation of resources, due to the restriction of animal movement within an enclosed area, which can result in local extinction if the area is not managed correctly (Ostfeld 1994; Bond & Loffell 2001; Boone & Hobbs 2004; Hayward & Kerley 2009). Populations may also be at risk of becoming isolated because of the lack of animal movement, which can reduce genetic variation (Haag *et al.* 2010; McManus *et al.* 2015) facilitated by inbreeding (Soulé & Mills 1998), leaving the population vulnerable to disease, or reduced reproductive success (Kissui & packer 2004). Consequently if numbers drop too low to recover within an isolated population local extinction can occur (Pullin 2002). A similar scenario can occur through restricted movement of species due to habitat fragmentation (Swanepoel *et al.* 2013) which can be enhanced by the presence of fences (Pullin 2002).

Considering the widespread use of fences there is surprisingly little known how the condition affects large mammal communities living either side of the fence, or how changes in the mammalian community composition and distribution may affect vegetation. Todd & Hoffman (1999) and Olofsson *et al*. (2001) have shown that grazing pressure from livestock and reindeer *Rangifer tarandus* changes vegetation composition. Nevertheless in many countries including South Africa there are a mixture of wild, introduced and domestic animals which will have a combined impact on the vegetation and will likely add to the effect a fence has on the community and therefore the extent of habitat fragmentation.

1.11. Apex predators

Due to the threats they pose to humans, lions and spotted hyenas in South Africa have been mainly restricted to fenced reserves; with minimal isolated pockets of wild animals (Funston 2008; Stuart & Stuart 2015). The last wild lion strong hold is located in the north of Limpopo. The fact that leopards are able to scale fences more readily than other carnivores (Hoare 1992; Balme *et al.* 2009a) qualifies them as the largest free-roaming apex predator of South Africa. It is only rivalled by the brown hyena in size and distribution (Mills 1982, Mills 1991). Even though the hyena is capable of hunting, this is considered rare and they are thought to consume a high amount of carrion, small animals, insects and fruit (Stuart & Stuart 2015).

1.12. Leopard ecology

Leopards are the most widely distributed of all *Panthera* species, spanning two continents ranging from South Africa through to the Amur valley, Malaysia and Indonesia (Sunquist & Sunquist 2002; Stein & Hayssen 2013). Though it is their highly elusive nature and known adaptability which may have been significant factors contributing to the leopard being overlooked in terms of conservation concern (Jacobson *et al.* 2016). Until 2008, leopards were classified as “least concern” on the IUCN red data list (IUCN 2016). The estimated decline from 37% of its former range over the previous 100 years (Ray *et al.* 2005) prompted its re-classification to “near threatened” (Henschel *et al.* 2008). However a global comparison of leopard research by Jacobson *et al.* (2016) suggested their range may have diminished by as much as 63-75%, signifying leopards may be at greater risk than previously considered, provoking a further re-classification to “vulnerable” in 2016. The full extent of the leopard’s decline and population numbers are unknown due to insufficient field data (Lindsey *et al*. 2011; Jacobson *et al.* 2016), hence the particular focus on the leopard in this study.

Typically leopards are solitary (Bailey 1993; Estes 1997) except for mating, when a female has cubs or rare occasions when small congregations of adult leopards have been observed (Kiffner *et al.* 2013); these maybe related animals or sharing a carcass (Jenny 1996; Pirie *et al.* 2014). Mating can occur up to 3.8 times an hour, over 2.8 days (Owen *et al.* 2010). Females are estimated to have cubs for 90% of their adult lives (Caro, 1989 in Skinner & Chimimba, 2005), with a birthing interval of 6-8 months after the independence of the previous litter (Balme *et al.* 2013). Time to cub independence can vary from a year (Owen *et al.* 2010) to an average of 19 months old (Balme *et al.* 2013). However where prey abundance or leopard density in adjacent areas is high, dispersal from the maternal range can be later (Bailey 1993). Infanticide was found to be the cause of 40% of known cub mortalities in the Sabi Sands game reserve, part of the Greater Kruger National Park (Balme *et al.* 2013). Interactions between males and their offspring are rarely documented, but have been observed within the Sabi Sands game reserve, which maybe an adaptation to reduce infanticide (Pirie *et al.* 2014) where leopard densities are suggested to be high (Bailey 1993; Maputla *et al.* 2013).

Both sexes are known to be territorial, defending against the same sex, displaying ownership through vocalisations, urine, and visual signs such as faeces and tree scratches (Estes 1997, Balme & Hunter 2004). Home range size, defined as the area used over a given time period (Börger *et al.* 2006), can vary considerably from 14km^2 (Balme *et al.* 2009b) to 1,160km^2 (Stander *et al.* 1997a), depending on the local density of leopards, prey availability and habitat (Gittleman & Harvey. 1982). Therefore leopards in arid environments have larger home ranges than those in humid habitats because of a reduced prey density (Odden & Wegge 2005; Sanei *et al*. 2011). This is further supported by findings by Stander *et al.* (1997a) who reported a significant positive relationship between leopard biomass and prey biomass. Male leopards often cover greater distances than females (Swanepoel 2008; Chapman & Balme 2010) with home ranges overlapping those of several females (Skinner & Chimimba 2005; Svengren & Björklund 2010).

1.12.1. Leopard hunting behaviour and diet

The diet of a leopard is often termed as catholic, with a recorded 92 prey species (Hayward *et al*. 2006) it has a wide dietary range compared to other large predators (Balme *et al.* 2007). Although rodents, birds, giraffe *Giraffa camelopardalis*, crocodile *Crocodylus niloticus* and the occasional gorilla *Gorilla* spp. (Fay *et al.* 1995; Hayward *et al*. 2006) are among the named species, preferred prey species weigh between 10-60kg (Hayward *et al*. 2006) and include impala, nyala *Tragelaphus angasii*, and bushbuck *Tragelaphus sylvaticus*, with some individual leopards developing a preference for other prey items (Jenny & Zuberbuhler 2005). An average daily meat intake of between 1.6–4.9kg is required, with prey size averaging 25kg which corresponds to the optimal prey size of 23kg for leopard (Hayward *et al.* 2006). Females with offspring have been found to have a higher average rate of return on their hunting efforts (2.45kg/km/day) compared to lone females (0.28kg/km/day) and males (0.35kg/km/day; Svengren & Björklund 2010).

Leopards are also known to kill and consume smaller carnivores including African civet (Bailey 1993), cheetah, jackal and genet *Genetta* spp., but seem to avoid brown hyena and other species capable of inflicting injury (Hayward *et al*. 2006). Baboons are a curious prey item as a few studies have documented them as being actively hunted, more so at night while they roost (Busse, 1980; Cowlishaw 1994). However they in turn can retaliate and kill leopards (Cowlishaw 1994). Indeed two male baboons were witnessed killing a leopard in the Waterberg by the early 20th century naturalist Eugene Marais (Gutteridge 2008).

The flexible hunting behaviour observed across its range could be accounted for the by anti-predator avoidance of tigers (Odden *et al*. 2010), lion and spotted hyena (Durant 2000). In forests, leopard can be diurnal or crepuscular (Jenny & Zuberbuhler 2005), while leopards in savannah and rocky areas show predominantly nocturnal activity patterns (Bailey 1993; Martins & Harris 2013). Differences have also been noted in caching behvaiour; leopards in savannah avoid kleptoparasitism by hoisting carcasses into trees, which is rarely observed where the densities of other carnivores are low (Balme *et al*. 2007). Leopard will also scavenge from other predators if given the opportunity (Hayward *et al.* 2006).

The main leopard hunting methods are to stalk and ambush, adapting each technique to particular habitats, with ambushing documented more in dense forest (Hart *et al.* 1996). Stander *et al.* (1997a*)* found a leopard needed to be within a mean distance of around 4.4m in savannah woodland for a hunt to be successful. Balme *et al.* (2007) later suggested although vegetation of 20cm is sufficient cover to enable a leopard to stalk close enough for this to occur, more cover is favourable to avoid detection by prey. They also speculated that thick vegetation may be difficult for leopard to locate prey even though density maybe high, and that attacks maybe hindered. Therefore they concluded hunting opportunities may be dictated by habitat, rather than prey density as once previously thought.

1.12.2. Leopard habitat preferences

A variety of habitats are accepted by leopards (Hayward *et al.* 2006), from dry arid deserts to tropical forests. However Swanepoel *et al.* (2013) considered physical and vegetation attributes from known leopard populations within South Africa, and suggested that only 20% of the country contained suitable leopard habitat. Suitable areas were mainly forest, thicket or savannah habitat types which were found to be highly fragmented from human presence (Mucina *et al.* 2008; Swanepoel *et al.* 2013). Of the total suitable habitat only 32% was thought to be located within conservation or protected areas (Swanepoel *et al.* 2013). Grassland was considered an unsuitable habitat. Other studies have found leopard will significantly avoid crossing open grassland within savannah, which could be anti-predation behaviour or to reduce the risk of detection by prey, or both (Balme *et al.* 2007).

Most of the information about South African leopards, including density estimates, is based on leopard populations within large protected reserves incorporating the savannah biome (Balme *et al.* 2010b; Chase-Grey 2013; Swanepoel 2015; see Appendix 1). A documented exception to this is a leopard population residing within a protected area encompassing fynbos and succulent karoo in the Cederberg Mountains, South Africa (Martins & Harris 2013). Interestingly here leopards are half the size of their counterparts in the rest of the country (Hayward *et al.* 2006, Stein & Hayssen 2013); males average 30.9kg and females 21.2kg compared to males in the north and east 58.2-63.1kg and females 34.9-37.5kg (Skinner & Chimimba 2005). Their diet consists mainly of klipspringer *Oreotragus oreotragus* and rock hyrax *Procavia capensis*, and have relatively large home ranges ranging from 74 to 910km^2 (Martins 2010) compared to the larger relatives.

1.12.3. Leopard-human conflict

The unrestricted movement of leopard and other carnivores outside protected reserves inevitably results in an increase in human-related mortality (Balme *et al.* 2009a). The removal of five members of the large carnivore guild from much of South Africa has already caused an increase in meso-predators which causes problems for livestock owners across the country (Bergman 2013). Relatively little is known about the last free roaming members; however it is known the leopard has undergone a dramatic decline in range (Jacobson *et al.* 2016). Leopard density estimates within protected areas containing favourable habitat, such as forest and savannah, are generally higher than those in unfavourable habitats or outside protected areas (Appendix 1) where the threat of conflict of hunting is considerable. In 2008 South Africa the number of CITES permits was raised from 120 to 150 of the 2,648 African CITES permits, which were then re-allocated to each of the nine provinces (Balme *et al.* 2010a). Concerns have been raised about the decrease in leopard distribution (Jacobson *et al.* 2016) and a trophy hunting ban was put in place at the beginning of 2016 which is to be re-assessed at the end of the year (Anon 2016b). However damage causing animal (DCA) permits can be issued to legally remove an animal found to attack livestock; although animals may also be removed illegally (Balme *et al*. 2009b). This is dependent on how tolerant people are towards leopards and other carnivores (Pitman *et al.* 2016) and will likely increase as human distribution expands and farm numbers rise, which may lead to further restriction on movement and increase the isolation of leopard populations (McManus *et al*. 2015).

1.13. Other predators

Relatively little is known about brown hyena and meso-predators beyond the basic ecology in South Africa compared to other predators, although it is known many can be a threat to livestock (Bergman *et al.* 2013; Stuart & Stuart 2015), including mongoose and large spotted genet *Genetta tigrina* which can attack poultry (Stadler 2006).

1.13.1. Habitat preference

Brown hyena; caracal, honey badger, *Melivora capensis*, striped polecat *Ictonyx striatus*, slender mongoose *Galerella sanguine*, small spotted genet *Genetta genetta*, and African wild cat *Felis silvestris cafra* are relatively widespread across South Africa. Some species are more habitat selective with Cape fox *Vulpes chama,* black-backed jackal*,* yellow mongoose *Cynictis penicillata*, aardwolf *Proteles cristatus* and bat-eared fox *Otocyon megalotis* associated with grassland and more arid regions, and side-striped jackal *Canis adustus*, large spotted genet, African civet *Civettictis civetta*, serval *Leptailurus serval*, and many of the mongoose species inhabiting savannah (Stuart & Stuart 2015).

1.13.2. Canidae, Herpestidae and Viverridae

Rodents, insects and small vertebrates are usually consumed by all members, with the diet often supplemented with berries or fruit (Stuart & Stuart 2015). However the side striped jackal may also feed on cultivated maize, groundnuts and pumpkin. Cape fox has been known to sporadically consume new born lambs, while black backed jackal are known to be problematic to sheep and goat farmers (Bergman *et al.* 2013). The volume of food and distances traversed by wild dogs has brought them into serious conflict with humans (Gusset *et al.* 2009). Often a successful pack will hunt morning and afternoon and are capable of killing large ungulates (Estes 1997; Creel & Creel 2009).

1.13.3. Felidae and Mustelidae

Members of both genera tend to be pure meat eaters, with prey size consumed increasing with carnivore size. Although honey badgers tend to feed mainly on rodents and invertebrates, they can also supplement their diet with fruit and carrion and have on occasion been thought to take poultry, or small livestock (Stuart & Stuart 2015) and will break into beehives. Servals are well adapted to hunting rodents and small mammals in long grass with anatomical features such as their large ears and long legs however they may also prey on small antelope the size of klipspringer (Pirie *pers. obs*.; Estes 1997) Unfortunately cheetah and caracal experience high levels of persecution due to predation on livestock (Selebatso *et al.* 2008; Bergman *et al.* 2013).

1.13.4. Hyaenida

Brown hyena is considered to be a specialized scavenger (Van der Merwe *et al.* 2009). Subsequently where apex predators occur large mammalian content is higher in the scat compared to areas without apex predators and hyena densities are considerably higher where apex predators do occur (Yarnell *et al.* 2013). Although aardwolf are also a member of the Hyaenidae they are myrmecovores, feeding on the nastute harvester termites (genus *Trinervitermes*). A record of an individual attacking a captive goose was documented, however this is considered extremely rare (Yarnell & MacTavish 2013).

1.13.5. Interactions

Although interactions among the African large carnivore guild (including lion, wild dog, cheetah, leopard, spotted hyena) have been widely investigated (Hayward *et al.* 2009; Durant *et al.* 2010; Pettorelli *et al.* 2010), research on interactions with meso-carnivores are limited, with the exception of the black backed jackal. Genet species are considered to be most the likely to experience competition with other meso-carnivores due distribution and diet overlap, with mongoose and small canids more likely to be subject to intra-guild predation (Caro & Stoner 2003). The predation by black backed jackal of the Cape and bat-eared foxes has been found to affect the behaviour and ecology of the two species, while Cape fox densities were also found to be suppressed by the presence of black backed jackal (Kamler *et al.* 2013). Inter-specific competition is thought to occur between black backed jackal and brown hyena in the absence of apex predators from evidence found in scat of both species (Yarnell *et al*. 2013). It is largely unknown how leopard abundance affects other carnivores in the absence of other large predators although intra-guild predation is known to occur (Hayward *et al.* 2006) and therefore could be extremely important for the regulation and conservation of different species.

The solitary, nocturnal, often elusive nature and low densities of many of South African carnivores make studying these cryptic creatures challenging (Balme *et al.* 2009b; Stuart & Stuart 2015). Historically indirect evidence such as scat and spoor were used to quantify species and record distributions of a range of carnivores including leopard, snow leopard, cougar, lion, caracal, tiger and pine marten *Martes martes* (Beier & Cunningham 1996; Zalewski 1999; Hussain 2003; Melville & Bothma 2006; Sharma *et al.* 2005; Houser *et al.* 2009; Sanei *et al.* 2011; Sheehy *et al.* 2014). However, advances in technologies such as radio and GPS tracking collars, camera traps and associated computer software, combined with field techniques, are allowing researchers to collect more accurate data on species ecology and behaviour.

1.14. Methods for studying carnivores

Radio and GPS tracking collars have been utilised in many studies of carnivores (e.g. black bears *Ursus americanus,* Amstrup & Beecham 1976; wolves Jedrzejewski *et al.* 2001*;* polar bears, Amstrup & Durner 1995; Ferguson *et al.* 1997; leopards*,* Simcharoen *et al.* 2008). They prove useful in determining potential home range sizes and behaviour patterns (Stander *et al.* 1997a); however they can be extremely expensive; US$350 standard VHF up to US$ 3,000 for a GPS collar alone (Emslie 2014) plus the cost of capturing and tranquilizing the animal. Although rare, injury or death through the capture process (Arnemo *et al.* 2006) can occur or once the animal has a collar on, as it may be fitted incorrectly, later causing harm (Krausman *et al.* 2004; Cid *et al.* 2013; Collins *et al*. 2014). The process or an ill-fitting collar may also affect the animal's behaviour, providing inaccurate data (Coughlin & van Heezik 2015; Collins *et al*. 2014).

Camera traps on the other hand are relatively inexpensive (around US$170), are non-invasive and provide data on a range of species and individuals (e.g. tigers, Karanth & Nichols 1998; leopard*,* Swanepoel *et al.* 2015; snow leopard, Jackson *et al.* 2006; Rowcliffe & Carbone 2008; carnivore biodiversity, Pettorelli *et al.* 2010; ocelot, Trolliet *et al.* 2014) rather than a single animal. However concerns have been raised about abundance and density estimations based on camera trap data due to variation in the likelihood of detection of different species (Krebs 2016). To limit this, it is typical to bias camera trap locations in areas which are likely to increase detection, particularly when focusing on low density animals (Karanth & Nichols 1998, Maputla *et al.* 2013). Computer software can be used to take detection probabilities into account, or these can be added as an effect in models (Fiske & Chandler 2011; Efford 2015).

1.15. Study site

This study was conducted at Thaba Tholo Wilderness Reserve and in the surrounding farmland which is located within Mpumalanga, South Africa. Savannah covers 39% and grassland 61% of the second smallest province (Mucina *et al.* 2008). The property borders farmland, with livestock (mainly cattle), and a small section with game farms which contains introduced game and colour variants. Cultivation also occurs in the surrounding area, which predominately includes citrus and maize crops. The property encompasses 55km^2 and has been managed as a commercial reserve since 2009. Many of the mammal species located on the reserve are naturally occurring, with a few key species (giraffe, Burchell's zebra*,* wildebeest *Connochaetes taurinus* and impala) being introduced (Appendix 2). There are no other megafauna (e.g. lions, spotted hyena, cheetah, wild dog) on site. The mountainous terrain extends from 1100m ASL in the valley, which is defined as central bushveld (an eco-region of savannah), to 2000m at the highest peak, where mesic highveld grassland occurs. Rainfall is typically greater in the summer which averages between 600-900mm; summer maximum temperatures reach the high 30^{o}Cs, and winter days reach the high 20^{o}Cs, dropping to a minimum of -4^{o}C at night.

Aims and objectives

The purpose of this study is to investigate the effect of humans and habitat on leopard and other large mammals in a South African commercial game reserve, lying at the boundary of two diverse biomes. In this study I:

1. Assess the effectiveness of methods to be used in the study by comparing spoor (tracks) directly with camera traps records to investigate the efficacy of both.

2. Investigate how the presence and permeability of a typical game fence affects the distribution of large mammals inside and outside a small reserve and if there is habitat heterogeneity either side of the fence.

3. Calculate the density of the local leopard population within a small game reserve and surrounding area and investigate how the relative abundance of leopard and other carnivore species may be affected by habitat or other large carnivore presence.

4. Investigate if there has been any change over the past five years in terms of farming practices and consequent changes in behaviour towards carnivores by local farm owners to understand how likely carnivores may be removed from the local area.

5. Explore the South African distribution of erythristic leopards, an unusual colour form and potential reasons for the relatively high abundance recorded at the study site.

Chapter 2

Limitations to recording larger mammalian predators in savannah using camera traps and spoor

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2.1. Abstract

Traditionally, spoor (tracks, pug marks) have been used as a cost effective tool to assess the presence of larger mammals. Automated camera traps are now increasingly utilized to monitor wildlife, primarily as the cost has greatly declined and statistical approaches to data analysis have improved. While camera traps have become ubiquitous, we have little understanding of their effectiveness when compared to traditional approaches using spoor. Here, we a) test the success of camera traps in recording a range of carnivore species against spoor; b) ask if simple measures of spoor size taken by amateur volunteers is likely to allow individual identification of leopards and c) for a trained tracker, ask if this approach may allow individual leopards to be followed with confidence in savannah habitat. We found that camera traps significantly under-recorded mammalian top and meso-carnivores, with camera traps more likely under-record the presence of smaller carnivores (African civet 64%; genet spp. 46%, Meller's mongoose 45%) than larger (jackal sp. 30%, brown hyena 22%), while leopard was more likely to be recorded by camera trap (all recorded by camera trap only). We found that amateur trackers could be beneficial in regards to collecting presence data; however the large variance in measurements of spoor taken in the field by volunteers suggests that this approach is unlikely to add further data. Nevertheless, the use of simple spoor measurements in the field by a trained field researcher increases their ability to reliably follow a leopard trail in difficult terrain. This allows researchers to glean further data on leopard behaviour and habitat utilisation without the need for complex analysis.

2.2. Introduction

The successful conservation of any species is predicated on our ability to understand its abundance and distribution (Stander 1998; Hussain 2003; Gusset & Burgener 2005; Houser *et al.* 2009; Trolliet *et al*. 2014). While some taxa (e.g. birds) have the benefit of being relatively well studied, many species such as the larger mammalian carnivores are notoriously difficult to directly monitor in the field (Stephens *et al.* 2006). Traditionally, indirect methods such as locating den sites, and scat or spoor (tracks, pugmarks) surveys have been utilized as a highly cost effective method (Gusset & Burgener 2005) to determine the presence or absence, abundance or population density for species such as the leopard, snow leopard, cougar, lion, caracal, tiger and pine marten *Martes martes,*(e.g. Beier & Cunningham 1996; Zalewski 1999; Hussain 2003; Melville & Bothma 2006; Houser *et al.* 2009; Sharma *et al.* 2005; Sanei *et al.* 2011; Sheehy *et al.* 2014).

It has been suggested that there is enough subtle individual variation in the measurements, shape and natural features (or caused by injuries) of *Panthera* spp. and cougar spoor to enable determination of the sex of an animal (Bothma 1984; Stander *et al*. 1997b; Stander 1998; Sharma *et al.* 2003; Sanei *et al.* 2011; Gu *et al.* 2014) or perhaps even individual leopard, snow leopard, tiger, white rhino *Ceratotherium simum* and black rhino *Diceros bicornis* (Stander *et al.* 1997b; Karanth & Nichols 1998; Riordan 1998; Jewell *et al.* 2001; Sharma *et al.* 2005; Alibhai *et al.* 2008). However, using spoor alone to estimate tiger densities in the field has been criticized for giving inaccurate results in the past (Karanth *et al.* 2003). Established methods were to take plaster casts or tracings of spoor on acetate from which measurements were taken (Lewison *et al.* 2001). Sharma *et al.* (2005) highlighted that data gathered in this way were of poor quality and inconsistently collected. Most feline spoor studies have been investigated in snow (Hayward *et al.* 2002), tropical (Sanei *et al.* 2011) or moist habitats in clay, (Garcia *et al.* 2010) sandy loam, (Lewison *et al.* 2001), or thick soil (Sharma *et al.* 2005), which are often more than 5mm in depth. Lewison *et al.* (2001) found linear measurements from tracings to be more accurate in thick sandy loam. Sharma *et al.* (2005) also found that a substrate depth of 0.5 – 1cm was most effective for detecting tiger spoor and gathering data in the form of tracings and photographs, which were scanned and measured utilizing computer software; a technique which has later been used for white rhino and puma with a good level of accuracy in small populations (Alibhai *et al.* 2008; Garcia *et al.* 2010). However it is not always possible to have these optimum substrate depths in more arid environments which often contain sandy substrates overlaying hard ground. Such habitats are typical of much of the range of species such as leopard in parts of eastern and southern Africa. Nevertheless, while simple spoor measurements are considered likely to be unreliable in determining individual identification (e.g. to determine population size), it is not clear if such measurements would allow tracking of individuals in a single tracking period. If this were so, then a set of spoor that is broken due to unsuitable terrain or crossed by another individual could be reliably followed, allowing further information to be gleaned by relatively untrained fieldworkers on the movement patterns and habitat utilisation of the species of interest.

Conversely, the recent widespread availability of camera trap technology has resulted in a great change in the approach taken to monitoring larger terrestrial mammals of conservation concern across the world (e.g. leopard*,* Trolle & Kery 2005; tigers, Chauhan *et al.* 2005; snow leopard, Jackson *et al.* 2006; Rowcliffe & Carbone 2008; ocelot *Leopardus pardalis*, Trolliet *et al.* 2014). Camera-trapping has been utilised since the early 20th century (Rowcliffe & Carbone 2008), but was initially limited in use by expense and technology. Since then camera traps have been used to estimate relative or absolute densities of rare or cryptic species (Karanth & Nichols 1998; Jackson *et al.* 2006; Silveira *et al.* 2003; Kelly. 2008; Maputla *et al.* 2013), assessing carnivore communities and home ranges (Kauffman *et al.* 2007; Gil-Sánchez *et al.* 2011; Stein *et al.* 2011; Ngoprasert *et al.* 2012; Lynam *et al.* 2013), in short and long term population monitoring (Bridges *et al.* 2004; Negroes *et al*. 2012), animal behaviour (de Almelda Jácomo *et al.* 2004), discovering new species (Rovero *et al.* 2008) and recording plant and animal interactions (Soley & Alvarado-Díaz 2011; Trolliet *et al.* 2014).

In addition, camera traps offer the benefit of allowing species identification with relative ease, and in identifying individuals for species which show variation in pelage markings or natural features (Karanth & Nichols 1998; Trolle & Kery 2005; Jackson *et al.* 2006; Negroes *et al.* 2012; Maputla *et al.* 2013, Pirie *et al.* 2014). They can have a significant advantage over indirect means of recording individuals, often allowing the population size of cryptic species (notably the large cats) to be estimated using capture-recapture models. This was first used to estimate tiger abundance (Karanth 1995) and subsequently this methodology has been adapted for other species of interest (e.g. Karanth & Nichols 1998; Trolle & Kery 2005; Jackson *et al.* 2006; Royle *et al.* 2009; Chapman & Balme 2010b; Negros *et al.* 2012; Maputla *et al.* 2013; Tobler & Powell 2013).

Although it has been accepted that abundance can be estimated relatively accurately when using camera traps (Chapman & Balme 2010) providing that the probability of detection is high and camera avoidance is low (Maputla *et al.* 2013), there remains a lack of a standardized method of camera trap-based mark-recapture (Kelly 2008) and issues such as camera performance and efficiency have still not been satisfactorily addressed (Maputla *et al.* 2013; Urlus *et al.* 2014). However, it is detectability which presents the greatest challenge in effectively sampling the species abundance in a surveyed area (Royle & Nichols 2003) as little is known about how species vary in their likelihood of being recorded by camera traps (e.g. Balme *et al.* 2009b; Ballard *et al.* 2014). In most studies the proportion of individuals which enter the camera trap range and fail to trigger the unit is unknown, resulting in under-estimation of distribution and/or abundance.

Balme *et al.* (2009b) recommend comparing populations of known numbers with camera trap results; this is unlikely to be logistically possible for most studies. Nevertheless camera traps are likely to be used to estimate the population size of target species because direct methods are difficult to implement in the field (Stephans *et al.* 2006; Trolliet *et al.* 2014).

The most accurate approach for comparing spoor and camera trap results is to focus on the two methods' ability to record known individuals (Ballard *et al.* 2014). Lyra-Jorge *et al.* (2008) found that compared to spoor, film cameras with a trigger delay of one second collectively under recorded by 1.65 times puma, maned wolf, striped hog-nosed skunk *Conepatus semistriatus*, armadillo *Dasypus* sp. and forest rabbit *Sylvilagus brasiliensis*. Balme *et al.* (2009b) evaluated spoor counts and camera trap images as population estimators against a known radio-collared population of leopards. Camera traps were found to be more effective than spoor despite the fact only spoor from known collared individuals was utilized. However, spoor is usually recorded in sand traps, which maximises the likelihood of successfully recording a passing individual. In field work such pristine recording opportunities are rare and conditions often affect data collection (Lyra-Jorge *et al.* 2008).

In this paper we report the results of a study of large to medium mammalian predators of the African savannah, where we explore a) the effectiveness of camera traps compared to spoor recorded in natural settings by trained amateur trackers for a variety of predators ranging in size from leopard to Meller's mongoose *Rhynchogale melleri* and b) if observer accuracy in recording measurements and substrate depth may limit the utility of using simple measurements of spoor in arid environments to attempt to track individual animals. We studied the latter using two approaches; first using a cast of a leopard print, we investigated inter-observer variation in spoor measurements. Second, using one observer following three leopards in two depths of fine sand substrate types we measured intra-observer variation in spoor measurements.

2.3 Methods

2.3.1. Study location

The study took place in July and August 2013 and was conducted at Thaba Tholo Wilderness Reserve, Mpumalanga, South Africa (Latitude: 24^{o}57”404 S, Longitude: 30^{o}21”105 E; Figure 1). The reserve was established in 2002 as a 1,500ha privately owned game reserve, rehabilitating land previously used for cattle and small pockets of cultivation, evidence of which still remains. In 2009 the boundary was increased to 5,400ha and it is now run as a commercial reserve with South African giraffe (*Giraffa camelopardalis giraffe*), plains, bush and mountain antelope and a number of carnivores, the largest being the brown Hyena and leopard.

The area is situated between the Steenkampsberg and Mauchsberg mountain ranges and lies on the cusp of two major biomes formally classified as savannah in the valleys and northern section of the reserve and grassland on top of the mountains in the southern section of the reserve. Altitudes range between 1100-2000m and it has an average annual summer rainfall of 700-900mm falling mainly during October-February. Rock types include granite, gneiss and sandstone in the mountains with mudstone, sandstone, quartz, shale and gneiss in the valleys. The vegetation is mixed veld, predominantly *Vachellia* spp., *Combretum* spp. and *Commiphora* spp, *Themeda triandra, Hyperthelia* spp. and *Cymbopogan* spp.

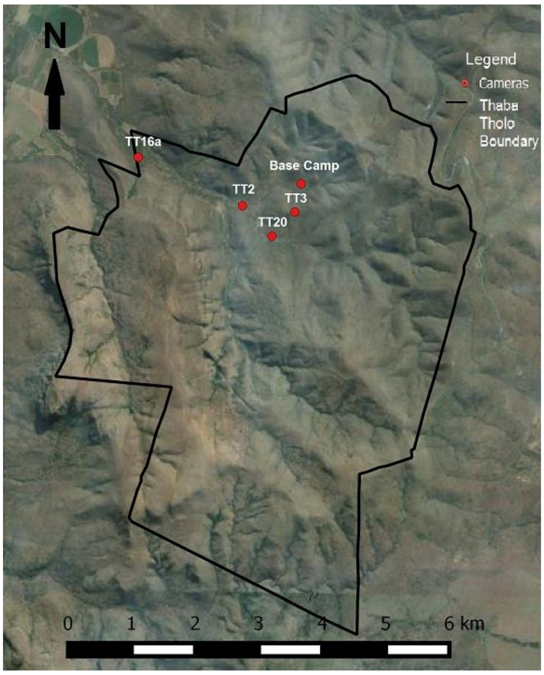

Figure 1: Map of Thaba Tholo Wilderness Reserve, South Africa showing the four camera sites which were surveyed and their relation to base camp. (Google Maps, 2016 and QGIS 2.6.3).

2.3.2. Camera Traps Placement

This work was part of a wider study of the ecology of South African leopards, utilising a network of over 30 camera traps across an area of 5,400ha. Camera traps were sited along unpaved dirt roads, which tend to be used as highways by many animals (Rowcliffe & Carbone 2008).

Four sites (Figure 1) were chosen among these to a) maximise the likelihood of recording high numbers of predatory mammals, b) have the correct natural substrate for spoor recording and c) were within walking distance of base camp in order to collect data before movement of vehicles occurred and safety factors were taken into consideration.

2.3.3. The cameras

Little Acorn 5210A (Ltl Acorn, Green Bay, Wisconsin) camera traps were utilised in this study. Each camera unit had a trigger time of one second and were set to photo mode, at normal sense level. The cameras have three sensors, with two requiring activation before an image is taken. The sensors detect motion and heat and can be triggered up to 15m away. Images were taken in bursts of three and the interval between captures was set at 30 seconds to reduce battery depletion resulting from moving vegetation or large groups of animals passing by the site.

A single camera was placed at one side of a “T” junction at four study sites, to increase the probability of capturing an animal. The camera unit was attached to a metal stake which was pushed into the ground resulting in the lens being positioned approximately 45cm off the ground with the sensors at 40cm. This height allowed for a range of species including meso-carnivores to trigger the sensors. The camera was angled 45 degrees to the road to allow an animal to be in range of the lens during the one second delay between the sensors being triggered and the capture once an animal has been detected. Camera sites were checked every morning, with cards and batteries being exchanged once a week during the spoor surveys to ensure the cameras worked constantly during the study period. As the sites were part of a longer running study in a commercially utilized part of the reserve we felt the daily human activity would not impact greatly on the normal movement of animals living in the area. However to check for this we compared spoor located inside and outside of the trap zone as discussed under spoor surveys. Additionally, we compared image capture rate in weeks preceding and following the study, and found no difference in image collection rates (data not shown). Any vegetation which could trigger the camera or hinder the view of an animal in the image was removed prior to the survey and during monitoring. Leopard, brown hyena, African civet, Meller's mongoose, genet spp. and jackal spp. (grouped; see below) were used in later analysis.

2.3.4. Spoor surveys

Spoor surveys were carried out for 38 consecutive days on foot during the early morning, by a minimum of two people who had received spoor recognition training for a week prior to the survey. This is the best time of day to locate and view tracks as the angle of the sun creates shadows in the spoor (Liebenberg 2005).

Spoor of leopard, brown hyena, African civet, Meller's mongoose, genet spp. and jackal spp. were recorded. Genet species cannot be distinguished by spoor so were grouped and there are difficulties in separating black-backed jackal and side-striped jackal so these were also grouped (Liebenberg 2005; Gutteridge and Liebenberg 2013). Carnivores were studied owing to the relative ease of species spoor recognition compared to that of herbivores and their general solitary nature reduced confusion and therefore error when collecting spoor samples of individuals. The general nocturnal activity of carnivores reduced the possibility that their spoor would be damaged by diurnal species and vehicles overnight which increased chances of locating and recording clear spoor in the morning. In order to check for camera shyness, 25m either side of the camera trap were surveyed for spoor.

The whole survey area was swept clean of all prints by walking from one end of the area to the other, using a feather duster to sweep the whole road; ensuring spoor found the following day was fresh. This was the only way the substrate was manipulated and otherwise was left in a natural state, open to all elements such as wind and dew which can affect substrate conditions (Alibhai *et al.* 2008; Lyra-Jorge *et al.* 2008). Spoor which was situated within the range of the cameras took priority and was marked as being at the camera. Spoor outside this area was marked as not at the camera.

A photograph was taken with a Nikon D3100 SLR for each carnivore spoor located at all sites, with a standard mm ruler zeroed from the back point of the metatarsal or metacarpal pad in the frame for size reference (Figure 2). The thickness of substrate was recorded as being below 2mm or over 2mm (rarely more than 5mm). Only complete and clear spoor were recorded. Partial prints were not recorded to avoid misidentification. Species identification from spoor recorded in the field were checked by observers using

Liebenberg (2005) and re-checked from the image by an experienced tracker. For both camera trap and spoor surveys, presence of a given species was logged once per night per location, irrespective of the number of spoor and/or images recorded.

Figure 2: Representative image of leopard spoor taken for confirmation of species identification with measurement zeroed at the back of the metatarsal or metacarpal.

2.3.5. Inter-observer variation in spoor measurements

A plaster cast of a clear leopard print was made from a spoor found in fine mudstone sand over 2mm thick. Hairspray was used to fix the track to avoid the particles moving during the casting process. A plastic ring 35mm high, 105mm in diameter was placed over the track and sand built up outside in order to stop any plaster from leaking out. Baby powder was sprayed lightly over the track to stop the particles from sticking to the cast. Plaster was then poured over the back of a spoon towards the side of the ring to avoid damaging the spoor and was allowed to set for twenty minutes (Anton Van Loggerenberg, *pers. comm*). The cast was used to make twenty prints in fine mudstone sand over 2mm thick, by one individual, using similar pressure each time. Four measurements were taken (Figure 3) directly from prints made in the substrate. All measurements were taken from the ridge made by the pad or toe indent. Each measurement was made by four independent observers using a single mm rule. Three observers were novice trackers who had been given a week's training (observers 1, 2, 4) and the fourth was the experienced field researcher (observer 3).

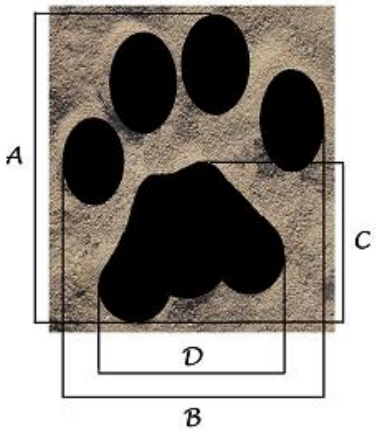

Figure 3: Spoor size was recorded in four dimensions. Full spoor length was taken as the tip of the longest toe to the furthest point of the tarsal pad (A), widest part of spoor (B), length of hind pad (C), width of hind pad (D).

2.3.6. Measurements of spoor from an individual animal

Three separate spoor trails were found by an experienced tracker of three individual leopards walking on hard ground covered in fine mudstone or sandstone sand and each was followed for 1 - 2km. If there was a break in the trail of more than five metres, the trail was considered terminated for that animal. Spoor was selected and recorded every 5m along each trail to ensure the same individual was being measured. Hind feet were recorded due to spoor registering; where the hind foot is placed directly on the front spoor, which obliterates the spoor of the front foot (Riordan 1998; Alibhai *et al.* 2008). Spoor was then separated as left or right and the substrate was recorded as before and measurements taken by a single observer.

2.3.7. Statistical analysis

All analyses were conducted using Minitab 16 (Minitab Inc. 2014) and R (R Core Development Team 2012). To ensure that cameras were optimally placed and that we had no evidence of animals avoiding camera trap locations we compared the number of spoor outside the camera trapping area with numbers located inside using a G-test. The effectiveness of the cameras in detecting each species compared to spoor was analysed using a paired t-test. In order to meet assumptions of normality +1 was added to the data then Log_{10} transformed prior to analysis. Detection rate was calculated by dividing number of total images or spoor by number of hours of exposure (840 hours; following Lyra-Jorge *et al.* 2008).

We investigated a possible relationship between the size and length of the study species and under-recording by camera trap compared to spoor located using the percentage difference between the two methods with a one-tailed Pearson's correlation.

A Friedman test was used to analyse the spoor measurements taken by four different observers from the same track and MANOVA was used to analyse the measurements taken by a single observer from three different animal trails in two substrate thicknesses in the field. Values for full spoor width were analysed following Box-Cox transformation and hind pad width following Johnson transformation to ensure data met assumptions of normality.

2.4. Results

2.4.1. Camera trap placement

We found significantly more spoor inside the camera trap area, supporting the hypothesis that camera traps were optimally placed ($G_5 = 13.3$, $p = 0.02$; Table 2) and that there was no camera avoidance.

2.4.2. Camera traps and spoor efficacy

A total of 153 recordings were collected over 35 nights from the four study locations, 48 images and 105 spoor; providing a mean of 0.114 total recordings of species/camera/hour. For spoor in the trap area, a mean of 0.25 species/trap area/hour was recorded, suggesting that overall spoor recorded the presence of a species more than twice as frequently as the camera traps. There was no significant difference between the number of nights species were recorded using the camera traps or using spoor located within the trapping area when leopard was included ($t_5 = 2.57$, $p = 0.23$;

Table 3). However when leopard was omitted from the analysis the result became highly significant ($t_4 = 2.78$, $p < 0.01$), indicating camera traps significantly under-record compared to spoor. Leopard was recorded on three occasions by camera trap during the study, but not by spoor inside the trap area. These were identified as study individuals MS24, MS24 and FS7. There is a significant correlation between carnivore species recorded by both methods ($R_S = 0.81$, $N = 6$, $p < 0.05$; Figure 4) indicating the increase in activity is detected by both methods.

Table 2: Number of spoor recorded inside and outside of the camera trap area for each species during the study.

Species	**Spoor found inside the trap area**	**Spoor found outside the trap area**
Brown hyena	15	10
Jackal spp.	25	11
Meller's mongoose	9	8
Genet spp.	60	23
Leopard	0	5
African civet	10	3
Total	119	60

Table 3: Number of recordings per species during the study period as camera trap images alone, spoor alone, or both images and spoor.

Species	**Only images recorded**	**Only spoor recorded**	**Both spoor and image**
Brown hyena	4	8	3
Jackal spp.	5	17	9
Meller's mongoose	3	8	0
Genet spp.	8	40	11
Leopard	3	0	0
African civet	1	8	1
Total	24	81	24

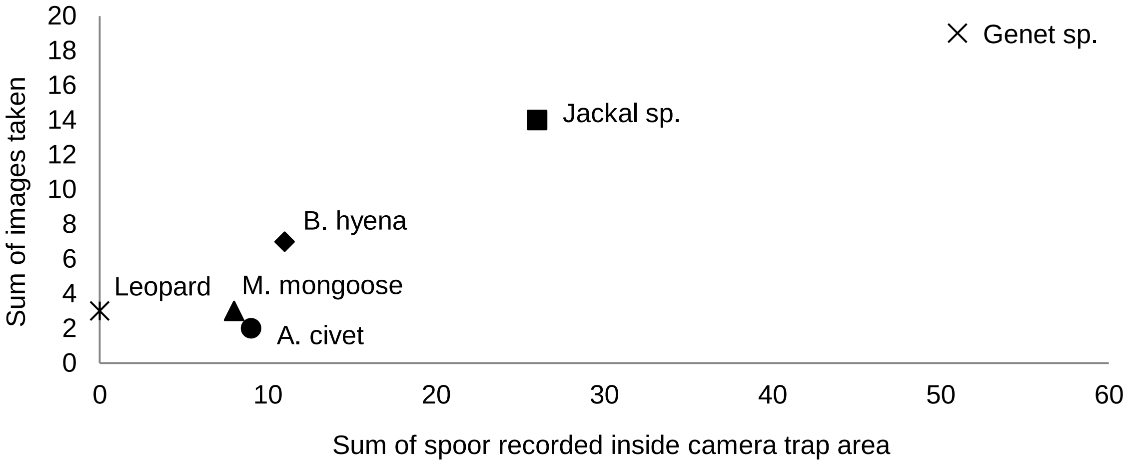

Figure 4: Sum of each study species recorded inside the camera trap area by either spoor or camera trap images.

Each species' mass and length (including tail where this is visible) were taken as the mean values for the male and female of each species (from Kingdon 2003 and Skinner & Chimimba, 2005). The percentage difference in recording between camera traps and spoor was found to be non-significant for mass, but there was a borderline trend with length (one-tailed Pearson r = -0.724, N = 6, p = 0.052; Figure 5), suggesting that relatively short species such as the genet spp. or Meller's mongoose may be more likely to be under-recorded than longer species like hyena and leopard.

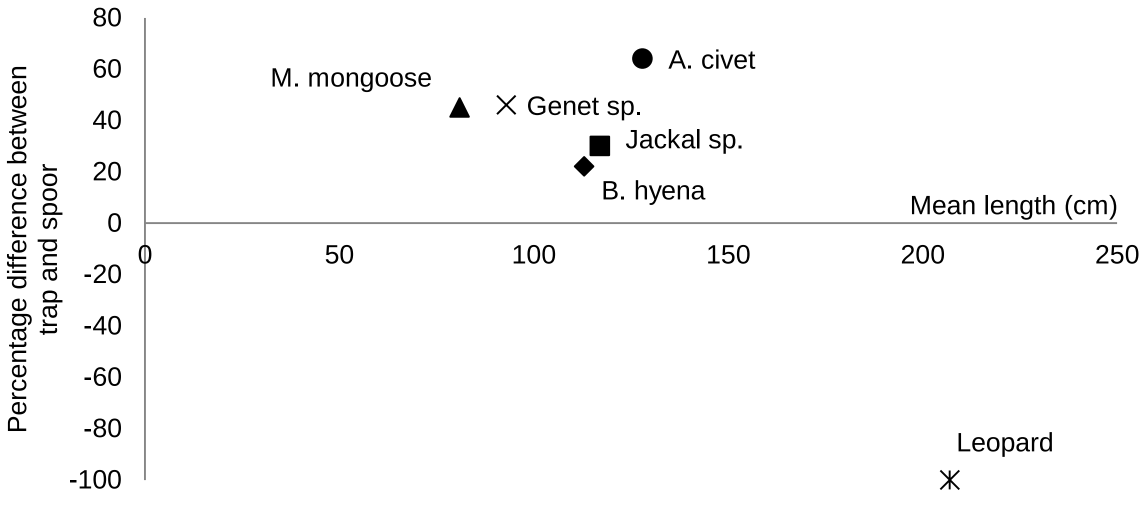

Figure 5: Relationship between study species body length (cm) and likelihood of being under-recorded by camera trap (considering the percentage difference between spoor and image records) in this study.

2.4.3. *Inter-observer variation*

Of the 20 prints made, 19 were useable and in one print measurement D was not possible due to damage during recordings. There was a highly significant difference between observers for each measurement (See Table 4). The experienced researcher had a greatly reduced variation between measurements compared to the three novices.

Table 4: Inter-quartile and median artificial spoor dimensions (mm; see Figure 3) as recorded by four observers. Values for Friedman analyses are provided below each spoor dimension.

	Full spoor length (mm)					**Full spoor width (mm)**				
Ob.	1	2	3	4	Total	1	2	3	4	Total
	n=19	n=19	n=19	n=19	n=76	n=19	n=19	n=19	n=19	n=76
Min.	81	85	90	83	81	73	75	72	74	72
Q1.	88.5	90	92	95	90	77.5	80	75	77	75
Median	91	95	95	97	95	78	80	75	78	78
Q3.	92	100	96	100.5	97	81.5	87.5	76	82.5	82
Max.	99	105	98	106	106	86	90	80	88	90
Diff.	18	20	8	23	25	13	15	8	14	18
	S = 19.92 (d.f. = 3) p < 0.001					S = 28.22 (d.f. = 3) p < 0.001				
	Hind pad length (mm)					**Hind pad width (mm)**				
Obs.	1	2	3	4	Total	1	2	3	4	Total
	n=19	n=19	n=19	n=19	n=76	n=19	n=19	n=18	n=19	n=76
Min.	39	45	45	41	39	52	50	55	53	50
Q1.	46	50	48.5	51.5	47	55.5	55	55	60	55.5
Median	48	53	50	56	51	58	63	56	63	59
Q3.	51	55	52	57.5	55	58.5	70	58.5	69	63.5
Max.	55	67	56	62	67	66	75	62	74	75
Diff.	16	22	11	21	28	14	25	7	21	25
	S = 25.95 (d.f.= 3) p < 0.001					S = 21.28 (d.f. = 3) p < 0.001				

2.4.4. *Intra-observer variation*

Hind right measurements were omitted from the analysis due to only one animal registering in substrate <2mm and two animals only registering in substrate >2mm. With the exception of hind pad width, there was a highly significant difference in all measurements between the animals and a significant difference was found between the two substrates for all measurements (Table 5) suggesting that substrate depth affects spoor size. The full spoor length was found to be the most distinct between each animal, supporting results of Sanei *et al.* (2011), followed by hind spoor length, with full spoor width only showing a difference in substrate >2mm (Table 6).

Table 5: MANOVA values for each spoor measurement (mm; Figure 3) for three leopard hind left spoor sets taken in the field. None of the interaction terms were significant.

Variable	**Effects**	***D.f.***	***F***	**P**
Full spoor length (A)	Animal	2, 48	37.06	0.001
	Substrate	1, 48	5.36	0.025
Full spoor width(B)	Animal	2, 51	5.06	0.010
	Substrate	1, 51	13.50	0.001
Hind pad length(C)	Animal	2, 49	17.51	0.001
	Substrate	1, 49	9.37	0.004
Hind pad width(D)	Animal	2, 49	1.46	0.244
	Substrate	1, 49	4.68	0.036

Table 6: Mean and range (mm) of spoor measurements (Figure 3) for three leopards hind left spoor, recorded under two substrate conditions in the field.

	Hind Left: Substrate <2mm				**Hind Left: Substrate >2mm**			
Measurements	A	B	C	D	A	B	C	D
Leopard 1								
Min.	75	61	36	44	73	55	37	45
Mean	78	62	38	46	81	63	44	48
Max.	80	62	40	50	88	67	50	52
n	4	4	3	3	8	9	8	7
Leopard 2								
Min.	85	55	45	45	89	58	45	45
Mean	87	60	47	47	93	63	52	51
Max.	90	63	49	49	97	70	58	60
n	3	3	2	2	16	15	16	16
Leopard 3								
Min.	82	60	41	43	80	61	40	42
Mean	87	62	45	46	88	69	47	50
Max.	95	67	49	51	95	76	55	60
n	13	14	14	14	5	7	7	8

2.5. Discussion

The ability to document the presence (and potentially abundance) of species of conservation concern is of great interest to field ecologists (Karanth & Nichols 1998; Trolle & Kery 2005; Jackson *et al.* 2006). Understanding the limitations of the main means of recording these species is therefore of considerable importance. In this study of mammalian carnivores inhabiting savannah habitat in South Africa, we found that camera traps significantly under-record the number of animals passing a trapping area when compared with those identified using spoor. This under-recording ranged from 22% for brown hyena to 64% for African civet and there is a suggestion that animal size may affect the likelihood of being recorded. This study illustrates that spoor can provide us with an opportunity to calibrate camera traps. However, the ability to detect and/or identify spoor is affected by the tracker's expertise as well as ground characteristics (Alibhai *et al.* 2008; Lyra-Jorge *et al.* 2008) which do need to be taken into consideration, but could be controlled where necessary.

The use of spoor for the identification of individual large cats by extracting measurements from casts and tracings is controversial and we found that the inter-observer variation in our study meant that measurements of leopard spoor size collected by amateur volunteers are unlikely to provide useful data beyond the presence/absence of leopards. However, experienced researchers were able to collect data which allowed them to follow three individual leopards in the field with some certainty, although spoor size was influenced by substrate, as well as other factors such as terrain and speed of the animal's movement (Riordan 1998; Liebenberg 2005; Sanei *et al.* 2011). We found that mean leopard spoor size was significantly larger in substrate with a depth of >2mm when compared with those recorded in <2mm, which may result from the greater displacement of the toes from the metatarsal pad as the foot pushes further into the substrate. Full spoor length was found to be highly significantly different between animals, which was more apparent in substrates >2mm depth, although we advise that measurements taken directly in field are best done in <2mm sandy substrate as this reduces variance. This is in contrast to Lewison *et al.* (2001) and Sharma *et al.* (2005), who found thicker soil to be more beneficial for tracings and photographs, especially for digital measurements. Therefore, while simple spoor measurements collected directly in the field in sandy soil may not reliably allow the identification of individuals, single leopards can be reliably tracked by trained researchers once spoor is located. Where the trail is broken, size measurements provide evidence that the same individual leopard's trail has been relocated.

Images of the spoor can be recorded for computer analysis as described by Sharma *et al.* (2005), although optimum substrate could be a limitation in more arid habitats. Research conducted on white rhino spoor has been undertaken in similar environments; however there are many lines and creases in the rhino foot to compare during computer analysis (Alibhai *et al.* 2008). Nevertheless under the right circumstances, spoor may still provide additional useful information on individual leopards in terms of movement and behaviour which will prove useful in developing conservation strategies.

In contrast, camera traps readily allow identification of species and individuals when variable pelage markings are evident, and often their general size or sex can be determined from which density and abundance estimates can be calculated providing detectability is accounted for. Increasing the likelihood of detecting focal species is extremely important to avoid under-recording (Maputla *et al.* 2013). Our work suggests that this could be a more significant factor to consider when utilizing camera traps than perhaps previously thought.

Trolle and Kery (2005) found dirt roads to be more effective than game trails in capturing carnivores on camera, so we are likely to have maximised our capture rate, but evidently many individuals were not recorded by the camera traps. While the results for leopard are based on a small sample, results from our long term study (unpublished) also suggest camera traps record the presence of this species approximately twice as often as spoor. All four sites were picked partly because of the ideal substrate conditions, although these can alter daily due to changing temperatures, humidity, rainfall and wind strength (Alibhai *et al.* 2008; Lyra-Jorge *et al.* 2008). On two occasions during the experiment, a leopard was pictured and the individual registered on ideal substrate outside the camera trap zone and was recorded, but failed to register a full recognisable spoor inside the trap zone because of these slight variations in the substrate where it walked. Partial spoor was not recorded to avoid misidentification, so was not recorded as being inside the trap zone. This may have biased the results for the larger species which may have been under-recorded to a greater extent; however the purpose of this study was to compare the effectiveness of cameras at recording species compared to amateur trackers and shows both methods are able to gather presence data.

Overall, under-recording appears to occur more frequently with smaller species. Previous studies (Kelly 2008; Lyra-Jorge *et al.* 2008, but see Negros *et al.* 2012) support this view. In contrast, Urlus *et al.* (2014) found that larger Australian mammals were more likely to be under-recorded by camera traps. It is likely that this is as a result of the much greater size difference in their study, with smaller mammals having a more restricted home range around the traps, and their use of bait stations to attract smaller species (Urlus *et al.* 2014). Trigger time, the interval between sensors detecting movement and an image being taken, may also play a role in under recording given that small animals may not trigger the sensors or move more rapidly out of the capture zone once the sensors have been activated. Negroes *et al.* (2012) found having two cameras per station was on average 29% more effective than a single camera based on photographic rate. In addition, camera traps can vary greatly in their likelihood of capturing different species (e.g. Urlus *et al.* 2014; Swan *et al.* 2014) and understanding how equipment varies is of considerable importance.

Assessing predator abundance and distribution in savannah remains a challenge. While using spoor alone to produce reliable species abundance is controversial and relies on skill and field conditions (Hayward *et al.* 2015), we argue that the traditional approach of using spoor and the skills associated with tracking in the field still have a place in monitoring the larger mammalian predators of savannah habitat in two key ways. First, spoor can allow us to evaluate how effective camera traps are at recording the study species; our study species were 37% more likely to be recorded by spoor than by our camera traps, which may have been higher if incomplete spoor was recorded and expert trackers used. This study supports the notion that camera trap studies should be calibrated against other methods (Gompper *et al.* 2006; Balme *et al.* 2009b) in order to gain more accurate data to determine actual density, relative abundance and movements of species. Camera traps are beneficial but their reliability in capturing each animal that triggers the sensors is uncertain and depends on the camera model, habitat and as we show, species. Second, while it is unlikely that direct spoor measurements can be used to reliably identify unknown leopards due to inter-observer variation, spoor measurements enable known individuals to be followed by experienced field trackers with some certainty, allowing researchers to link records at static camera trap locations with the wider movements of an individual. We therefore suggest that while camera traps are an exceptionally helpful addition to the ecologist’s armoury, we should take care to ensure that the benefits of good field craft are not neglected.

Chapter 3

Fencing differentially affects domestic, introduced and wild South African mammals

Submitted to the Journal of Wildlife Management

3.1. Abstract

Fences are utilized throughout the world to restrict the movements of wildlife, protecting them from various threats and reducing human-wildlife conflicts. In South Africa the number of privately-owned fenced game reserves has increased greatly in recent years, and little is known about how fencing affects the distributions of larger mammals. We surveyed the complete fence line (approximately 30km) of a recently established commercial game reserve in South Africa. We surveyed 2m either side of the fence looking for signs of animal presence (spoor, scat, foraging or other field signs) while also recording damage (holes) to the fence. Every 250m we carried out 100m transects either side of the fence, recording signs of animal presence as well as vegetation cover and height within 2m of the transect line. Transects were also carried out where holes (over 10cm) were found in the fence. We found that livestock (largely cattle) were excluded from the reserve, but 17% of records for large game species introduced to the reserve were recorded outside of the fence line. Fifteen wild species were found to be using both sides of the fence, but we found more evidence of their presence inside the reserve. We also found evidence that the construction of the fence had led to a change in vegetation structure. Therefore while fencing was highly effective at preventing movement of livestock, commercial game animals were able on a limited basis to cross the boundary. Wild mammals frequently crossed the boundary, in part due to holes in the fence line. This work shows that the efficacy of the most common approach to preventing animal movement around protected areas depends on the species being considered.

3.2. Introduction

Fences mark boundaries and act as barriers to the movement of people and wildlife (Hoare 1992, Boone & Hobbs 2004). In the context of wildlife management, fences can help protect wildlife from persecution (Hayward & Kerley 2009), predation (Lokemoen *et al*. 1982, Rimmer & Deblinger 1992), poaching, and can help reduce the spread of disease from wildlife or domestic animal reservoirs (Andrews 1990, Vanak *et al*. 2010). Fences have also been used to reduce the possibility of conflict with humans by inhibiting the access of larger wild mammals to crops (Thouless & Sakwa 1995) or livestock (Treves & Karanth 2003), reducing economic losses (Treves & Naughton-Treves 2005), or to prevent direct risks to humans, such as through colliding with vehicles on roads (Putman 1997; Woodroffe *et al.* 2014) or through attack (Sukumar 1991).

However, fences have resulted in large-scale negative effects. For example, the construction of dingo exclusion fences in Australia led to mass mortality in kangaroos *Macropus* spp. due to exclusion from seasonal resources (Caughley *et al.* 1987; Hayward & Kerley 2009) and other native mammals from the increase in populations of mesopredators such as foxes and domestic cats (Dickman *et al*. 2009; Hayward & Kerley 2009). Furthermore, the presence of veterinary fences in Botswana has led to considerable declines in migrating southern African ungulates (Mbaiwa & Mbaiwa 2006; Williamson & Williamson 2009; Hayward & Kerley 2009). Fencing can also alter dispersal routes (Boone & Hobbs 2004), indirectly disrupting gene flow, which in turn can potentially cause inbreeding which may contribute to local extinctions (Hayward & Kerley 2009).

Aside from creating a direct barrier effect, the initial disturbance of erecting the fence and differing levels of herbivory on either side can result in an edge effect (Todd & Hoffman 1999; Olofsson *et al*. 2001; Vanak *et al*. 2010). Historically, natural habitat edges have been thought to be beneficial, due to an increase in biodiversity in both flora and fauna (Leopold 1933), although specialised species are unlikely to benefit (Yahner 1988). Some studies have suggested that there is a higher level of predation along edges compared to interiors (Marini *et al*. 1995; Šáleka *et al.* 2010). Šáleka *et al.* (2010) found predator abundance was associated with an increase in prey at the boundaries of habitats, although other hypotheses have yet to be thoroughly tested (Marini *et al*. 1995; Dijak *et al*. 2000; Šáleka *et al.* 2010; Vanthomme *et al*. 2013).

Fences typically enclose a fixed area. The presence of fences around relatively small wildlife reserves can directly affect the behaviour of apex predators such as lions in terms of habitat utilization (Kettles & Slotow 2009), wild dogs in their prey selection (Davies-Mostert *et al*. 2013), or by restricting the movement of mega-herbivores such as giraffe (Bond & Loffell 2001) and elephant (Vanak *et al.* 2010). These species require large areas to forage (Vanak *et al* 2010), resulting in the over-exploitation of resources which can result in the local extinction of species (Ostfeld 1994; Bond & Loffell 2001; Boone & Hobbs 2004). Fenced populations require effective management to avoid this outcome (Hayward & Kerley 2009; Kettles & Slotow 2009).

Fences are therefore of considerable economic and conservation importance, as they provide the means to isolate species of concern from external threats (Woodroffe *et al.* 2014). Fences are often considered to be impermeable but this is not so for all species. Universal game fences usually consist of posts and steel wire strands and depending on the type of game or livestock enclosed they may be electrified (Hoare 1992). In South Africa, antelope species such as waterbuck *Kobus ellipsiprymnus*, kudu *Tragelaphus stepsiceros* and eland *Taurotragus oryx* are able to jump fences; the latter two species are able to clear 2m fences and indeed eland are able to break some fences (Hoare 1992; App 2000). Other species, including warthog *Phacochoerus aethiopicus*, bushpig *Potamochoerus larvatus*, bushbuck, crested porcupine *Hystrix cristata*, and many mammalian carnivores can dig or crawl under fences, while leopard and other arboreal species may simply jump over (Hoare 1992) if trees or rocks allow. Furthermore, all species can traverse a fence if any holes present are large enough to permit free passage. Together, these behaviours render many barriers semi-permeable (i.e. the fence does fully restrict the rate of movement of some mammals), with permeability determined by fence construction and condition.

There has been a lack of research on the effect of semi-permeable barriers on mammal communities (Cozzi *et al*. 2013). This is surprising considering that the effects of other barriers, such as roads and railway lines, on animal movements have been widely studied (Adams & Geis 1983; Forman & Alexander 1998; Ng *et al.* 2004; Ito *et al.* 2005; Shepherd *et al.* 2008; Farig *&* Rytwinski 2009; Frantz *et al.* 2012). Many of these studies conclude that although passable, roads have a significant negative impact on wildlife movement and survival (Trombulak & Frissell 2000; Jaeger & Fahrig. 2004; Ng *et al.* 2004; Shepherd *et al.* 2008; Kerth & Melber 2009; Farig *&* Rytwinski 2009; Abbott *et al.* 2012). Although roads and railway lines could be viewed as permeable barriers, they are fundamentally different to fences. Barrier characteristics are an important factor in determining the movement of species (Cozzi *et al*. 2013; Forman & Alexander 1998) and each will differ in outcome.

With the increasing number of small privately owned game reserves in South Africa (there are an estimated 9000 private game farms enclosing over 200,000 km^2 in South Africa; Cousins *et al.* 2008; Lindsey *et al.* 2009; Taylor *et al.* 2016), increased habitat differentiation and consequent changes in large mammal distribution are likely (Cozzi *et al.* 2013). However, little is known about how introducing fencing affects the abundance and distribution of larger mammalian species, the consequences for plant community structure, and how fence condition (the presence of holes) can affect the passage of animals. Working at a small commercial game reserve in north eastern South Africa, we asked how the introduction of a boundary fence six years prior to the study has a) affected the distribution of larger mammals, both in terms of commercial status and with regards feeding guild, b) whether this is influenced by the presence of holes in the fence and c) what the consequences have been for the local plant communities.

3.2. Methods

3.2.1. Study area

The study took place during July and August 2015 and was conducted at Thaba Tholo wilderness reserve (TTWR), Mpumalanga, South Africa (Latitude: 24°57”404 S, Longitude: 30°21”105 E). The 1,500-ha privately owned game reserve was established in 2002, integrating smallholdings of land previously used for cattle. Evidence of cultivation such as terraces thought to be dating back from the Iron Age (Pistorius 2014), still remains on site. The perimeter increased to incorporate an area of 5,400ha in 2009 (Figure 6), and is now a commercial reserve with a variety of game including South African giraffe, however it excludes all but the leopard of the ‘big five’ (Pirie *et al*. 2016a; Chapter 2). The reserve boundary is shared with low intensity livestock farming with naturally occurring game, except for 3.3 km of the boundary (highlighted in white; Figure 6) which is shared with another game farm stocking similar species with the exception of eland, sable *Hippotragus niger*, gemsbok *Oryx gazelle*, and Burchell’s zebra.

Altitudes range from 1100-2000m due to the site being located between Steenkampsberg and Mauchsberg mountain ranges with rock types including granite, sandstone, quartz, shale, mudstone and gneiss. The vegetation is mixed veld, predominantly *Vachellia* spp., *Combretum* spp., *Commiphora* spp., *Themeda triandra, Hyperthelia* spp. and *Cymbopogan* spp. and lies on the transition zone between two major biomes formally classified as savannah covering approximately 69% of the reserve (found mainly in the valleys and northern section of the reserve) and grassland, covering approximately 31% (found on top of the mountains mainly in the Southern section of the reserve; Mucina & Rutherford 2006; Pirie et al. 2016a; Chapter 2). The area receives summer rainfall mainly between October-February averaging 700-900 mm.

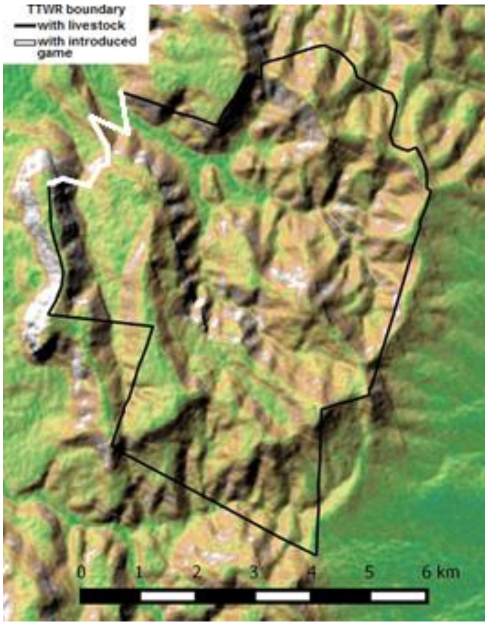

Figure 6: Perimeter fence of Thaba Tholo Wilderness Reserve showing the shared boundary with cattle farms (black) and game only farms (white). Produced using digital elevation model, downloaded 17 March 2015, Earth explore, USGS; in Quantum GIS 2.8.

3.2.2. Fence characteristics

The perimeter fence (29.3km; Figure 6) was erected in 2008/2009 to incorporate the new property acquired and confine species introduced into the reserve including Burchell's zebra, blue wildebeest, eland, gemsbok, impala, nyala, sable, South African giraffe and waterbuck. The fence was 2.2m high and consisted of 22 strands of galvanized steel wire, 2.5mm in diameter (Figure 7). The bottom four strands were 5cm apart, the rest were separated by 10cm. The lowest wire was flush with the ground and the last wire was flush with the top of the fence post. Each strand was attached by wire to a solid metal dropper located every meter along the fence and was threaded through a main fence post every ten metres. Corners and points over 200m from corners were strengthened by large metal posts (10cm in diameter), which were bolstered by thinner metal posts and guide wires. All metal posts were dropped 80cm into the ground. It is worth noting that there were two large gaps in the fence due to the presence of sheer rock faces; although difficult to traverse these could allow movement for agile species such as klipspringer, baboon, kudu and leopard.

Figure 7: Example of the Thaba Tholo Wilderness Reserve game fence.

Due to the length of the perimeter and ruggedness of the terrain, data were collected in subsections of the complete fence over the two month sampling period. Researchers walked along the perimeter fence collecting data, stopping every 250m to conduct transects, with the number of daily transects completed varying with terrain and weather conditions.

3.3.3. Mammal presence along the fence line

Accurate species abundance is challenging to achieve through field sign collection (Hayward *et al.* 2015) however, as shown in chapter 2, spoor can provide reliable presence and level of activity data compared to camera traps under the right conditions; therefore for this study spoor, scat and other field signs were used as primary indicators of species presence and activity rather than camera traps. Although the later may reduce the ambiguity associated with field signs, deployment of cameras to cover the same distance and number of replicas would have been extremely challenging. Two teams of three observers simultaneously walked in single file along both sides of the fence, with an experienced field guide at the rear to ensure data were not missed on either side of the fence. Terrestrial mammal evidence (spoor, scat, foraging or other field signs) was recorded if within two metres of the fence line (Figure 8); GPS location (model; Garmin E-trex) and species found were noted. Most terrestrial and arboreal mammals present on TTWR were found (Appendix 2). However, species smaller than lagomorphs (<40cm long; Stuart and Stuart 2001) were omitted from the study due to their ability to easily traverse the fence and difficulty in locating and differentiating their field signs.

3.3.4. Hole utilisation

Holes were located based on the disturbance of the substrate or damage to the wire due to force, indicating they were created or utilized by animals. The size of hole was categorised based on permeability to key species: a) lagomorphs or smaller <10cm (small), too small for an adult leopard to easily utilize, but could allow mesopredators, dwarf antelope, grey duiker *Sylvicapra grimmia* and klipspringer through, b) >10cm - <25cm (medium), large enough for an adult leopard head and body without much struggle, and c) >25cm (large; mean zygomatic width for adult leopards in Namibia: male, 15.6cm, female 11.3cm [Stein & Hayssen (2013); while hip or shoulder widths are more likely to be the restrictive factor in ability to traverse a fence (Stulken & Kirkpatrick 1953), no such measurements were available]. Hole utilisation was recorded based on the absence of debris or presence of flattened vegetation, both indicators of recent animal movement (Liebenberg 2005). The presence of a game trail passing through the hole was also recorded which served as an indication of the hole being utilized over a longer time period. When a transect location landed within 3m of a medium or large hole it was adjusted to be taken at the hole. The distance to the next transect point was then taken from where the original point would have landed.

3.3.5. Transects

Transects were taken every 250m along the boundary fence line commencing from the main access point onto the reserve. One hundred metres was marked either side perpendicular to the fence. Vegetation cover; recorded as Bare Ground (BG), non-woody plants including grasses / sedges / flowers / *Lampranthus* spp. (O) and woody plants such as trees and bushes (T), height and species were recorded at each ten metre point along each transect using the point-intercept method (Figure 8). The height of the vegetation was categorized as 1: 0-20cm; 2: 20cm-1m; 3: 1-2m; 4: 2-3m; 5: 3-4m and 6: > 4m. GPS co-ordinates and altitude were recorded at the fence and at the ends of each transect. Vegetation was identified to species where possible following Schmidt *et al*. (2002), Van Oudtshoorn (2012) and Manning (2009). Where this was not possible taxa were recorded to morphospecies.

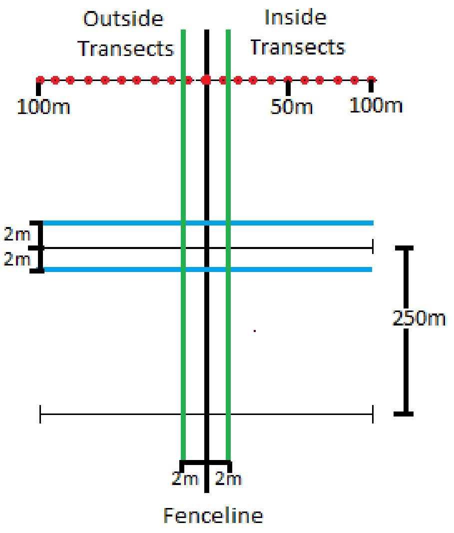

Figure 8: Transects were taken every 250m perpendicular to the perimeter fence line both inside and outside the fence. Vegetation characteristics were recorded every 10m (red circles) for 100m on both sides using the point intercept method. Animal evidence (spoor, scat, other signs) and distance from the fence line was recorded within 2m of the transect line (blue lines). Animal evidence and GPS location was also recorded within 2m of the fence along the entire perimeter fence line (green lines).

Species, distance from fence line and type of evidence (spoor, scat, field sign) of mammals >40cm in length were recorded two metres either side of the transect line. Scat identification was based on size, shape and colour (Murray 2011) and recorded when there were three or more pieces of scat to compare and the shape was intact. Isolated piles were classed as a single count. Herbivore scat was not recorded where only single pellets were found or squashed rendering them unidentifiable. Spoor was identified using Liebenberg (2005), and was only recorded if it was clear, entire and could be identified with certainty. Partial spoor was not recorded. Taking a conservative approach, each spoor from a single species at a single site was recorded as one individual unless clear trails from different individuals were seen. Game trails bisecting the transect line were also recorded. If a transect location was found to be too dangerous to sample, a replacement was located at the closest possible point to the original and the distance subtracted from the next 250m point.

3.3.6. Statistical Analysis

Inspection showed that the data were unsuitable for parametric analyses. Where appropriate P-values for all tests were adjusted using sequential Holm-Bonferroni calculations to avoid errors associated with multiple tests (Holm 1979). All analyses were conducted using R (R Core Development Team 2012).

A Jaccard index (Jaccard 1901) was used to calculate vegetation community similarity either side of the fence. Paired Wilcoxon tests were used to compare maximum and median vegetation heights, amount of plant diversity at each transect point, bare ground, woody and non-woody plant cover either side of the fence. Paired Wilcoxon tests were also used to compare the different maximum vegetation heights and diversity close to the fence (0-50m) and far from the fence (50-100m) inside and outside.

The total abundance of holes within 50m and 100m buffer zone of each transect along the fence line was compared using discrete probability distribution, and replicated for each size category and finally for regularly used holes and unused holes of each size. Spearman's rank was then used to test for trends with vegetation characteristics inside and outside the fence. The effect of hole size on utilization and presence of game trails, were also compared using G-tests (Sokal & Rohlff 1995). Paired Wilcoxon tests were used to compare vegetation characteristics and mammal presence either side of the fence for transects with holes and transects without holes separately.

A Jaccard index was used to calculate large and meso-mammal community similarity either side of the fence based on scat and spoor evidence recorded along the fence line and transects. Paired Wilcoxon tests were used to compare animal evidence, diversity and game trails either side of the fence and then counts close to the fence (0-50m) and far from the fence (50-100m) inside and outside. G-tests were conducted to test for differences in evidence located either side of the fence for a) introduced and naturally occurring wild species and livestock, b) five diet guilds; carnivores, omnivores, grazers (feed on grass only), browsers (do not feed on grass), termite feeders, c) species located (See appendix 1 for classifications).

3.4. Results

3.4.1. Differences in vegetation and mammal activity.

One hundred and sixteen transects were completed (Figure 9); 15 were incomplete due to cliff edges and were omitted from further analyses.

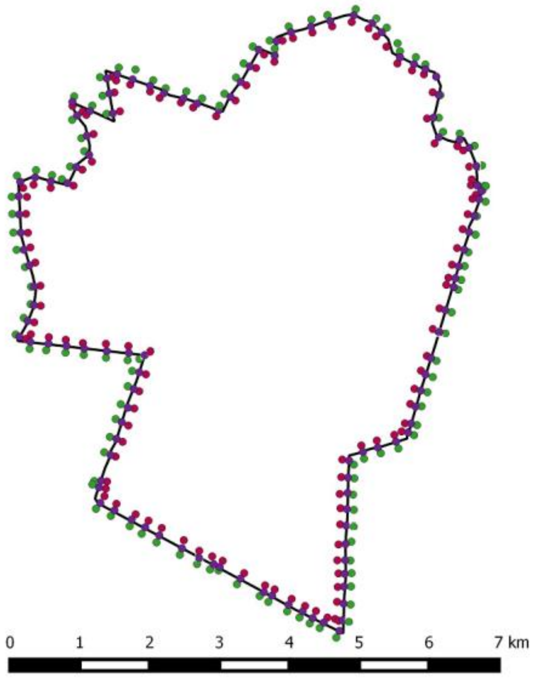

Figure 9: Transect locations taken around the perimeter of Thaba Tholo Wilderness Reserve. Pink represents the furthest transect point inside the reserve, green represents the furthest point outside the reserve and purple represents the 0m at the fence.

Eighty-four plant species were identified; five woody plants and fewer than ten non-woody plants were not identified to species. The Jaccard Index showed an overall difference of 37% (C_J=0.63) between plant communities either side of the fence line. Plant diversity along the transects and percentage of non-woody plant cover was significantly higher inside the reserve (Table 7) however no significant differences were found with the maximum height of vegetation or species diversity and distance from the fence either inside or outside the reserve.

Table 7: Results of paired Wilcoxon signed-rank tests for vegetation attributes either side of the fence from complete transects and transects without holes, with p-values adjusted following sequential Holm-Bonferroni correction.

Transect data	**Attribute**	**Median inside**	**Median outside**	***Z***	**n**	**Adj. *P***
All excluding incomplete	Vegetation diversity	6	5	3559	101	<0.001
	Max. vegetation height	2	2	1187	101	NS
	Median vegetation height	2	2	1247	101	NS
	Percentage of bare ground	9	9	1616	101	NS
	Percentage of non-woody plant cover	73	64	3471	101	0.019
	Percentage of woody plant cover	18	18	2009	101	NS
Without holes	Vegetation diversity	6	5	535	81	<0.001
	Percentage of non-woody plant cover	73	65.7	738	81	0.004

A total of 35 wild mammal species were identified (Appendix 2) through spoor, scat or field signs. There was a 24% difference (C_J=0.76) between the assemblages of wild mammals found inside and outside the fence line, the differences were primarily because of introduced species to the reserve which were absent outside the fence. The number of game trails and amount of animal evidence located was significantly higher inside of the reserve, suggesting there was a higher level of animal activity compared to outside the fence (Table 8, Figure 10). Introduced and wild mammals were significantly more likely to be found inside the reserve as were all diet guilds (Table 9), which remained unchanged when data from the thirteen transects taken on the neighbouring property containing introduced species were omitted from the analyses. There was no significant difference in distance from the fence and evidence located for any of the diet guilds or counts of game trails.

Table 8: Results of paired Wilcoxon signed-rank tests for animal evidence (spoor, scat or field signs), diversity and game trails either side of the fence found on all complete transects, transects with holes only and without holes only, with p-values adjusted following sequential Holm-Bonferroni correction.

Transect data	**Attribute**	**Median inside**	**Median outside**	***Z***	**n**	**Adjusted *P***
All excluding incomplete	Animal evidence	15	11	4589	101	<0.001
	Animal diversity	5	4	4008.5	101	<0.001
	Game trails	12	4	4710	101	<0.001
Without holes	Animal evidence	13	10	987	81	0.03
	Animal diversity	5	4	540.5	81	0.001
	Game trails	13	5	664.5	81	<0.001
With holes	Animal evidence	10.5	9	108.5	19	NS
	Animal diversity	5	3	145	19	NS
	Game trails	9.5	2	128	19	NS

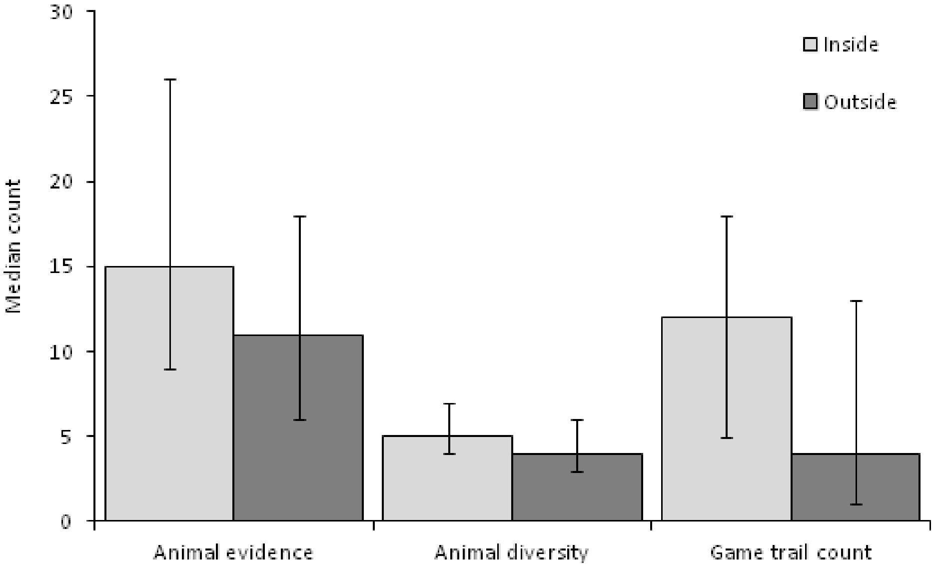

Figure 10: Median count values (+/- inter-quartile range) for animal diversity, animal evidence (spoor, scat and other field signs) and game trails located from all complete transects taken inside and outside of the TTWR perimeter fence.

Table 9: Results of G-tests showing the likelihood of locating evidence of introduced and wild species, and each diet guild based on transect evidence excluding incomplete transects and transects from the 3.3km boundary with the neighbouring game farm, with p-values adjusted following sequential Holm-Bonferroni corrections.

Attribute	**Count inside**	**Count outside**	***G***	***d.f.***	***Adjusted P***
Introduced game	762	100	576.3	1	<0.001
Wild game	1301	790	126.2	1	<0.001
Livestock	0	356	482.5	1	<0.001
Browser	801	488	76.8	1	<0.001
Carnivore	17	6	5.5	1	0.038
Wild grazer	936	216	485.2	1	<0.001
Omnivores	284	148	43.6	1	<0.001
Aardvark	32	29	0.2	1	NS

3.4.2. Hole utilization

A total of 1697 holes were recorded along the reserve fence line (735 small; 444 medium; 518 large; mean of 3 holes > 10cm in size per 100m of fence). Small holes were more likely to be present than medium or large ($G_1 = 72.6$, adjusted $p < 0.001$, $G_1 = 37.8$, adjusted $p < 0.001$) with large holes more likely to be present than medium ($G_1 = 5.7$, adjusted $p = 0.017$). Large holes were more likely to be used recently and contain a game trail than either medium ($G_1 = 17.86$, adjusted $p < 0.001$) or small holes ($G_1 = 24.84$, adjusted $p < 0.001$). Small holes were more likely to be unused compared to medium and large holes ($G_1 = 183.89$, adjusted $p < 0.001$, $G_1 = 150.7$, adjusted $p < 0.001$ respectively; Figure 11). All three sizes had similar proportions of either a game trail present only or had been recently used and game trails were more likely to be present where evidence was found at a hole ($G_1 = 8.62$, p=0.003; Figure 11).

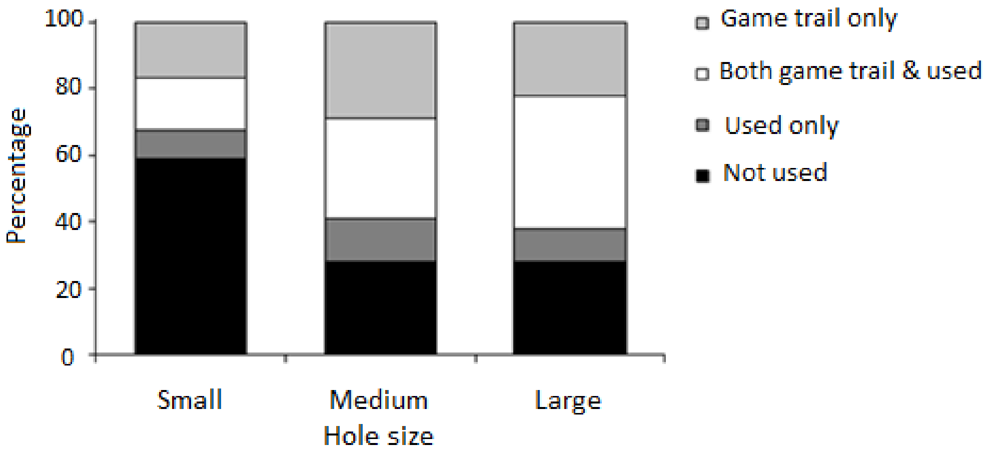

Figure 11: Percentage of unused and used (game trail only, used only, both game trail and used) holes found along the TTWR fence line, divided into non-used, used, game trail present and used with a game trail present.

Of the total, 691 holes were located within 50m of a transect location with 1486 holes located within 100m of a transect line. Holes were found to be randomly distributed along the fence line, however when the holes were categorized, medium holes were still randomly distributed while the remaining sizes were clumped (Figure 12). On further inspection regularly used holes (which had a game trail a present and evidence of use) and unused holes for each category were also clumped (Figure 12). There was a significant correlation between the total number of large and small holes found within 50m of a transect line (R_s = 0.24, p = 0.009) which remained with regularly used holes of the same categories (R_s = 0.34, p < 0.001), although only a significant correlation was found between unused medium and large holes (R_s = 0.29, p = 0.002). However no significant correlation was found between vegetation traits and hole count within 50m of the transects. Fifteen mammal species were identified from scat or spoor located in the hole, utilizing 33 holes in total (Table 10); animals were more likely to be recorded when a game trail was present at the hole (G_1 = 8.62, adjusted $p < 0.001$).

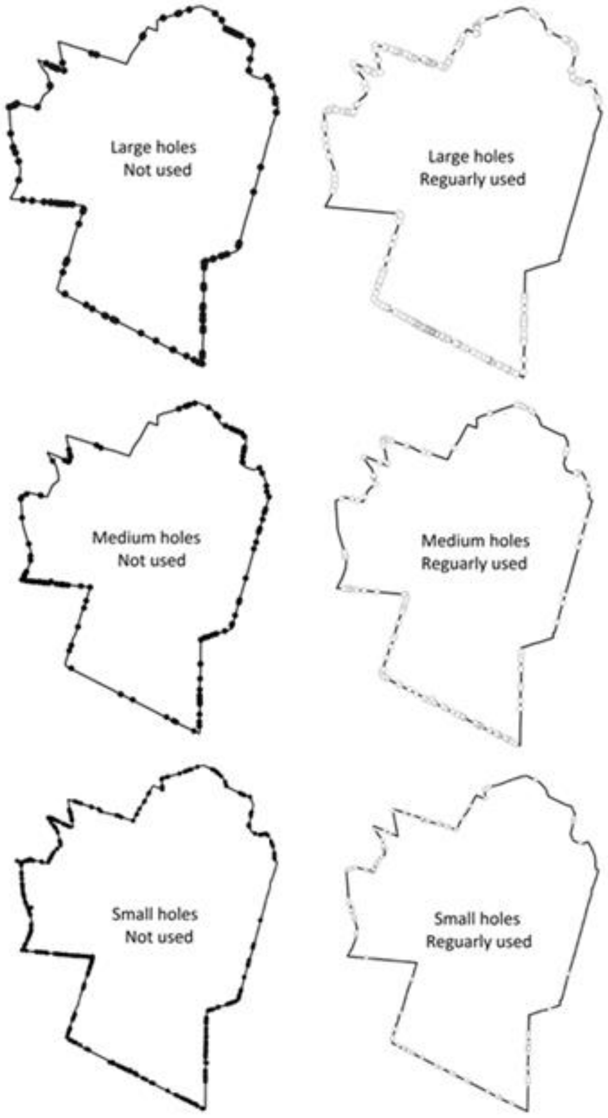

Figure 12: Distribution of regularly used and unused holes for each size category around the TTWR fence line.

Table 10: Number of records for each species recorded within a hole, the size of hole and whether there was a presence of a game trail at the hole where the evidence was recorded.

Hole	Species present	Binomial name	Count	Game trail presence
Small	Rock hyrax	*Procavia capensis*	1	1
	Smith's rock rabbit	*Pronolagus rupestris*	1	1
Medium	Baboon	*Papio ursinus*	4	4
	Meller's mongoose	*Rhynchogale melleri*	1	1
	Vervet monkey	*Chlorocebus pygerythrus*	1	1
large	Bushbuck	*Tragelaphus scriptus*	1	1
	Samango monkey	*Cercopithecus mitis*	1	1
	Serval	*Leptailurus serva*	1	0
Small and medium			0	
Medium and large	Aardvark	*Orycteropus afer*	2	2
	Brown hyena	*Hyaena brunnea*	6	3
	Duiker	*Sylvicapra grimmia*	3	3
	Warthog	*Potamochoerus porcus*	2	2
	Crested porcupine	*Hystrix cristata*	2	2
	Genet species	*Genetta spp*	4	3
	Klipspringer	*Oreotragus oreotragus*	3	2
All three			0	

Of the total complete transects 20 were located at holes, which primarily were in the medium category. There were no differences in vegetation or mammal attributes either side of the fence line for transects at holes, yet significant differences in vegetation diversity, percentage of non-woody plants (Table 7) and all mammal attributes remained for non-hole transects (Table 8).

3.4.3. Mammal activity at the fence line

Data from the 3.3km section of the boundary were omitted from the perimeter fence analysis. Thirty-one mammal species were identified along the fence line, with evidence more likely to be located inside the fence for both introduced game and wild species (Table 11, Figure 13) however when livestock were included in the introduced guild the difference became insignificant. Mirroring the results from the transect data, all diet guilds were significantly more likely to be found inside the reserve except for the myrmecovore (aardvark *Orycteropus afer*, Table 11). Species with <10 samples recorded on both sides of the fence were omitted from the individual species G-tests. Evidence for six of the 16 species, five which were introduced, was more likely to found inside the reserve (Table 11, Figure 14).

Table 11: Significant G-tests results showing the total counts of evidence located for each status guild, diet guild and individual species immediately either side of the fence, with the data from the 3.3km boundary with the neighbouring game farm removed and p-values adjusted following sequential Holm-Bonferroni correction.

Status/species/Guild	Count inside	Count outside	G_1	Adjusted *P*
Introduced	395	57	284.06	<0.001
Wild	956	650	58.66	<0.001
Domestic and introduced combined	395	442	2.64	NS
Browser	627	408	46.69	<0.001
Grazer	420	88	235.89	<0.001
Omnivore	257	115	55.60	<0.001
Carnivore	37	18	6.70	0.009
Greater kudu	300	190	24.80	<0.001
Blue Wildebeest*	49	10	28.09	<0.001
Burchell’s zebra*	68	3	70.19	<0.001
Eland*	180	39	97.35	<0.001
Gemsbok*	42	0	51.45	<0.001
Nyala*	29	2	2814	<0.001

* Species introduced to the reserve

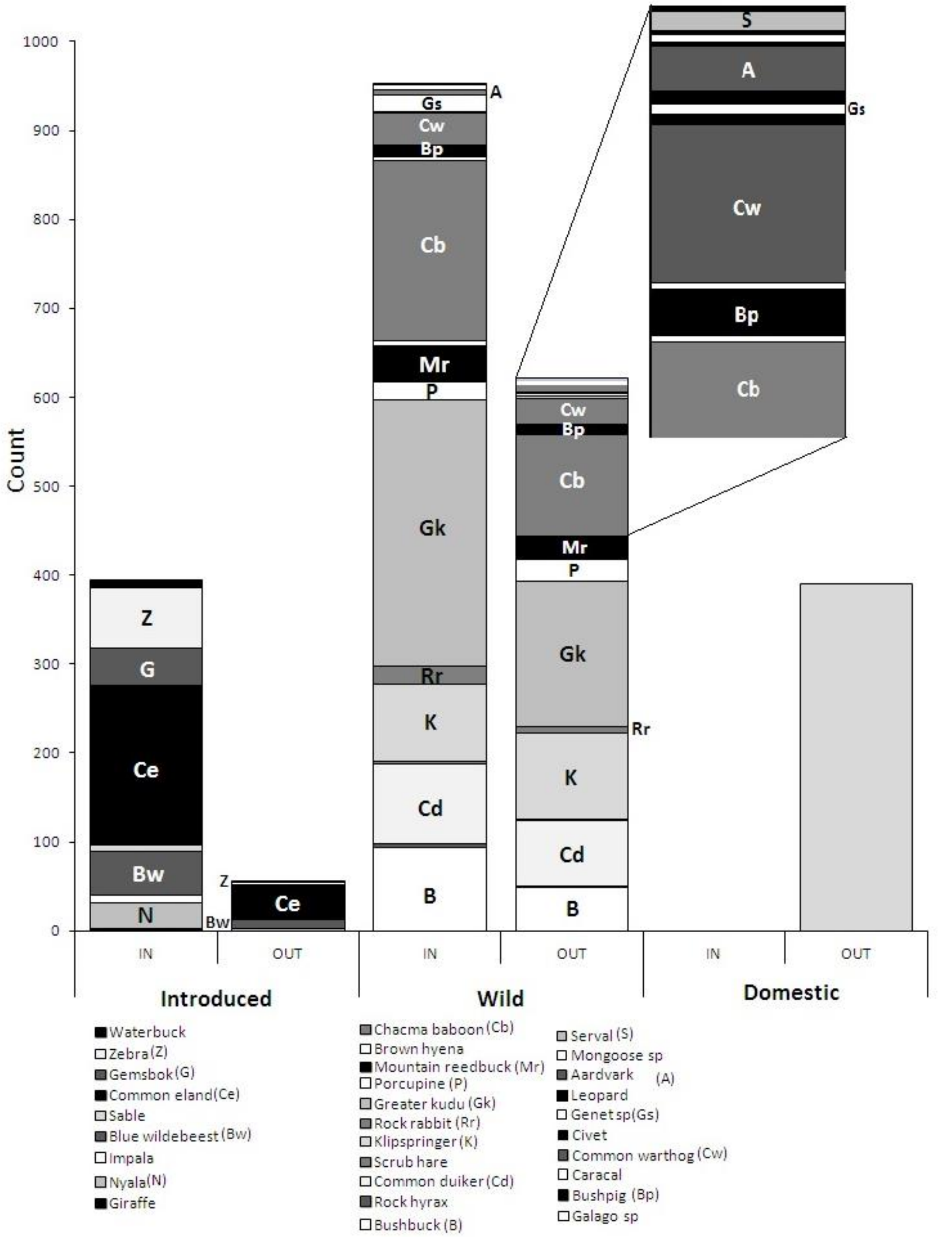

Figure 13: Total counts for each species recorded immediately inside and outside of the fence categorized by status, with the data from the 3.3km boundary with the neighbouring game farm removed.

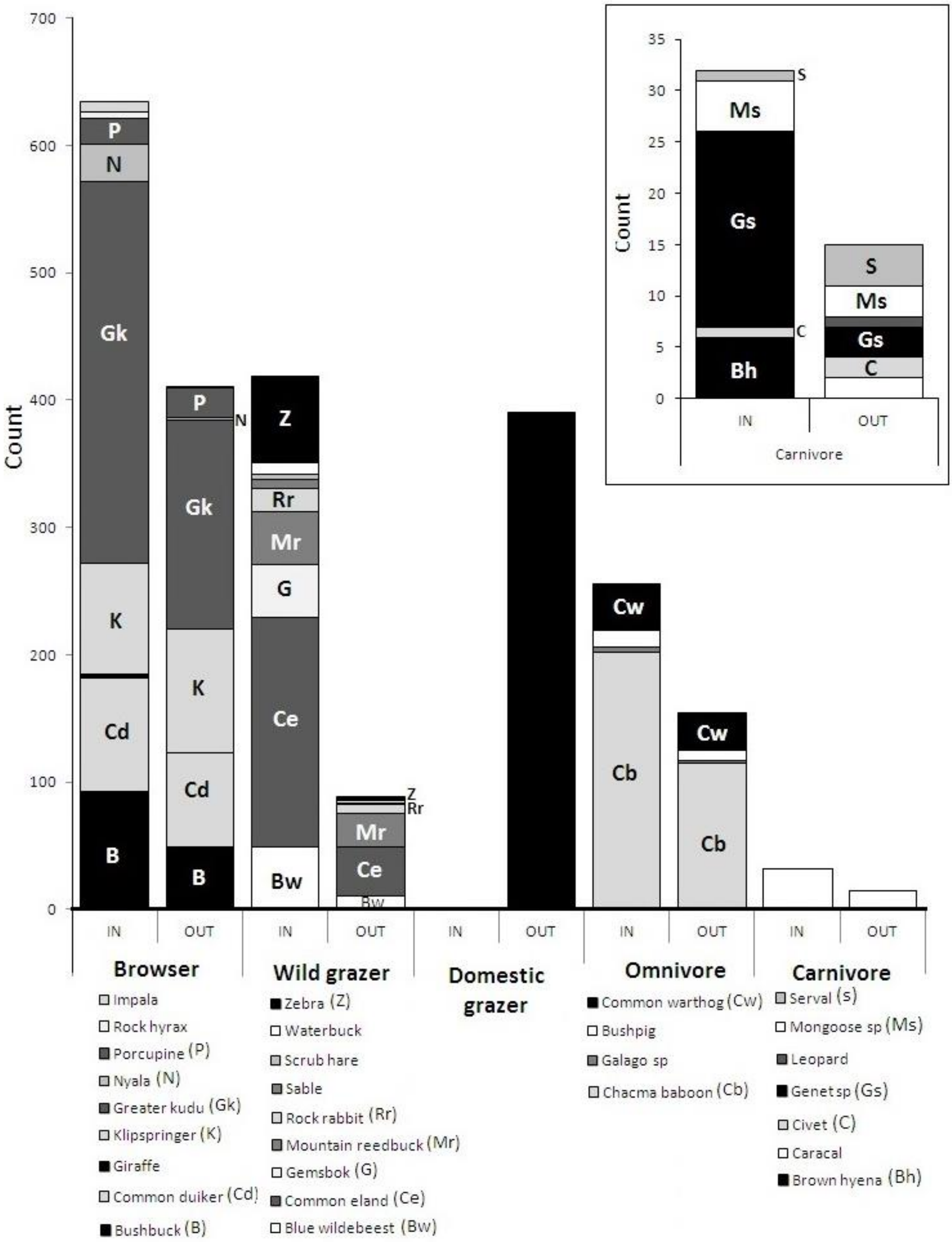

Figure 14: Total counts for each species recorded immediately inside and outside of the fence categorized by diet with data from the 3.3km boundary with the neighbouring game farm removed.

3.5. Discussion

Fences are ubiquitous, playing a central role in isolating larger species of conservation or economic concern from threats (Thouless & Sakwa 1995; Hayward & Kerley 2009; Packer *et al.* 2013), to ease management and to reduce the spread of disease between domestic and wild species (Andrews 1990; Vanak *et al.* 2010). The recent, rapid growth in numbers of small commercial game reserves in countries such as South Africa (Cousins *et al.* 2008; Taylor *et al.* 2016) has resulted in a substantial increase in the number of pockets of populations of wild and introduced game often surrounded by agricultural land maintained for crops and livestock (Lindsey *et al.* 2009). Here, we report the results of a study investigating how the erection of a fence around a relatively new small commercial game reserve affected the distribution of larger wild, introduced and domestic mammals, finding that while domestic animals were restricted to agricultural land, there was evidence of some movement across the boundary of introduced game species, and sizeable movement of large wild mammals across the fence line. We found direct evidence of fence condition (measured by the presence of holes in the fence) affecting movement, with larger holes being associated with more indications of use. The introduction of the fence has resulted in a change in vegetation structure, which in turn is likely to alter the distribution and abundance of a wider range of species.

We considered the effect of the fence on the distribution and behaviour of animals by searching for evidence of their presence a) along the fence line itself, and b) by the use of 100m perpendicular transects conducted approximately every 250m along the fence line. Both approaches found significantly more animal evidence, diversity and game trails inside the fence line of the game reserve. However, when we consider the nature of the animals, whether through the perspective of their relationships with humans (domestic, commercial game species, wild mammals) or their feeding guild, differing patterns emerge. Although every effort was made to limit the misidentification of species using guides and an experienced field guide, we acknowledge it can still be possible to misidentify signs; however by having large number of replications and classifying species into guilds, the margin of error should be further reduced. We found no evidence of movement of domestic animals (almost all cattle) across the fence. In contrast, Chigwenhese *et al.* (2016) found that cattle would utilise holes in fences at Gonarezhou National Park, Zimbabwe, while buffalo only crossed where the fence was completely removed as a result of elephant damage. However, with introduced game there is evidence for some movement across the fence line (17% of records for introduced game were found outside of the game reserve. Although these species are not considered to be naturally present in the local mammal community, there is a slim possibility they may have been in the area previously. Records of wild game were more even (61% of wild game records were collected inside the reserve), but these could be the result of the formation of two populations, isolated by the introduction of the fence. Indeed, when we consider individual species, it is noteworthy that the greatest differences in evidence along the fence line are for introduced game species (wildebeest, zebra, eland, gemsbok, nyala) and domestic animals. The only ‘wild’ game species to show a significant difference in evidence across the fence line was greater kudu, which was more abundant inside the reserve.

Indeed, it is evident that the TTWR fence line is not an impermeable barrier. Some animals can directly cross through or over the fence; however damage may have increased the opportunity for movement across the boundary line. We found 962 holes larger than 10 cm along the boundary. While fewer than half of small holes showed evidence of use (presence of a game trail and/or animal signs), over 70% of medium and large holes were used. As expected, smaller species (rock hyrax, Smith's rock rabbit *Pronolagus rupestris*) used small holes, while larger holes were used by a wide range of species, including brown hyena, grey duiker and klipspringer. Although regularly used holes of each category were clumped in areas along the fence line; there were no significant correlations between number of holes and vegetation traits, however there were significant correlations with used and unused holes of different categories, suggesting there is a pattern of movement which may be driven by something other than physical attributes. Over 40% of holes were within 50m of a transect, and almost 90% of holes were located within 100m of a transect line, which may explain why we were unable to detect any differences in vegetation or mammal activity from transects with holes as mammals are mobile and their effects are unlikely to be limited to narrow areas.

Nevertheless, when we consider the feeding guilds of the non-domestic mammals [browsers, grazers, carnivores, omnivores, and a myrmecovore], we find that all apart from aardvarks *Orycteropus afer* (no difference) are more frequently recorded inside TTWR fence line. This suggests that in spite of the opportunity for movement of animals (notably medium sized and smaller) across the fence line, the reserve could be acting as a preferred habitat for these species. The presence of livestock could be affecting the habitat choice of wild game through direct (Madhusudan 2004) or indirect (Adams 1975) competition for food, with game potentially avoiding areas of high livestock density, however further research would be required to confirm this hypothesis.

Despite the fact fences can protect wildlife and humans (Sukumar 1991; Hayward & Kerley 2009) as well as lead to rapid population growth for species of conservation concern (e.g. a brown hyena population increased by almost four-fold in 10 years following fencing; Welch & Parker 2016), their use is controversial among conservation biologists (Creel *et al.* 2013, Woodroffe *et al.* 2014). They can result in fragmented landscapes, and where habitat fragments are small, predators and large mammal populations can rapidly decline (Woodroffe *et al.* 2014). Fences prevent herbivores from tracking changes in vegetation availability over a landscape scale (Caughley *et al.* 1987), and where water is seasonal, reduce access to this resource too (Williamson & Williamson 2009). Such constraints can lower the carrying capacity of the fenced area, as well as resulting in habitat degradation through over-grazing. For example, Cassidy *et al.* (2013) found significantly reduced vegetation inside a fence surrounding a wildlife management area in Botswana. Notably, woody cover and tree diversity was half that outside the fence, an area used for tribal grazing.

It is unsurprising that such patterns are evident, and to a large extent will depend on stocking, density and management. While the fence has only been fully in position for six years, we found greater overall plant diversity inside the fence line, and an increase in the contribution of smaller (non-woody) plants to ground cover, suggesting that grazing intensity is much higher in the surrounding farmland. However, woody cover was not different, suggesting the distribution of browsers either side of the fence was potentially equalizing the effect on woody plants, reflecting similar findings by Augustine *et al.* (2011), who found wild browsers mixed with livestock reduced bush encroachment. We acknowledge that our analysis of plant community structure is relatively simple, and fails to capture the complexity of patterns seen on the ground. For example, thorn bushes are mainly located at lower altitudes in TTWR, and there are visible differences in cover, with greater cover inside the fence line. These differences are hidden by variation in vegetation with altitude. Nevertheless, there are clear differences in plant community structure, which are likely to reflect grazing pressure (notably by cattle and introduced game), leading to rapid change in plant communities and hence wild herbivore communities either side of the fence line (*cf.* Todd & Hoffman 1999). We were surprised to find no evidence of edge effects, with no significant difference in amount of animal evidence or vegetation characteristics recorded up to 50m and 50-100m from the fence line, however a study by Laurance *et al.* (2011) showed edge effects could occur at distances over 100m, outside of our transect length. Alternatively the lack of an edge effect may be a consequence of the relatively free movement of game at the study site. Therefore replications at other sites with varying states of fence condition would be recommended to further examine the results found in this study.

Although controversial, fences do fulfil the basic role of species separation; however maintenance plays a large role in permeability which can be costly and difficult in challenging terrain, typical in countries like South Africa. The use of specialised fence-gaps at a Kenyan wildlife conservancy has been investigated with encouraging results, allowing the passage of large mammals, including elephants, but preventing movement of black rhino (Dupuis-Désormeaux *et al.* 2016). Maintaining specific sized holes in a fence to allow movement of target species could potentially reduce genetic isolation of populations either side of a fence and in doing so may limit the negative effects of the fence (Augustine *et al.* 2011). Further research is needed to ascertain whether seasonal differences or other factors could explain the differences found in usage of certain holes.

3.5.1 Management implications

Fences are ubiquitous and their use in conservation is controversial (e.g. Caughley *et al.* 1987; Mbaiwa & Mbaiwa 2006; Williamson & Williamson 2009; Dickman *et al*. 2009; Hayward & Kerley 2009). In some circumstances, fences can be beneficial, yet we have little understanding of how effective they can be. Although the study was limited to one site here we show that fences can be effective barriers against the incursion of domestic animals into protected areas, but less so in terms of introduced and commercially valuable game animals. The fence was much less effective at limiting the movement of other wild large mammals; the latter in part may be associated with damage to fences and the variation in the agility of some species. The erection of a standard game fence has relatively quickly resulted in changes in vegetation structure, changes that are likely caused by the different feeding pressures either side of the fence (Todd & Hoffman 1999), however it is plausible these effects may be limited by allowing the movement of wild fauna (Augustine *et al.* 2011) through specific sized holes in a fence. We recommend further investigation at sites with varying fence conditions in order to fully examine this. In addition this could also potentially reduce the risk of genetic isolation of highly mobile and endangered species in areas where alternate barriers or conservancies are not feasible, while still restricting the movement of more valuable introduced species and livestock.

Chapter 4

Habitat influences the structure of mammalian predator assemblages on the border between two distinct habitats: a case study in South Africa.

4.1. Abstract

Although many of the megafauna are located within protected reserves in South Africa, leopard and other meso-predators are found outside of these formally protected areas. Little is known about carnivore community composition and habitat preferences in the absence of lion and other large predators. Here we report density estimates of a leopard population at a transition zone between savannah and grassland eco-regions. Using camera traps, we investigated how leopard presence and habitat composition may affect the presence and abundance of other large mammalian carnivores. Mean leopard density was between 3.04 (S.E. +/-1.55) and 4.97 (S.E. +/-2.14) leopards per 100km^2, which is lower than densities previously recorded in savannah dominated habitats. We found no significant differences in use between the two habitats for leopard, but there was for six of the sixteen predator species recorded, with significantly higher relative local abundance of brown hyena, Cape fox, caracal and serval in grassland and large spotted genet and Meller's mongoose showing preference for savannah. Many of the carnivores including caracal and both jackal species showed a significantly lower relative local abundance in the wet season, which may be linked to these species hunting livestock during seasonal birthing in surrounding farmland. Habitat was more important than local leopard, brown hyena or caracal relative abundance levels in explaining the relative local abundance of other carnivores. While Thaba Tholo Wilderness Reserve is clearly a source for leopard, the relatively low numbers recorded compared to other savannah areas implies that other factors may be limiting local population increases.

4.2. Introduction

4.2.1. Habitat and prey

Vegetation structure directly and indirectly determines the distribution and abundance of most terrestrial mammal species (Andrews & O'Brien 2000). Herbivore distribution and abundance is largely driven by resource availability, quality and abundance (Bailey & Provenza 2008) which in turn influences carnivore density and distribution (Stander *et al.* 1997; Fuller & Sievert 2001). Nevertheless, habitat underpins carnivore distribution and abundance due to herbivore regulation through the bottom up process (Power 1992). This can be extremely restrictive for prey specialists such as aardwolf (Matsebula *et al.* 2009), but less so for a generalist such as leopard. Not only can the vegetation characteristics influence the effectiveness of prey detection and catchability (Balme *et al.* 2007), it can provide concealment for meso-predators from apex predators which can influence intra-guild effects (Janseen *et al*. 2007; Ritchie & Johnson 2009). Consequently this can enhance or suppress carnivore densities and distribution (Gommper *et al.* 2016) and are therefore key aspects in the conservation of carnivores.

4.2.2. Interactions

The avoidance of apex predators by smaller predators can be a limiting factor in their distribution and composition within areas of suitable habitat and prey availability (Vanak *et al.* 2013; Gompper *et al.* 2016) which can be either the result of intra-guild predation (Palomares & Caro 1999); the effects of which can provoke a change in behaviour from just scent alone (Leo *et al.* 2015), or through inter-specific competition for prey (Durant 2000; Caro & Stoner 2003; Vanak *et al.* 2013). In Africa, species interactions with lions has been widely investigated and results have found members of the large carnivore guild demonstrate a degree of avoidance of lions, which was more pronounced in cheetah and wild dog than leopard (Hayward & Slotow 2009; Durant *et al.* 2010; Pettorelli *et al.* 2010). However effects of apex predator abundance on smaller predators where lions are absent have rarely been explored hence potential relationships are relatively unknown. Some areas have experienced the complete removal of apex predators such as cougar (Ripple & Beschta 2006), coyote (Crooks & Soulé 1999), and dingo (Letnic & Kock 2010), which has resulted in meso-predator release, highlighting the important regulatory role apex predators play in an ecosystem. Similarly apex carnivores can also directly or indirectly affect herbivore abundance and composition (Hopcraft *et al.* 2009) and therefore plant community structure (Schmitz *et al.* 2000) through a tropic cascade effect.

4.2.3. Mammal distribution in South Africa

South Africa encompasses nine vegetation biomes (Mucina *et al.* 2008) which are further sub-divided into eco-regions that share similar physical and biotic features (Rutherford *et al.* 2006). Some mammal species are associated with individual biomes, while others are less specialised (Apps 2000). Generally the large charismatic mega-fauna (e.g. lion, elephant, and giraffe) are associated with the savannah biome (App 2000) which is the largest South African biome covering approximately 32.5% of the country. It dominates the north and east of the country (Mucina *et al.* 2008) and is characterized by a co-dominance of trees and grasses; although the ratio between the two varies considerably depending on the savannah eco-region (Higgins *et al.* 2000). It is home to the greatest diversity of mammals in South Africa, with numbers decreasing westwards (Gelderblom *et al.* 1995; Andrews & O'Brien 2000). Conversely although grassland is the second largest biome (27.9% of land area), and is found mainly on the high altitude plateau located in the central part of South Africa (Mucina *et al*. 2008). The biome and subsequent eco-regions generally lack mega-fauna but contains fifteen of the 34 mammals endemic to South Africa including springbok *Antidorcas marsupialis*, mountain reedbuck *Redunca fulvorufula*, blesbok *Damaliscus pygargus* phillipsi, and black wildebeest *Connochaetes anou* (App 2000).

4.2.4. Predator distribution in South Africa

The mega-fauna found in savannah are now mainly confined to large government protected reserves and National Parks, or to some of the 9,000 (Taylor *et al*. 2016) privately-owned fenced game reserves (Hayward *et al.* 2007b; Hayward & Kerley 2009; Stuart & Stuart 2015). Large protected reserves are thought to cover 9.3% (Swanepoel *et al.* 2013) and privately owned reserves 16% of the total country (Taylor *et al*. 2016). These private reserves can be utilized for tourism, hunting or farming (Taylor *et al.* 2016) and may incorporate a combination of wild and introduced species (Hayward *et al.* 2007b; Pirie *at al*. submitted a; Chapter 3) which could have implications for the native and introduced species alike. However leopard and smaller mammals are still free-roaming across parts of the country, with some species able to traverse fences into or out of reserves more readily than others (Hoare 1992; Cozzi *et al.* 2013; Pirie *et al.* submitted a; Chapter 3).

Of the 35 terrestrial carnivores in South Africa, aardwolf, African wild cat, brown hyena, caracal, honey badger, slender mongoose, small-spotted genet and striped polecat are considered to be more widely distributed across the biomes. African civet, large spotted genet, serval, side striped jackal and many of the mongoose species show preference for eco-regions within savannah, whereas bat-eared and Cape foxes, black-backed jackal, and yellow mongoose are associated more with grassland eco-regions and other biomes in the west of the country (Stuart & Stuart 2015). The leopard is known to be highly adaptable (Hayward *et al.* 2006) and is considered to be widespread throughout South Africa (Stuart & Stuart 2015) which qualifies the leopard as the apex predator outside large protected areas (Martins & Harris 2013), rivalled only by brown hyena for size and distribution across the country (Mills 1982, Mills 1991). Although brown hyena is capable of hunting (Stuart & Stuart 2015), they are regarded as a specialized scavenger (Van der Merwe *et al.* 2009).

Twenty percent of South Africa is thought to contain the most suitable leopard habitat, mainly located within the forest, thicket or savannah biomes (Freidmann & Traylor-Holzer 2008; Mucina *et al.* 2008; Swanepoel *et al.* 2013) providing a lot of cover and abundance in prey, whereas grassland is thought to be unsuitable for leopards (Swanepoel *et al.* 2013). Indeed Balme *et al*. (2007) and Durant *et al.* (2010) found that leopards were less likely to be in open grassland within savannah either due to an increase in the chance of being detected by prey due to lack of cover, or to avoid larger predators such as lions. Although similar in appearance the presence of an upper woody layer and differing herbaceous species distinguishes savannah from grassland (Cowling *et al.* 2004). Relatively little is known about the population densities of leopard in these less favourable habitats or in the transition zones of these habitats (Appendix 1).

4.2.5. Consequences of game reserves

The increase in small reserves has likely contributed to the fragmentation of the land (Swanepoel *et al.* 2014) and a major consequence of the disjointed nature of these small game reserves is the increased likelihood of human-carnivore conflict from predators living on the edge of these reserves and moving between them. While carnivores are not always responsible for the killing of livestock (Poliser *et al.* 2003) the perceived threat can be enough to prompt requests for a Damage Causing Animal (DCA) (Balme *et al.* 2009a; Pitman *et al.* 2016) permit to legally remove the animal with some species (caracal and black backed jackal) which can be removed without a permit in some provinces (Anon 2013a). In addition illegal retaliatory killings do also occur (Treves & Naughton-Treves 2005; Woodroffe *et al.* 2007; Lindsey *et al.* 2013; Swanepoel *et al.* 2014). Most estimates of leopard density have been based on animals living inside large protected game reserves (Appendix 1). Only two studies have reported leopard densities outside of large protected areas where leopards are exposed to legal and illegal removal; both of which were conducted within suitable habitat in the Limpopo province (Appendix 1). In light of the recent study which concluded leopard distribution has been reduced to 25% of its former range (Jacobson *et al.* 2016), it is therefore of conservational concern that leopard densities are quantified in areas which may be less suitable for leopards and where permits may be allocated to allow informed decisions regarding permit allocations and reserve management to be made.

Historically studies on carnivores have been difficult to achieve due to the nocturnal and elusive nature of many focus species (Karanth & Nichols 1998; Stuart & Stuart 2015) which makes them challenging to study. However the use of camera traps as a tool for monitoring and surveying these species has increased greatly in recent years (e.g. for tigers, Karanth & Nichols 1998; leopards, Trolle & Kery 2005; snow leopard, Jackson *et al.* 2006; Rowcliffe & Carbone 2008; carnivore biodiversity, Pettorelli *et al.* 2010; ocelot, Trolliet *et al.* 2014). In addition, powerful statistical approaches have been developed which can utilise data from camera traps, particularly in order to estimate density and relative abundance based on occupancy levels (Fiske & Chandler 2011; Efford *et al.* 2009; Efford 2015). In particular maximum likelihood based spatially explicit capture-recapture models are becoming more widely used in their application for density estimates of secretive species with small sample sizes but have unique patterns for identification. (e.g. jaguar, Sollmann *et al.* 2011; bobcat *Lynx rufus,* Thornton & Pekins 2015; leopard, Gray & Prum 2012; Swanepoel *et al*. 2015; Braczkowski *et al.* 2016).

It is becoming increasingly essential to gain more intricate knowledge of the ecological mechanisms which influence carnivore abundance due to the increasing pressures on the taxa from the loss of habitat, prey and direct removal by humans and environmental changes (Pettorelli *et al.* 2010). It is therefore important to understand how habitat may affect not only apex predator density and abundance but other carnivore abundance and composition as well and similarly how apex predator abundance may affect that of other carnivores in order to maintain healthy ecosystems within the confines of fenced reserves which could be crucial for species survival (Swanepoel *et al.* 2014) and biodiversity (Ritchie & Johnson. 2009; Pettorelli et al. 2010).

We addressed these issues using a long term camera trapping approach at Thabo Tholo Wilderness Reserve, a private game reserve where the grassland and savannah biomes meet. Here we will a) determine the leopard population density in the reserve; b) investigate whether leopard density changes seasonally; c) determine whether habitat explains any variation in leopard density; d) investigate the relationships between mammalian carnivore species and e) determine if habitat explains differences in the likelihood of recording predators.

4.3. Methods

4.3.1. Study area

The study was conducted at Thaba Tholo Wilderness Reserve (TTWR), Mpumalanga, South Africa (Latitude: 24^{o}57”404 S, Longitude: 30^{o}21”105 E) between 01 October 2012 and 30 September 2015. The reserve is approximately 55km^{2} in area and is run as a commercial reserve containing a wide variety of wild and introduced ungulates, and wild carnivores.

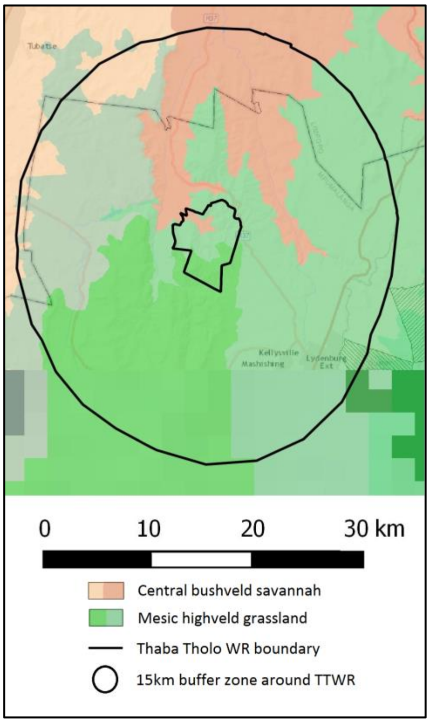

Figure 15: Thaba Tholo Wilderness Reserve boundary showing the eco-regions within the reserve and the 15km buffer zone highlighted in grey. (Downloaded from http://www.sanbi.org/ and manipulated in Quantum GIS 2.8.4).

The reserve lies between the Steenkampsberg and Mauchsberg mountain ranges, with altitudes ranging between 1100-2000m. The site incorporates savannah, the central bushveld eco-region, characterized by

Combretum spp. and *Vachellia* spp. mainly located in the north western areas and valleys, and grassland, the mesic highveld grassland eco-region (Mucina *et al.* 2008, Figure 15) mainly found in the south eastern part and mountains, characterized by very short grasses, forbs and the presence of isolated outcrops of *Protea* spp. (Bloem *et al.* 1993; Lötter *et al.* 2002). The mountainous grassland is recognised as being part of the Lydenburg centre of plant endemism (Lötter *et al.* 2002; Mucina *et al.* 2008). The central bushveld covers 39% of the Mpumalanga province and the remaining 61% is covered by mesic highveld grassland, of which 45% has been disturbed by farming and mining (Mucina *et al.* 2008; Fourie *et al.* 2015). The area has a local average annual rainfall of 700-900mm falling mainly in the summer between October and February.

4.3.2. Data collection - Camera traps

Although camera traps were found to significantly under record meso-carnivores compared to spoor located (Pirie *et al.* 2016a, Chapter 2), cameras were found to be the most reliable when recording leopard and can provide individual identification through coat recognition which can allow for more accurate calculations of density based on capture recapture models (Karanth & Nichols 1998; Trolle & Kery 2005). The fact cameras are indiscriminate allows for other carnivore data to be collected which can still allow for relative comparisons by using software to produce occupancy based abundancy estimates which consider values taken at other locations (Royle 2004).

The camera traps used in the study were all little acorn 5210A (Ltl Acorn, Green Bay, Wisconsin) units. Each was set to a normal sensitivity level, requiring two of the three heat and motion sensors to be activated for an image to be taken. Three images per trigger were taken after one second delay from activation, which could occur up to 15m from the unit. In order to avoid depletion of battery life from multiple triggers caused by wind or large groups of animals, an interval of 30 seconds between triggers was used. The cameras were positioned at 45 degrees to the road, using a metal stake with the lens 45cm off the ground (Pirie *et al.* 2016a, Chapter 2).

At each trapping point, two camera traps were positioned within each 1.6km x 1.6km square of a grid spanning the study site and participating surrounding farmland. The minimum known home range of an African female leopard in savannah is 14km^2 (Balme *et al*. 2009b). To ensure detection of all leopards potentially living within the study area, camera sites were therefore no more than 2.7km apart with ≥ 2 camera sites within a minimum leopard home range (Balme *et al*. 2009b). The core trap network of 26 sites consisted of one camera per site in order to cover a larger area without increasing camera distance and risk a leopard going undetected (Henschel 2008; Tobler & Powell. 2013). The units were operational for 1,095 days from 01 January 2013 to 30 September 2015 and covered an effective area of 70 km^2, which was used for both the habitat and density analysis (Figure 16). A further seven sites were operational on farmed properties outside the reserve (Figure 16), three between 01 January 2013 and 30 September 2015, three between 01 July 2014 and 30 September 2015, and one between 01 January 2014 and 30 June 2014.

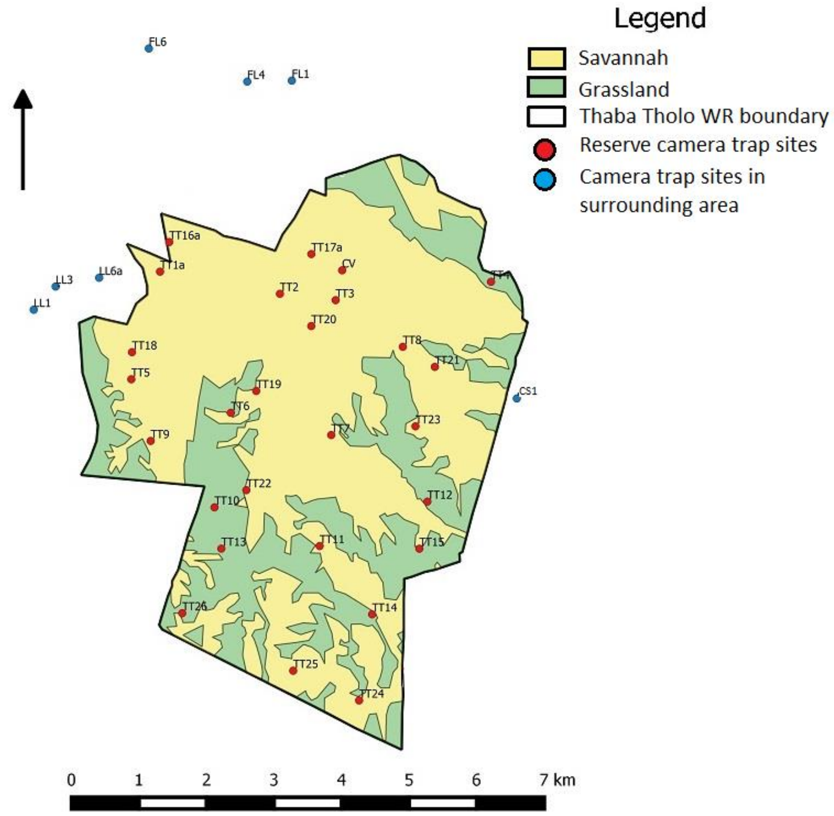

Figure 16: Camera trap locations inside (red) and outside (blue) Thaba Tholo Wilderness reserve and distribution of grassland (green) and savannah (yellow) biome within the reserve (Produced using Quantum GIS 2.8.4).

Detection is extremely important for density and abundance estimates (Karanth & Nichols 1998; Chapman & Balme 2010; Maputla *et al*. 2013), so core units were located on dirt roads to increase the potential of detection. Other studies have shown dirt roads can be used up to 90% more than game trails and other routes (Gusset & Burger 2005, Trolle & Kery 2005, Rowcliffe & Carbone 2008). Cameras were also positioned opposite game trails, road junctions (Pirie *et al.* 2016a, Chapter 2) or at natural funnels in the land to further maximize the rate of detection.

4.3.3. Data collection - Leopard and other carnivore image data

Over the duration of the study detailed identification kits were produced in order to identify individual leopards by their pelage pattern (Karanth & Nichols 1998, Balme *et al.* 2009b, Negroes *et al*. 2012, Pirie *et al.* 2014). To avoid double counting, unknown animals which had only the right side pictured were omitted from the analyses and any unclear pictures were rejected. Each individually identified animal was allocated a number and where possible sex and age were determined, however for the purpose of the analyses an animal was defined as an “adult”, “sub-adult” or “cub”. Adult was defined as being over two years old, sub-adult was used if the animal aged between a year and two years old and independent of the mother, and cub was used if the individual was pictured with the mother (Balme *et al.* 2009b). All records of carnivores which were identifiable to species were recorded for each camera trap location. As it was not possible to identify common large spotted genet *G. maculate*, and South African large spotted genet *G. tigrina* apart (Stuart & Stuart 2015) they were grouped together as large spotted genet.

4.3.4. Data collection - Habitat descriptors

A grid of 0.8km x 0.8km squares was superimposed over the map of the study site. Each intersection was numbered 1-49 and a random number generator was used to produce 26 points to survey. The area where the intersection fell was located in the field and a stone was thrown by one person, over their shoulder, to locate the first corner of the 50m^2 quadrats, which were then constructed and corners marked. Vegetation data were recorded at every 10m x 10m point. Here, the type of cover was recorded as bare ground (BG); non-woody (grass/ forbs/succulents: NW); and woody (trees, bushes, shrubs: W). The height of the vegetation was recorded as 0-1m, 1-2m, 2-3m, 3-4m and >4m. Where possible, vegetation was identified to species following Schmidt *et al.* (2002), Van Oudtshoorn (2012) and Manning (2009). Where this was not possible taxa were recorded to morphospecies. Data were collected in a similar manner around each camera trap site, except that the centre of the quadrat was located where the camera trap was placed.

4.3.5. Analysis - Leopard density estimation

The ability to identify individual leopards through their coat patterns (Karanth & Nichols 1998, Balme *et al.* 2009b) and relatively high numbers of detections allowed us to use a mark, capture-recapture model to calculate leopard density.

The data were analysed at two temporal scales. First, the calendar year was divided into quarters (91 days): 1) 01 Jan-01 Apr; 2) 02 Apr-01 Jul; 3) 02 Jul-30 Sept; 4) 1 Oct-31 Dec. This was to ensure assumptions of population closure were met (Otis *et al.* 1978; Stanley & Burnham 1999; Efford 2015) and to highlight any change due to seasonal variation (Stander *et al.* 1997a). Second, data were analysed using full years running from October 01 to September 30 for three years, to coincide with a full seasonal cycle of wet and dry periods, in order to increase detection rates and incorporate the full extent of area which the animals may utilize during different seasons. We acknowledge this would not meet the necessary assumption of closure; however the relatively long observational period allowed us to omit animals which would violate the assumption.

A recording event was defined as a single animal pictured at a single site over a 24 hour period (00h00 – 23h59). Cubs pictured with the mother were omitted from the study. Cubs which were >1 year old and not pictured with the mother were classed as sub-adult and used in the total animal model (Athreya *et al.* 2013) for the year analyses, but omitted from the adult only model and the quarterly data analyses. Densities were then calculated for each session using the likelihood of capture, utilising spatial explicit capture-recapture (secr) in R (Efford 2015). Camera trap information including the co-ordinates of each trap, basic habitat (grassland, savannah), altitude, percentages of bare ground, trees and other vegetation within a 50m^2 quadrat, and the camera activity for each 24 hour period (working, not operational) were recorded.

Non-operational periods could be due to battery failure, SD card or camera malfunction, camera removal by an animal, or the destruction of a camera by an animal or fire.

Leopard capture history included the individual animal identification number, sex, trap site code and particular 24 hour period it was recorded. A "mask" of potential home range points was also uploaded to the program. These points were spaced 580m apart within a buffer zone of 15km for which was plotted from the outermost camera traps (following Braczkowski *et al.* 2016) which excluded areas which were unlikely to contain the home range centre, such as fenced citrus farms and the town of Lydenburg (Figure 13).

There are three parameters in the secr likelihood analysis; the probability of detection at the home range centre (g0), the rate of reduction in detection as distance increases from the home range centre (sigma), and the leopard density (D) (Efford 2015). We fitted models to include a basic constant (.), behaviour changes towards all cameras after a single capture from a camera (b), learned response to a single site after a capture at that site (bk), transient response which depended on the previous capture at the site (Bk), heterogeneity (h2) and sex as effects on the location of the home range centre and basic habitat type, altitude, percentage of bare ground, woody and non-woody vegetation and sex which may affect the density estimate. The best model for each session was chosen using the Akaike Information Criterion (Akaike 1974, Efford 2015) by first comparing models based on each covariate, then comparing the best model from each of these with the basic model (Braczkowski *et al.* 2016). This was done for each of the three month data sets over the three years and year data sets for adult animals only and for independent animals over a year old (Bailey 1993).

4.3.7. Analysis - Habitat

Mann-Whitney U-tests were used to compare proportions of bare ground (BG), woody plants (W) and non-woody plant (NW) cover at quadrat sites containing a camera and the random sites to test for any bias in camera site habitat locations. Quantum GIS (2015) and local knowledge was used to select areas with tree cover (savannah: 64% of sites) and without dense tree cover (grassland: 36% of sites) within the study site to produce relative proportions of the two biome types.

4.3.8. Analysis - Relative abundance

Data from the three year period were used in order to reduce the error of detection for each species by the camera traps (Pirie *et al.* 2016a, Chapter 2) to generate relative local abundance estimates at each site for the carnivore species using the R-package "Unmarked" (Fiske & Chandler 2011), specifically using an N-mixture model (Royle 2004) with day as the temporal sampling unit (Brodie & Giordano 2013). N-mixture models consider variation in abundance at each site based on site covariates of all sites to produce reasonable estimates of abundance (Royle 2004). Due to the generally solitary nature of African carnivores (Estes 1997), the data were formatted into a matrix which included a single detection per site per 24h period (00h00 – 23h59) as 1 in order to avoid over-estimation due to repeated capture of the same animal on the same night. Sites where no animals were photographed were recorded as 0. The detection function was set to include the number of sampling occasions per site based on the number of 24h periods each camera was operational. We then looked at the effect of woody cover only on each of the carnivores. We then assessed various models which included altitude and proportions of woody, non-woody and bare ground as covariates for the abundance function. The best model was chosen based on the lowest Akaike Information Criterion (Akaike 1974; Efford 2015) and highest AIC weight. The relative abundance at each site for each carnivore was calculated using the “predict” command.

4.3.9. Analysis- Habitat preference

Mann-Whitney U-tests were used to test for differences in the local relative abundances for each carnivore between the two biomes. Relative local abundance estimates for each camera site were then calculated for three month periods termed the “wet season” (January to March, when vegetation is abundant and water readily available) and the “dry season” (July to September, when water is scarce and vegetation reduced). Paired Wilcoxon signed-rank tests were used to test for differences between the seasons at each site for all carnivores. Holm’s sequential Bonferroni (Holm 1979) was used to correct for any errors associated with performing multiple tests.

4.3.10. Analysis - Species Interaction

Relative local leopard, brown hyena and caracal abundance was used as the only covariant and modelled to investigate possible relationships between each of the three carnivores and the other meso-predators. The relative local abundance values for leopard, brown hyena and caracal were then added as extra covariates for each individual carnivore. Models including leopard, brown hyena and caracal either singly or as a combination were included with and without the vegetation characteristics for each carnivore. The best model was chosen based on the Akaike Information Criterion (Akaike 1974, Efford 2015) and highest AIC weight.

4.4. Results

Over the three year period (1,095 trap days), the 26 core trap sites were operational for an average of 79% of the time, producing a total of 21,057 trap sampling days and capturing 41 mammalian species (Appendix 2) of which 16 were carnivores (46% of the total South African carnivore species). There were a total of 5,393 images containing large carnivores of which 1020 were African civet, 767 brown hyena, 35 Cape fox, 114 caracal, 269 honey badger, 237 black backed jackal, 157 side striped jackal, 1283 large spotted genet, 948 leopard, 395 Meller’s mongoose, and 139 serval.

4.4.1. Leopard density

Over the three years we identified 28 leopards (Table 12) from a total of 1,568 recorded events. A single animal was omitted from the analysis to avoid double counting due to only the right side being pictured. Of the 18 adults, four (2 female, 2 male) were resident throughout the three years and seven were pictured ≥ 3 months (4 female, 1 male). Of the total of 1,568 leopard events recorded, 135 were not clear enough to identify the individual (mean 3.75 images per month); of those that could be identified, 54% were female and 46% male.

Table 12: Counts of individual leopards identified over 3 years.

Sex	Adult	Sub-adult	cub	Total
Female	12	2	1	15
Male	6	6		12
Unknown	-	-	1	1
Total	18	8	2	28

As we found no significant difference in leopard counts between savannah and grassland (see below), the habitat mask incorporated both habitats as suitable (Figure 17). However proportions of cover and overall habitat type were kept as covariates within the models. The "mask check" command in secr showed the 15km buffer was adequate with no change in log likelihoods with increases in buffer size.

Each quarterly period was found to meet the closure assumption using the closure test in secr (Efford 2015). Data from the fourth session in 2014 was limited so density estimates were not obtained. The mean number of animals captured was 6 (S.E. +/- 0.18) with a mean of 80 (S.E. +/- 5.8) re-capture occasions per quarter. The mean density was 3.04 (S.E. +/- 1.55) leopards per 100km^2. The majority of best models based on the AIC weight incorporated a learned response to a camera site after capture (Table 13) which all showed a positive response suggesting the animals were undeterred by the camera traps and regularly utilized roads.

Figure 17: Habitat suitability mask showing the unsuitable habitat (white) and potential home range centres every 580m (grey) within a buffer of 15km of the camera trap locations (crosses).

Table 13: The best basic model for each quarterly period based on the weighted AIC for adult leopards only (K= parameters, LL= log Likelihood, g0= detection probability at the range centre, σ = detection decline from range centre, D=density, CVD=coefficient variation estimates of the density).

Session	Model	AICc	AIC wt	*K*	LL	*g*0 (+/-SE)	σ (m) (+/-SE)	D/100 km^2 (+/-)	CVD
2012_4	*g*0 (.) σ (.) D (.)	662	1	2	-326	0.02 (0.004)	2402 (601)	3.11 (1.85)	0.59
2013_1	*g*0 (.) σ (.) D (.)	434	0.96	2	-213	0.02 (0.006)	1896 (371)	4.81 (2.33)	0.48
2013_2	*g*0 (bk) σ (.) D (.)	646	0.86	3	-314	0.01 (0.003)	3185 (962)	2.36 (1.50)	0.64
2013_3	*g*0 (sex) σ (.) D.)	889	0.77	3	-429	0.04 (0.009)	2740 (460)	2.04 (1.17)	0.57
2013_4	*g*0 (bk) σ (.) D (.)	850	0.90	3	-416	0.01 (0.004)	4180 (1427)	1.60 (1.13)	0.70
2014_1	*g*0 (bk) σ (.) D (.)	650	1	3	-316	0.01 (0.002)	2220 (427)	4.65 (2.20)	0.47
2014_2	*g*0 (bk) σ (.) D (.)	1085	0.98	3	-528	0.02 (0.003)	2330 (353)	2.76 (1.36)	0.49
2014_3	*g*0 (.) σ (.) D (.)	807	0.93	2	-399	0.02 (0.004)	2270 (343)	3.27 (1.50)	0.46
2015_1	*g*0 (.) σ (.) D (.)	691	0.53	2	-342	0.02 (0.003)	2417 (387)	3.04 (1.42)	0.47
2015_2	*g*0 (bk) σ (.) D (.)	1063	1	3	-522	0.01 (0.003)	2522 (370)	2.77 (1.27)	0.46
2015_3	*g*0 (bk) σ (.) D (.)	1002	0.99	3	-492	0.01 (0.003)	2390 (386)	3.04 (1.42)	0.47

Models containing habitat were not found to be significant suggesting habitat was not influencing the leopard home range centre locations. There was no significant change in density estimates. However this does suggest that younger animals are dispersing out of the immediate area rather than taking up residence within their maternal range and the lack of change in adult identity over the periods suggested a stable system in the area.

4.4.2. Annual densities

The density models based on year data also showed a learned response to a camera site after capture and showed a general positive trend in density. The mean density based on adult animals was 4.97 (S.E. +/- 2.14) leopards per 100km^2, with female leopard density averaging 3 (S.E. +/- 1.6) animals per 100km^2 and males 2 (S.E. +/- 1.3; Table 14). For all independent animals over a year old, the density was 6.7 (S.E. +/- 2.3) leopards per 100km^2. Based on these densities the mean population estimate for the mask area of 995 km^2 using the adult data only was 49 (S.E. +/- 19) and incorporating the independent animals over a year old was 78 (S.E. +/- 22).

Table 14: The best basic model for each year based on the weighted AIC for adult leopards only and female and male separately (K= parameters, LL= log Likelihood, g0= detection probability at the range centre, σ = detection decline from range centre, D=density, CVD=coefficient variation estimate of the density).

Session	**Model parameter**	**AICc**	**AIC wt**	***K***	**LL**	***G0* (+/- SE)**	**Sigma (+/-SE)**	**Density/ 100 km^2 (+/-)**	**CVD**
Y1 Adult only	*g*0 (h) σ (.) D (sex)	1175	1	2	-1265	0.03 (0.007)	2,410m (407)	4.43 (1.90)	0.52
Y2 Adult only	*g*0 (bk) σ (.) D (.)	3741	0.89	3	-1865	0.01 (0.002)	1,890m (294)	4.89 (2.14)	0.44
Y3 Adult only	*g*0 (bk.) σ (.) D (.)	868	0.99	3	-428.9	0.01 (0.003)	1,300m (137)	5.61 (2.40)	0.42

Session	**Female**	**CVD**	**Male**	**CVD**
Y1 Adult only	1.66 (1.05)	0.63	2.77 (1.43)	0.52
Y2 Adult only	3.49 (1.74)	0.47	1.40 (1.03)	0.71
Y3 Adult only	3.74 (1.90)	0.5	1.87 (1.33)	0.71

4.4.3. Habitat

Mann-Whitney U-tests showed that the proportion of bare ground was significantly different between the random quadrats and camera quadrats (W=222.5, n = 26, p=0.006), which was likely to be due to the presence of the unpaved road. Proportions of woody and non-woody cover were not significantly different, indicating camera trap locations were a fair representation of the study site habitat (Figure 18). Grassland was defined as being where tree cover covered <20% (Figure 19) and was largely mountainous grassland (Figure 20).

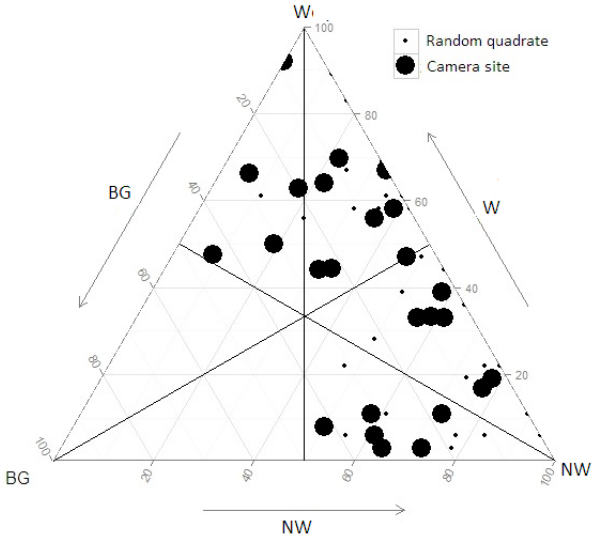

Figure 18: Proportions of bare ground (BG), non-woody cover (NW) and woody cover (W), taken from 50m quadrats around each camera site and at random sites across the study area.

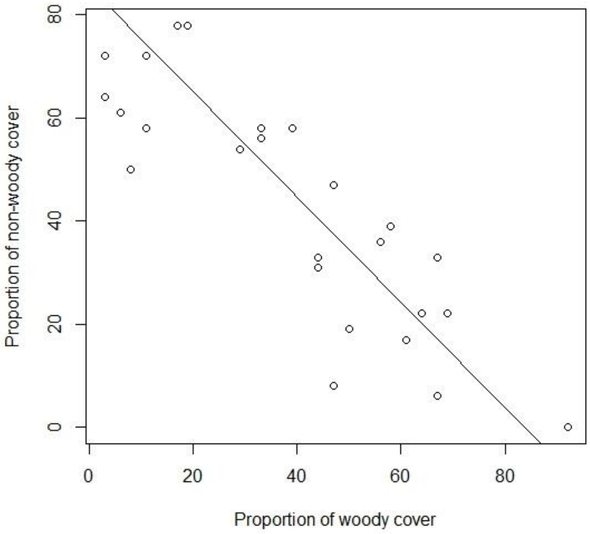

Figure 19: Relationship between relative proportions of woody and non-woody cover at camera sites; highlighting the difference between sites classed as grassland and savannah; with grassland defined <20% woody cover.

Figure 20: Example of mesic highveld grassland (left) and central bushveld (right).

4.4.4. Other carnivores

African wild cat, aardwolf*,* yellow mongoose*,* dwarf mongoose *Helogale parvula*, marsh/water mongoose *Atilax paludinosus*, and African clawless otter *Aonyx capensis* were omitted from analyses due to lack of data. Slender mongoose was also omitted. Although small spotted genet, Selous's *Paracynictis selousi* and white-tailed *Ichneumia albicauda* mongooses may occur in the area, we did not record any. We found no significant difference in mean relative local abundance indices for leopard between savannah and grassland sites, however brown hyena, Cape fox, caracal, large spotted genet, Meller's mongoose and serval did show significant differences between the two habitats (Table 15; Figure 21), with highly significant correlations with percentage of tree cover for many of the carnivores (Table 16). We also found no significant difference in leopard or brown hyena relative local abundance indices between seasons at all sites or sites within each biome, however six other carnivores did show significant differences (Table 15).

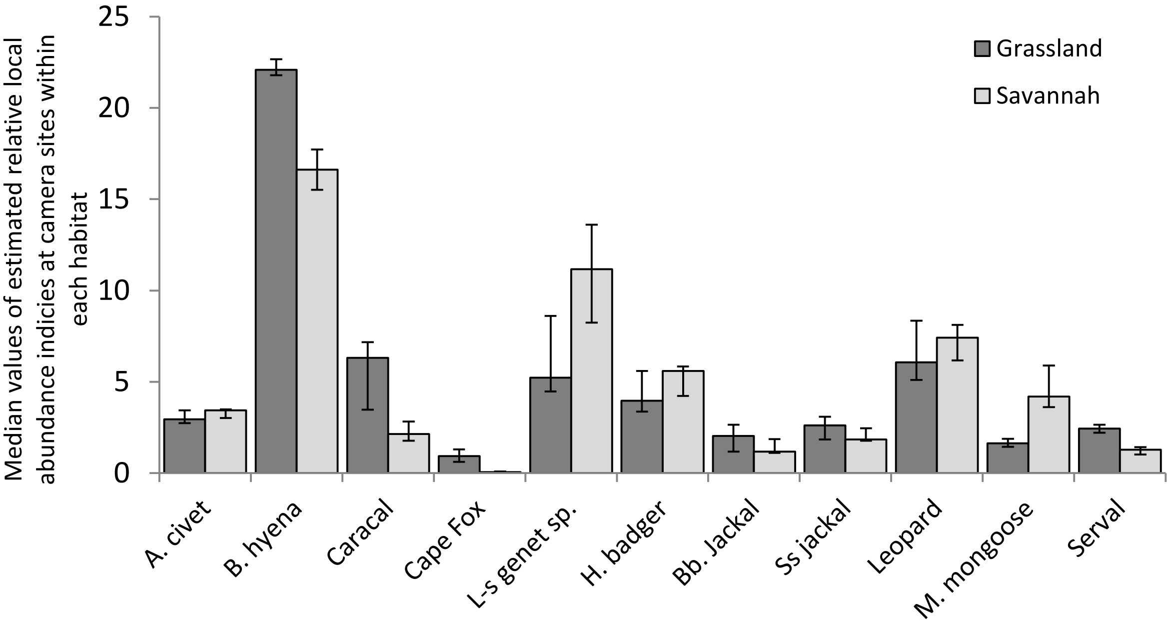

Figure 21: Median (+/- inter-quartiles) relative local abundance indices calculated from occupancy based models for selected predator species at each camera site within each habitat.

Table 15: Results of the Mann-Whitney U-tests between savannah and grassland camera sites and the Paired Wilcoxon signed-rank tests between the same sites over the "wet" and "dry" three month periods with adjusted p values (n=26). Median values of local relative abundance indices within each habitat type generated from occupancy based models at each camera site within each habitat.

Carnivore	**Sav. median**	**Grass. median**	**W**	**Adj. p**	**Wet median**	**Dry median**	**V**	**Adj. p**
African civet	3	3	-	-	1	2	67	0.028
Brown hyena	17	22	153	<0.001	4	4	-	-
Caracal	2	6	146	0.001	1	2	34	0.001
Cape Fox	0	1	153	<0.001	0.0001	0.01	-	-
Honey badger	6	4	-	-	2	4	20	<0.001
Black backed jackal	1	2	-	-	0	1	630	<0.001
Side striped jackal	2	3	-	-	0	1	630	<0.001
Large spotted genet	11	5	19	0.011	4	3	-	-
Leopard	7	6	-	-	4	5	-	-
Meller's mongoose	4	2	0	<0.001	0.9	1.1	67	0.028
Serval	1	2	153	<0.001	0.1	1	51	0.001

4.4.5. Interactions between species

Relative local leopard abundance indices were positively associated with those for African civet and large spotted genet numbers however there were no other significant associations between leopard and other species. Brown hyena and caracal indices showed a significant positive association; numbers of each were negatively correlated with large spotted genet and Meller's mongoose, and positive with serval and Cape fox respectively (Table 16). However many of these associations became non-significant when models containing habitat covariates were run together with the univariate models. Only Cape fox, side striped jackal, African civet, and large spotted genet had models which included larger carnivores as potentially affecting relative local abundance levels (Table 17). The African civet and Cape fox were the only carnivores to have a model which included larger carnivores only. Relative local abundance of African civet was positively associated with relative local leopard abundance while Cape fox was s negatively associated with leopard and caracal and positively by hyena (Table 17).

Table 16: Significant relationships between the relative local abundance of each carnivore and each univariate; woody cover, leopard, brown hyena and caracal, p values adjusted using Holm's sequential Bonferroni. (Weights for each mammal were taken from Stuart & Stuart 2015).

Carnivore	Woody Z	Woody Adj. p	Leo. Z	Leo. Adj. p	B. hyena Z	B. hyena Adj. p	Caracal Z	Caracal Adj. p
African civet (9-15kg)	-1.11	>0.05	14.9	<0.001	-	-	-	-
Brown hyena (35-58kg)	-3.83	0.001	-2.63	0.068	-	-	-	-
Caracal (7-19kg)	-3.13	0.012	-	-	2.65	0.048	-	-
Cape Fox (2.5-4kg)	-2.63	0.052	-	-	-	-	3.22	0.009
Honey badger (8-14kg)	1.83	>0.05	-	-	-	-	-	-
Jackal, black backed (6-12kg)	0.109	>0.05	-	-	-	-	-	-
Jackal, side striped (7.5-12kg)	-1.1	>0.05	-	-	-	-	-	-
Large spotted genet (1.5-3.2kg)	3.54	0.004	5.82	<0.001	-4.59	<0.001	-3.68	0.002
Leopard (60-90kg)	3.56	0.004	-	-	-	-	-	-
Meller's mongoose (1.7-3kg)	4.71	<0.001	-	-	-2.86	0.034	-3.20	0.009
Serval (8-13kg)	-2.23	>0.05	-	-	2.83	0.034	-	-

Table 17: The best model for each carnivore showing interactions with vegetation (W=woody cover, NW=non woody cover, BG= bare ground) and large carnivores (L=leopard, BH= brown hyena, C=caracal), based on the smallest AIC and highest AIC weight.

Carnivore	Best model	AIC	AICw	Coefficient
African civet	L	7863	0.37	0.035
Brown hyena	W,NW,BG	7295	0.56	W 0.020 NW 0.027 BG 0.026
Caracal	W	1419	0.37	-0.021
Cape Fox	L,BH,C	378	0.22	L -1.33 BH 1.24 C -9.85
Honey badger	BG	2947	0.27	-0.02
Jackal, black backed	BG	2428	0.21	0.03
Jackal, side striped	C	1807	0.21	0.184
Large spotted genet	W,NW,BG,L	9990	0.3	W 0.026 NW 0.012 BG 0.005 L 0.093
Leopard	W,NW,BG	7928	1	W -0.094 NW -0.091 BG -0.113
Meller’s mongoose	W	3178	0.52	0.024
Serval	W	1691	0.8	-0.016

4.5. Discussion

In our study we found that leopards were equally likely to be recorded in mountainous grassland and savannah. The lack of significant increase in leopard density estimates over the three years suggests younger animals are dispersing from the maternal home range and the system was stable. However, density estimates are lower than those estimated from interior savannah inside and outside formally protected areas in South Africa (Appendix 1). Brown hyena, caracal, Cape fox, and serval were found to have significantly higher relative abundances in the mountainous grassland than more wooded savannah, avoiding areas with higher tree cover. Several meso-predators showed a difference in relative abundance at each site between seasons; however leopard and brown hyena did not. Although there were significant relationships with leopard alone, habitat was found to be more significant in affecting most of the carnivore species’ abundance.

4.5.1. Leopard density and habitat use

This study has shown leopards will utilize open mountainous grassland in the absence of large predators. Balme *et al.* (2007) suggested that a minimum vegetation height of 20cm was needed for successful hunting by leopard, and although there was not any confirmation that hunting occurred in the mountainous grassland areas where grasses can measure <20cm, leopards are highly adaptable (Hayward *et al.* 2006). Martins & Harris (2013) showed that the nocturnal nature of leopard provided adequate hunting success in the succulent karoo where there is very little cover. Hence it is plausible that leopards could utilize mesic highveld grassland to disperse from source areas within the savannah interior due to their highly adaptable nature (Steyn & Funston 2009, Jacobson *et al.* 2016).

Estimates of leopard density were lower compared to those taken from the interior of the savannah biome regardless of location inside or outside of protected areas (Appendix 1, Bailey 1993; Balme *et al.* 2009b; Chase-Grey *et al.* 2013; Maputla *et al.* 2013; Swanepoel *et al.* 2015). There were a total of ten cubs raised throughout the duration of the study on TTWR and the densities were relatively unchanged over the three years suggesting the area was either at carrying capacity or other factors are restricting leopard density from reaching the same levels as the interior savannah areas. Stander *et al.* (1997b), confirmed leopard biomass was correlated with prey biomass, particularly animals of 15-60kg in mass, which includes many medium antelope (Stuart & Stuart 2015; Skinner & Chimimba 2005) which are the optimum mass for leopard in terms of the optimal foraging theory (Hayward *et al.* 2006). TTWR contains a wide variety of wild and introduced ungulates within the preferred weight range; including warthog, bushbuck, impala, nyala, klipspringer, blesbok and mountain reedbuck (Appendix 2). Many of these species are found outside the reserve boundaries, however higher abundance of evidence was found inside the reserve (Pirie *et al.* submitted a; Chapter 3). Further investigation is needed to confirm if prey abundance could be a limiting factor here or outside influences are impacting the density levels.

4.5.2. Carnivore habitat utilization

With the exception of leopard, there were significantly higher abundances of large carnivores in grassland, and the smaller carnivores showed a significant preference for savannah. Janssen *et al.* (2007) suggested that habitat structure could play an important role in intra-guild predation with greater cover providing more refuge from larger predators and reducing encounter rates between members of the guild, which could account for the significant increase in abundance of the smaller carnivores in savannah. Caracal, jackal, and African civet showed lower mean abundance levels in the wet season which is also when livestock have young. Both caracal and black backed jackal are known to attack livestock (Bergman *et al.* 2013) with the later specifically targeting birthing livestock (Yom-Tov *et al.* 1995) and game (Pirie *pers. obs*). A survey conducted on farmers in the area confirms they have possibly experienced losses of game and livestock to caracal and jackal (Pirie *et al.* submitted b, Chapter 5). This could account for the lower abundance levels during the wet season especially as the leopard and hyena showed no significant change in abundance during this time.

4.5.3. Relationships

Our results suggest that the relatively widespread leopard, brown hyena and caracal could potentially influence the abundance of other meso-predators, although the association is highly dependent on habitat and could be driven by other factors not included in the study. It was first considered to be different habitat preferences which accounted for the negative relationship found between Egyptian mongoose *Herpestes ichneumon*, and Iberian lynx *Lynx pardinus*, in Spain (Litvaitis & Villafuerte 1996), however Palomares *et al.* (1998) provided evidence in support for the relationship of a top-down interaction using path analysis which could not be used in this study due to the bias in camera trap placement. The negative associations found in this study between the caracal and brown hyena with smaller predators maybe from intra-guild predation or competition. Caro & Stoner (2003) highlighted that mongoose species were the most vulnerable to intra-guild predation, presumably on account of their size (Mills 1982) and it was also suggested that genet species were the most likely to have competitors within the carnivore guild due to overlap in distribution and diet, however the association may be driven by the preference for different habitat as the large carnivores showed a preference for grassland and the smaller for savannah. Nevertheless results suggest smaller carnivores may be associated with the presence of larger carnivores as there were highly significant positive associations between local relative abundance of African civet and large spotted genet with relative local leopard abundance. Although the large spotted genet did show a significant positive association with woody plant cover; leopard and the African civet did not.

Leopards have been recorded killing most other meso-carnivores, with the exception of honey badger. Bailey (1993) observed a honey badger being attacked by a leopard, but not killed, hence they may be unlikely to avoid leopard nor are they likely to be in direct competition, as rodents and invertebrates are their principle prey (Stuart & Stuart 2015). However leopard has been documented killing African civet and genet species in other areas (Bailey 1993; Hayward *et al.* 2006) and we found a carcass of an African civet during the study with tooth marks around the neck matching the canine diameter and distance of a leopard (Pirie *pers. obs*). African civet is known to supplement their diet with carrion (Stuart & Stuart 2015) and Moleón *et al.* (2015) showed that large spotted genet would feed on small carcasses; however we have recorded large spotted genet and African civet feeding on large carcasses within the study area (Pirie *pers. obs*.). Therefore in an area with a relatively high number of meso-carnivores it is possible they could be scavenging from carcasses left by leopard to supplement their diet. This might suggest leopard could have some influence on relative local African civet abundance on the reserve. However further research into the temporal separation between carnivores and the relative prey abundance would be needed to ascertain how realistic these associations might be or if there are other underlying mechanisms driving the association found in this study.

4.5.4. Conclusion

This associations found in this study suggests leopard, brown hyena and caracal may have some influence on relative local carnivore abundance; however this may also be highly dependent on vegetation characteristics (Janssen *et al.* 2007) and the relative local abundance of the apex predators. We have highlighted that not all associations between apex African predators and meso-predators may be negative, but could be positive, especially if there is benefit to be gained offsetting the potential for intra-guild predation. However further research is needed to investigate whether these associations are in fact driven by other factors, if they are observed at other sites and how population fluctuations may influence these potential associations in order to fully understand the potential implications should persecution of the larger carnivores continue to increase in the area and indeed across the country (chapter 5).

The presence of mountainous grassland does seem to have an impact on carnivore distribution with some species showing more tolerance to both biomes than others. Although grassland does not appear to affect leopard movement, density estimates based on adult information are lower compared to those from most of the interior savannah areas suggesting there could be a local factor or a combination of factors, such as prey abundance, or direct removal outside the reserve (Chapter 5) which could potentially be restricting the leopard density from reaching numbers seen in other parts of the country. Further research conducted outside the reserve would allow for a greater understanding of what may be influencing the low density estimates and further modelling based on the population dynamics found could allow future population estimates to be forecasted.

While at a wider population level, local leopards are clearly under threat, and the population may be coming increasingly fragmented, it is clear that TTWR is a source of leopards for the local population, rather than a sink. As the numbers of small, privately owned reserves like this increases, each can be a refuge for leopards and other persecuted predators. Understanding how both habitat and inter-specific interactions influence, and are influenced by, this charismatic big cat is the first step in helping develop approaches to mitigate the challenges they face today to ensure their survival.

Chapter 5

Increasing game prices may increase negative action towards leopards (*Panthera pardus*) and other carnivores in South Africa

Submitted to Peer J

5.1. Abstract

Human-carnivore conflicts occur globally, particularly in regions where large carnivores predate livestock. Retaliatory killings do occur, and although predation of livestock by carnivores happens, losses from other factors such as disease or injury can be misattributed because of farmer perceptions. Game farming for both trophy hunting and eco-tourism is becoming increasingly common in South Africa, and there has been a dramatic increase in the cost of animals over the last five years. This could increase conflicts between commercial game farmers and carnivores. We conducted two questionnaire surveys of farmers in 2010 and 2015 to investigate this. We investigated if there had been changes in farming practices, perceived predator activity, perceived livestock and game losses, and behaviour towards carnivores in a South African farming community. We found no significant change in farming types in the area or losses of livestock between the years. However, there was a significant increase in game losses and livestock and commercial game farmers were more negative towards carnivores in 2015 compared to other farmers, with a significantly higher percentage of commercial game farmers responding they would remove one or more carnivore species compared to livestock owners. We suggest that these changes could be a result of the increase in game price over that period, leading to greater financial losses when an animal is taken, which could increase the likelihood of retaliatory killings of carnivores.

5.2. Introduction

With ever increasing human populations, the occurrence of conflict with wildlife is predictable, particularly when people's livelihoods are negatively affected (Thirgood *et al.* 2005, Dickman 2010). The increased encroachment of people into wilderness areas is inevitable (Asibey 1974; Sillero-Zubiri & Switzer 2001) and limited resources often force wildlife into areas of pasture or arable land where conflict can occur (Sillero-Zubiri & Switzer 2001; Thirgood *et al.* 2005; Athreya *et al.* 2007; Dickman 2010). Conflicts arise for many reasons and with many taxa, including larger mammalian carnivores (e.g. tiger, Himalayan black bear, snow leopards, leopard: Sangay & Vernes 2008; wolves*,* Lynx*,* brown bears: Kaczensky 1999) and herbivores (elephant*,* bushpig, Naughton-Treves 1998). Human-wildlife conflict will undoubtedly continue to be a key factor in the decline of wildlife populations, particularly for carnivores (Woodroffe 2000; Dickman *et al*. 2009; Hoffman & O'Riain 2012).

Large mammalian carnivores can pose a threat to livestock (Yom-Tov *et al.* 1995; Meriggi & Lovari 1996; Wagner & Conover 1999; Odden *et al.* 2002; Sunquist & Sunquist 2002; Bagchi & Mishra 2006; Garrote *et al.* 2013) or people (Treves & Naughton-Treves 1999; Woodroffe et al. 2007; Neto 2011; Löe & Röskaft 2004). One of the most vulnerable times for ungulate livestock is during birthing, when species such as jackal are known to attack new-borns as they are born (Yom-Tov *et al.* 1995). Young animals are often more vulnerable than adults to attack from predators (Rosas-Rosas *et al.* 2008), particularly by species which are unlikely to predate conspecific adults (Yom-Tov *et al.* 1995). However, larger species such as tigers, black bears and snow leopards have been documented predating adult horses, yak *Bos grunniens*, sheep and cattle (Sangay & Vernes 2008) and leopards have been found to predate goats, sheep and domestic dogs (Kissui 2008; Yirga *et al.* 2012). Despite this, predators can often be wrongly accused of livestock predation, and losses may actually occur from theft (Rust et al. 2016), injury, disease, poor nutrition, or venomous snake bites (Poliser *et al.* 2003).

The removal of predators, whether legally or illegally, has been undertaken either by trapping and relocating (Linnell *et al.* 1997; Athreya 2006; Weilenmann *et al.* 2010) or through lethal control (Treves & Naughton-Treves 2005). As a result, ecological consequences such as meso-predator release and trophic cascades caused by the removal of apex predators have been documented across numerous systems (Crooks & Soule 1999; Schmitz *et al*. 2000, Letnic & Kock 2010). Preventative methods such as the use of guard dogs or donkeys (Ogada *et al.* 2003; Gehring *et al.* 2010), retaining horns on cows, mixing heifers with older and more experienced cows, synchronised calving, using calving camps and electric fencing (Reinhardt *et al.* 2012; Lindsey *et al.* 2013), or even using groups of adults rather than boys as herders (Svengren & Björklund 2010), have been used to reduce predation on livestock globally.

Compensation schemes have also been trialled globally from European countries (Boitani *et al.* 2011; Rigg *et al.* 2011), India and the USA (Agarwala *et al.* 2010) to South Africa (Anthony *et al.* 2010) to reimburse landowners for damage caused by wolves and other large carnivores. Although some areas have not noted any change in negative attitudes towards carnivores (Agarwala *et al.* 2010; Boitani *et al.* 2011), the State of Wisconsin, USA, started a scheme in 1982 and recorded a significant increase in wolf numbers over 30 years (Treves *et al.* 2009); however the increase was relatively low suggesting retaliatory killings may have still occurred (Chapron & Treves 2016). Alternatively performance payments have been used in Sweden instead, where successful conservation and carnivore reproduction earned reindeer herders a reward. The payment was calculated based on the number of carnivore offspring and the future damage these animals were predicted to cause (Zabel & Holm-Müller 2008). Although the scheme has been implemented for a decade and a local increase in wolverine *Gulo gulo* numbers was observed (Zabel *et al.* 2014), application in other situations has yet to be trialled.

Predation of livestock is thought to occur more often where natural prey abundance is low (Polisar *et al.* 2003; Kolowski & Holekamp 2006); therefore improving habitats for prey species has been recommended and the farming of game has been suggested as an effective way to promote the conservation of carnivores (Winterbach *et al.* 2015), especially when coupled with eco-tourism in order to produce viable income (Lindsey *et al.* 2013). In South Africa game farming has increased rapidly from an estimated 5000 farms in 2003 (Carruthers 2008) to just under 9000 in 2016 (Taylor *et al.* 2016). The breeding of economically valuable species including sable, roan antelope *Hippotragus equinus* and disease free African buffalo has increased in the last 30 years mainly for the purpose of trophy hunting (Taylor *et al.* 2016), rather than eco-tourism. It was estimated that trophy hunting generated R1.956 billion (US$136.7 million) of revenue 2014 (Taylor *et al.* 2016).

To a lesser extent trophy hunting of carnivores, especially felines, also occurs in South Africa, indeed 150 CITES (Convention on International Trade in Endangered Species of wild fauna and flora) permits were issued every year between 2005 and 2015 for the legal harvesting of leopards. However the leopard was reclassified in 2016 from ‘near-threatened’ to ‘vulnerable’ on the IUCN red data list due to concerns over the rapid decline in distribution (Jacobson *et al.* 2016). Furthermore a temporary hunting ban was introduced in the country earlier the same year (Anon 2016b). Although legal hunting is under review in South Africa, the illegal killing of predators in the form of poaching for trade in animal parts (Costa-Neto 2005; Doughty *et al.* 2015) or retaliatory killings through fear or actual conflict with humans, can be a common occurrence (Balme *et al.* 2009a) and may have a more detrimental effect on the viability of local populations than trophy hunting (Swanepoel *et al.* 2014). Leopards (Balme *et al.* 2009a, Swanepoel *et al.* 2015), brown hyena (Mills 1982) and meso-predators such as caracal and jackal species (Thorn *et al.* 2011; Kingdon 2013) are commonly found outside of formally protected reserves in South Africa and are therefore increasingly likely to come into conflict with local people which can result in retaliatory killings (Swanepoel *et al.* 2014) or requests for damage causing animal permits (DCA) to remove problem animals (Pitman *et al.* 2016). Understanding the reasons for conflict between local farmers and carnivores, in particular leopards due to their declining distribution, is important for the local conservation of carnivores, however it is equally important to understand if conflict does occur how likely it is to lead to illegal retaliatory killings of those species and where what impact this has on the local population (Swanepoel *et al*. 2014).

There is growing concern attitudes are used to predict behaviour towards carnivores however attitudes may not directly predict behaviour (Wallace *et al.* 2005, Heberlein 2012, Delibes-Matreos 2014, Gross 2016) and often surveys do not consider other factors which may influence the final behaviour (St John *et al.* 2010). Therefore in this study behaviour categories are based on actions taken towards each carnivore which is then used to highlight the potential of retaliation based on these actions already taken against one or more species. The use of a randomized response technique can be used to compensate for inaccurate answers to controversial questions by using a die to prompt the survey participant to give either false or true answer (St John *et al.* 2011). However this method was not widely known when the first survey was conducted in 2010 and in the interest of continuity we decided to repeat the original format. We decided not to evaluate predator activity, loss or cause of loss for this study as we were focused on the behaviour towards predators by farmers which would be driven by the farmers' perceptions regardless of what the reality was on the farm.

Understanding the reasons for conflict between local farmers and carnivores, in particular leopards due to their declining distribution, is important for the local conservation of carnivores, however it is equally important to understand if conflict does occur how likely it is to lead to illegal retaliatory killings of those species and what impact this has on the local population (Swanepoel *et al*. 2014). We conducted surveys of farmers in 2010 and 2015 to ascertain if farming practices, perceived predator activity, perceived losses of livestock and/or game and behaviour towards carnivores had changed in an area on the border between the Limpopo and Mpumalanga provinces, South Africa to understand if conflict is occurring in the area and what risk the local carnivores may be exposed to when they traverse between a small privately owned reserve and surrounding farmland. We also estimate the percentage of leopard which may have been removed from the area annually to understand how this may impact the population.

5.3. Methods

Identical surveys (Appendix 1) were conducted in 2010 and 2015 which engaged with farmers that had land over 20ha, used it to farm on and were located within a 30km buffer zone of Thaba Tholo Wilderness Reserve. This area included the towns and regions of Steelport, Burgersfort, Lydenburg and Ohrigstad, in the Limpopo and Mpumalanga provinces, South Africa (Figure 22). This selection process mainly incorporated farmers from an Afrikaans background. The survey which was based on a standard survey conducted by the Endangered Wildlife Trust, was approved by the ethics committee school of biological sciences #SBS 13-14 19. We were aiming to replicate the 2010 surveys with the same farmers, however some farmers were no longer in the area for various reasons and we were unable to make contact with others. To compensate for this the new farmers to the area were questioned along with other famers which were not part of the original survey. The interviews were conducted by a female Afrikaans speaking researcher either by telephone or in person and took an average of fifteen minutes to conduct. Before the survey was conducted the respondent was informed the survey was being undertaken by the researcher on behalf of the Ingwe Leopard Research and the University of Reading and asked if they would be willing to take part in the survey about carnivores on their property and if they consented they were asked if they would prefer to take part over the phone or face to face, most chose the former with five opting for the later in 2015.

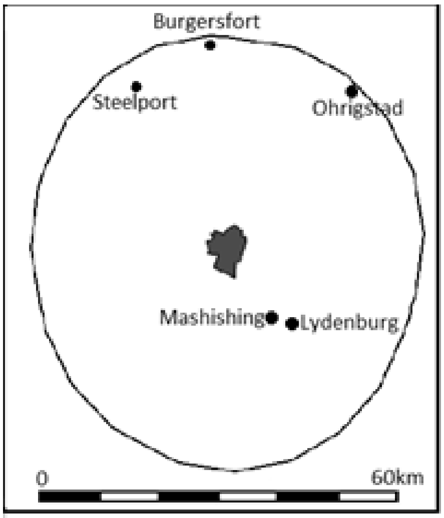

Figure 22: Location of area surveyed within South Africa (Produced using Quantum GIS, 10 July 2016).

The survey contained five sections of mainly closed-ended questions, which asked: A; general information about the farm size and location, B; type of farm activity (crops, livestock, wildlife), type of water source and terrain, C; infrastructure and management of livestock and game (monitored, guarded, placed in overnight camps or in camps permanently), D; open questions relating to perceived predator activity were recorded as visuals or spoor found on the property and perceived losses of livestock/game which were recorded as species lost and the perceived reason for the loss, E; behaviour towards each carnivore species (friendly, tolerant, trap, poison, shoot, no opinion). At the end of the 2015 questionnaire, respondents were asked an open ended question which required the respondent to state if their behaviour towards carnivores had changed over the last 5 years, regardless of whether they had participated in the previous survey or not, and if so, why.

Responses to the predator activity and potential causes of loss were categorised as caused by leopard, brown hyena *Hyaena brunnea*, caracal *Caracal caracal,* jackal (both *Canis mesomelas* and *C. adustus*), other (which included serval *Leptailurus serval*, civet *Civettictis civetta*, poachers, disease and feral dogs) and unsure, which was the response given if the farmer was unsure what might have been responsible for the livestock or game loss. Respondents were asked to categorise their behaviour towards eight carnivore species; leopard, brown hyena, caracal, jackal sp., serval, civet, genet sp., feral dog and other. They were given seven options; no opinion, shoot, poison, trap, tolerate (defined as no action taken although would prefer no carnivore presence), friendly (no action taken and like the presence of carnivores) and other.

Overall behaviours towards carnivores were categorised based on how the respondent reacted to each carnivore species. Positive meant that the respondent gave all “friendly” or “tolerant” responses to each carnivore; both was used when some of the responses were given as “friendly” or “tolerant” but where shoot/trap/poison was given for others; negative was used when there were no friendly or tolerant responses given towards any carnivore and a negative action was shown towards each carnivore.

5.3.1 Analysis

In the second survey a proportion of farmers had answered the first questionnaire. To ensure independence we analysed the data in two ways. First, we considered unmatched data, where only the second (2015) data set was used for those individuals who had answered both sets of questionnaires. Second, we performed a matched analysis just using the data from those who had answered both questionnaires. Where appropriate multiple tests were adjusted using Holm’s sequential Bonferroni corrections (Holm 1979).

5.3.2 Analysis - Unmatched surveys – All farmers

Mann-Whitney-Wilcoxon tests were used to investigate whether a change had occurred in farming practice and animal management, losses experienced and behaviour towards carnivores in the area over the five year period. Two farm owners had two separate properties which were treated as separate farms for all the questions except for the behaviour question. Some crop farmers did have game on their property which was not “farmed” hence the comparison was made between all farmers in this section.

5.3.3 Unmatched surveys – Stock farmers only

Only livestock farmers and farmers who stated they farmed game for commercial reasons, from here on referred to as commercial game farmers (rather than they just had wild game on their property) were considered in this section. Species included kudu, nyala, bushbuck, blesbok and zebra as well as colour variants of impala and wildebeest species. Two proportions z test were then used to test for differences between each year and farm type, management occurrence, numbers of losses and perceived reasons for losses for farms with livestock and/or commercial game only. Two farm owners had two separate properties which were treated as separate farms for all the questions except for the action taken towards carnivores.

5.3.4. Matched surveys-stock farmers only

A Wilcoxon signed-rank test was used to compare whether farming practice had changed between the same farmers, if there was any change in levels of losses and whether responder actions towards carnivores had changed between surveys.

5.3.5. Leopard mortality

The Mpumalanga Parks and Tourism Authorities were requested for a report on the number of CITES and damage causing animal (DCA) permits utilized in the area and any roads kills within the 15km area of TTWR since 2006. Additional information regarding retaliatory killings were contributed by farmers during the survey for the same period. An annual mean was then calculated using all known removals. Mean population estimates for leopard residing within the 15km buffer zone were calculated using the secr program (R statistics, 2016) based on the annual density estimates for adult animals only and all animals over a year old (Chapter 4).

5.4. Results

In 2010 we had a response rate of 90% which yielded a total of 63 completed surveys and a response rate of 47% in 2015 with 35 completed surveys. This was due to the inability to make any contact with previous farmers. We estimated there were 200 farms within study zone. Most respondents were farmers, with two managers of citrus farms responding in 2015. Twenty of those carried out in 2015 were with the same individual farmers as 2010, with the remaining 15 undertaken with new respondents.

5.4.1 Unmatched surveys – All farmers

In comparing the respondents who were questioned independently in 2010 and 2015 there was very little change between most responses. Farm type was either crops, livestock or wildlife, either natural or farmed, or a combination of two or all three types (mean proportions across both years for properties containing crops was 68%, livestock 60% and wildlife 84%). Cattle formed the majority of farmed livestock (Figure 23) and farm category size was variable (less than 300ha; 32%: between 300ha and 1000ha; 28%: over 1000ha; 26%).

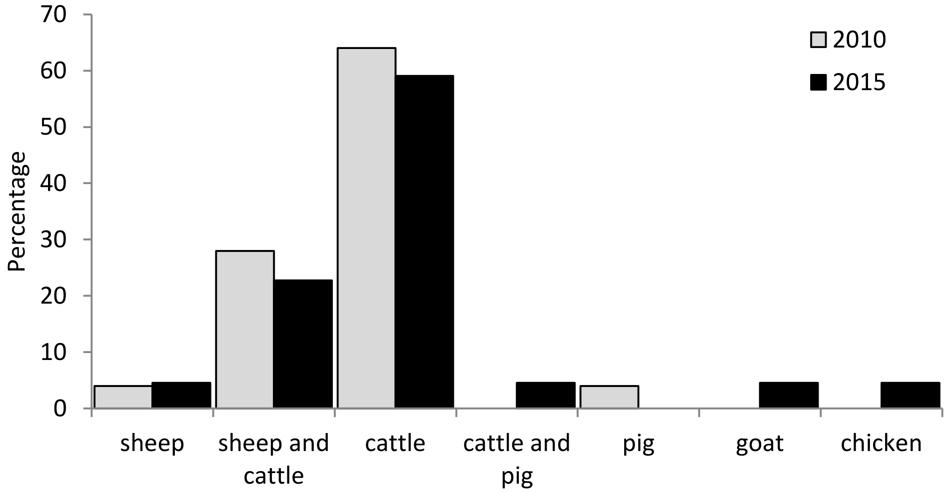

Figure 23: Percentage of livestock reared in surveyed farms, 2010 and 2015.

However there was a significant decrease in animal management, either by providing overnight camps, guarding by people or dogs, or monitoring young animals (W = 454.5, 2010 N = 43, 2015 N = 35, p = 0.001; Table 18). Additionally there was a highly significant increase in losses reported in the 2015 survey (W = 498, 2010 N = 43, 2015 N = 35, p = 0.003), although there was no significant difference in predators seen both years. Both leopard and caracal were thought to be the cause of more losses in 2015, however only responses for the believed caracal-caused losses were found to be significantly higher (W = 603.5, 2010 N =

43, 2015 N = 35, adjusted p = 0.045). Even though there was an increase in loss perceived to be caused by carnivores, there was no significant difference in behaviour towards the carnivores between the years, with 51% responding positively or at least tolerant towards carnivores compared with 20% who responded negatively to all carnivores (Table 18). However, there was a significant difference in behaviour towards carnivores between livestock and commercial game farmers compared to farmers who only had crop and/or naturally occurring game in 2015, with the former showing more negative behaviour (W = 176, N = 18, N = 9, adjusted p = 0.043). Conversely there were no significant differences between stock or crop only farmers in 2010.

Table 18: Percentage of farm type (some farms had a combination of two or three types), farm size (2010 N = 43, 2015 N = 35), type of management of livestock and game (2010 N = 43, 2015 N = 35) and behaviour (2010 N = 43, 2015 N = 33) based on actions taken for unmatched surveys.

Question	Response category	2010 %	2015 %
Farm type	Crop	65	71
	Livestock	58	63
	Wildlife	88	80
Size of farm	<300ha	35	29
	300-1000ha	28	29
	>1000ha	26	26
Management	Yes	92	60
	No	8	40
Behaviour	Positive	23	27
	Tolerate	26	27
	Both	33	24
	Negative	16	21

5.4.2 Unmatched surveys – stock farmers only.

Of the 43 independent 2010 responders there were 27 which either farmed livestock or game for commercial reasons. There were 26 responses with the same restrictions from the 2015 surveys, with no significant change in farming of livestock or commercial game within the time period (Table 19). Although management of stock in the form of fenced areas, guarding or monitoring, was less likely to occur overall in 2015, management of game, in the form of fenced camps, was more likely in 2015 (Z = -2.69, 2010 N = 3, 2015 N = 8, p = 0.007, Table 19). Livestock losses perceived to be caused by predators were not significantly different between the two years, however commercial game losses were more likely to occur in 2015 (Z = -2.55, 2010 N = 3, 2015 N = 8, p = 0.011, Table 19). There was no significant difference in perceived predator activity between the years and even though leopard and caracal were thought more likely to be responsible for both livestock and game losses in 2015, this was not significant (Table 20). There was no significant difference found in overall behaviour towards the carnivores between the years, nevertheless the percentage of respondents which would remove certain species increased for all focus carnivore species over the five year period (Table 19) and when responses were combined from both years, commercial game farmers significantly responded they would remove one or more carnivore species compared to the livestock farmers (Z = 2.43, game farmers N = 11, livestock farmers N = 44, p = 0.015).

Table 19: Percentages of responses for unmatched surveys from livestock and commercial game farmers only, including type of stock (some farmers had both livestock and commercial game; 2010 N = 27, 2015 N = 26), any management (2010 N = 27, 2015 N = 26), losses for livestock or commercial game (2010 N = 27, 2015 N = 26), and behaviour towards each carnivore (2010 N = 27, 2015 N = 24).

Question	Response category	2010 %	2015 %
(Of stock farmed)	Livestock	93	85
Type of stock	Exotic game	11	27
Management	Livestock yes	88	36
	Exotic game yes	0	86
Losses	Livestock	74	69
	Exotic game	25	86
Behaviour	Positive	15	21
	Tolerant	22	21
	Both	44	33
	Negative	19	25
Removal of species	Leopard	15	29
	Hyena	15	25
	Jackal	37	54
	Caracal	4	25
	Feral dog	26	21

Table 20: Percentage of farmers perceived causes of livestock and commercial game losses in 2010 (N = 27) 2015 (N = 26).

Cause of loss	Livestock 2010	Livestock 2015	Game 2010	Game 2015
Leopard	19	23	4	15
Brown hyena	19	19	4	4
Caracal	4	8	0	8
Jackal sp.	44	19	0	15
Serval	4	0	0	0
Feral dogs	0	0	0	4
Poachers	7	4	4	7
Disease	4	0	0	0
Unsure	11	23	4	12

5.4.3. Matched analyses – stock farmers only

There were 20 repeated surveys of which two farmed only crops in both years, these were omitted from further analyses. There was no difference in animal management (monitored, guarded, placed in overnight camps or in camps permanently) however perceived losses were found to have significantly increased in 2015 (W = 11, N = 18, p = 0.037). Actions taken towards carnivores were not found to significantly differ between the surveys.

5.4.4. Changes in behaviours

When farmers were asked if their behaviour towards carnivores had changed in the 2015 surveys, the majority remained unchanged, with fifteen continuing to be positive. Of the ten whose behaviour had changed, two farmers had replied they had become "more negative", one "due to the substantial loss he has sustained (40 nyala at R 30,000 (US$ 2,058) per animal) over the last four years". Eight stated that they had become more positive, two of whom said they had become "better informed" and "better educated to the fact they have a place". One farmer had become more positive because "they don't farm with cattle anymore". Most had replied there was no change. One farmer "accepted it was part of farming" however some would "allow a certain amount [of losses] but then I need to remove the problem, but there is no-one to help with this" and others responded "if they find predators are creating a big problem they will shoot them but don't want to shoot them" or if the predator attacks too much of the stock they would "put methods in place to fix it, like shoot them". Two farmers had commented they thought there was an "increase in the carnivore populations and activity due to towns increasing in size and therefore less land is available for the animals". Two farmers commented on their perceived increase in the use of snares and one farmer disclosed that he knew of ten leopards which had been illegally killed in the area over the last ten years because of livestock losses.

5.4.5. Leopard mortalities

Over a nine year period spanning 2006 to 2015 some 38–45 animals were removed from area radius of 15km from the study site. Sixteen CITES permits (23% of the total provincial permits over the period) were allocated to the area although no DCA permits were used and no permits were issued after 2014 (MTPA unpublished). Ten animals were reported to have been killed illegally in the area and between 12 and 19 animals were estimated to have been killed accidentally (Will Fox, *pers. comms*). Therefore potentially an average of 4–5 animals may have been removed within the 15km buffer zone of TTWR each year, assuming these were resident animals and not vagrants, there could have been 5 - 21%, of the population removed annually; based on the adult leopard population estimate of 49 (S.E. +/- 19, Chapter 4), or 3 - 12 % based on 78 leopards (S.E. +/- 22) which included animals ≥ 1 year old (Chapter 4).

5.5. Discussion

There was a significant increase in reported losses to predators between our repeated surveys of 2010 and 2015, which is possibly a result of the decrease in animal protection and management seen across the survey period. However, perceived predation of livestock by wild predators from the independent surveys did not change during the five year period, but there was a significant increase in perceived game losses. Farming of game species did not increase significantly in the area over that time period, but we did find management of game was significantly more likely to occur in the later year. While behaviours towards carnivores did not change between years, there was a significant difference between livestock/ commercial game farmers and crop farmers in 2015, with the former responding less favourably towards carnivores. In addition commercial game farmers were significantly more likely to remove one or more species of carnivore compared to livestock farmers.

A decrease in management of livestock in the area was reported, but there was no significant increase in losses perceived to be caused by large predators, however commercial game losses were significantly more likely to occur in 2015 despite protective camps were significantly more likely to be used in 2015. Although fences are designed to separate species (Woodroffe *et al.* 2014), they are not always flawless (Hoare 1992; Cozzie et al. 2013), indeed we have documented unhindered movement of many different African carnivores through a game fence (Pirie *et al.* submitted). Keeping game in relatively small camps could potentially allow predators such as leopard and caracal to hunt more effectively should they enter. The lack of space to outrun attackers would give predators an advantage; African wild dog, *Lycaon pictus* have been documented using fences to increase hunting success (Davies-Mostert *et al.* 2013). Ogada *et al.* (2003) found that livestock kept in kraals overnight were less likely to be attacked by predators such as lion, *Panthera leo,* leopard and spotted hyena, *Crocuta crocuta*, but this may be a consequence of the presence of watch dogs and high levels of human activity, rather than the presence of the barrier to predator movement. They also highlighted the behaviour of individual predators was an important factor and therefore losses could be attributed to one or two individuals which are able to cross camp fences in order to obtain the prey inside (Oganda et al. 2003).

Increased individual game losses may have been observed more in 2015 simply due to inflation in the monetary value of game, and hence a greater financial loss from the death of each individual animal (Table 21). Live game sales in South Africa were thought to generate an annual turnover revenue of R4.328 billion in 2014 (US$ 296 million, Taylor *et al.* 2016), a four-fold increase since 2012 (Pitman *et al.* 2016). Prices of animals such as nyala and impala have increased dramatically, with colour variants reaching unusually high prices (Table 21) which is likely to account for the increase in protection of game in 2015. In contrast there has been little change in the cost of live cattle (Table 21, Anon 2016c), or beef and mutton prices (Janovsky 2013) over the last five years.

Although Pitman *et al.* (2016) found a significant positive correlation between DCA permit requests in the North West, no DCA permits were issued by the MPTA during the study period. However retaliatory killings were divulged during the survey, which accounted for almost a third of removals, and although some farmers acknowledged they would kill leopard and other carnivores, we must acknowledge true actions may not have been admitted due to the directness of the question. Interestingly although randomized response technique may be used to account for inaccurate answers the study by St John *et al.* (2011a) found snakes and jackal to be targeted most by famers with caracal and leopard to a less extent and hyena the lowest, which was a similar finding to this study.

Table 21: Auction prices of game and cattle in South Africa for 2011, 2013 and 2015. US$ value calculated at an exchange rate of 14.31 Rand to the US$.

Ani.	Colour	Cost 2011	Ref.	Cost 2013	Ref.	Cost 2015	Ref.
Nyala	normal	R6,809 (US$ 476)	Anon 2013b	R10,706 (US$ 748)	Anon 2013b		
Nyala	red		Anon 2013b	R50,000 (US$ 3,495)	Anon 2013b		
Impala	normal	R1,106 (US$ 77)	Anon 2013b			R2,568 (US$ 179)	Erasmus 2016
Impala	black	R230,000 (US$ 16,077)	Erasmus 2016			R275,400 (US$ 19,251)	Erasmus 2016
Impala	white	R330, 000 (US$ 23,068)	Erasmus 2016			R2 million (US$ 139,803)	Erasmus 2016
Cattle		R18.36/kg[1] (US$1.28)	Anon 2016c	R18.28/kg (US$ 1.28)	Anon 2016c	R19.68/kg (US$1.38)	Anon 2016c

[1] Data for January 2012

While we acknowledge there were few responses for the 2015 surveys especially from commercial game owners, our findings suggest there may have been an increase in the management and protection of game, which could be a reflection of the increasing economic value of game (a trend also seen in Limpopo Province; Pitman *et al.* 2016). The significant difference in the potential removal of one or more carnivore species by commercial game owners compared to livestock farmers in 2015 further supports this theory and highlights a potential issue of an increase in retaliatory killings if game prices continue to rise. As one game farmer explained, he had become more negative because of the substantial financial loss, which has been shown to be a major motivator in retaliatory killings in other studies (Bagchi & Mishra 2006; Kissui 2008).

Although responses about leopard were not significantly different between farming categories or years, these numbers could be lower than actual actions due to the directness of the question or could be a reflection of the awareness about the important role of the leopard in the ecosystem and conservation concern as remarked on by one of the respondents. However the fact leopards have been removed illegally from the area, as revealed in the study, could be problematic for the local population especially if retaliatory killings escalate in the future. Swanepoel *et al.* (2014) suggested that retaliatory killings may have more of a negative impact on leopard populations than trophy hunting, due to removal being less discriminatory and may include the removal of breeding females and juveniles rather than large males. Although it is thought healthy leopard populations can withstand regulated harvesting (Balme *et al.* 2010a; Swanepoel *et al*. 2011), concerns have been raised regarding the long-term viability of South African leopards should unsustainable removal occur due to the random removal of females and cubs which can impact local populations (Sawnepoel *et al*. 2011). It is worth noting that many who said they would remove problem animals acknowledged that they did not want to do so, suggesting that they would be open to other strategies, which is an encouraging sign that retaliatory killings could be limited in the area with the right approach. Supporting this, other landowners noted that their attitude had become more positive in light of understanding that carnivores “had a place”.

4.5.1 Conclusion

Farms changed little over the five year interval between surveys, and there was no change in perceived losses of domestic livestock thought to be caused by carnivores, or significant increase in commercial game farmers. However, perceived losses of commercial game animals may be associated with a rapid rise in the economic value of game animals relative to that of livestock, which may be reflected by the significant increase in management of game, mainly fenced camps. It is therefore plausible that the significant difference in actions in 2015 between stock and non-stock farmers could be due to the increase in game prices as this seems to be the only factor which has changed over the time period. Stock farmers understandably show a more negative behaviour towards carnivores than non-stock farmers as they experience direct financial loss when stock is taken (Thorn *et al*. 2013) which could also account for the higher percentage of commercial game farmers responding they would remove one or more carnivore species compared to livestock owners. Even though the responses may not directly correspond with actual behaviour (Wallace *et al.* 2005), our study does suggest actions may be taken against carnivores in the area and retaliation killings do occur even towards protected animals such as leopards although there have been no DCA permits issued within the study area over the last ten years (Mpumalanga Tourism and Parks Authorities, *pers. comms*). Retaliatory killings have the potential to increase in the future if game value continues to rise and financial loss per animal is therefore higher, which should be acknowledged as a real threat to South Africa’s carnivores if left unaddressed. Therefore we advise further research should be conducted to understand the potential implications of this growing industry on carnivores across South Africa.

Chapter 6

Erythristic leopards *Panthera pardus* in South Africa

Published in Bothalia - African Biodiversity and Conservation

Pirie, T. J., Thomas, R. L., & Fellowes, M. D. E. (2016b). Erythristic morphs of the leopard *Panthera pardus* in South Africa. *Bothalia: African Biodiversity and Conservation,* 46: a2034.

6.1. Abstract

Background: Leopards (Panthera pardus) show genetically determined colour variation. Erythristic (strawberry) morphs, where individuals are paler and black pigment in the coat is replaced by a red-brown colour, are exceptionally rare in the wild. Historically, few records exist, with only five putative records known from India.

Objectives: To record the presence of erythristic leopards in our study site (Thaba Tholo Wilderness Reserve, Mpumalanga) and to collate records from across South Africa.

Method: A network of camera traps was used to record individual leopards at TTWR. We also surveyed local experts, searched the popular South African press, and used social media to request observations.

Results: Two out of 28 individual leopards (7.1%) recorded in our study site over 3 years were of this colour morph. We obtained records of five other erythristic leopards in the North West and Mpumalanga regions, with no reports outside of this population.

Conclusions: Erythristic leopards are widely dispersed across north-east South Africa, predominantly in the Lydenburg region, Mpumalanga. The presence of this rare colour morph may reflect the consequences of population fragmentation.

6.2. Introduction

There is a high degree of coat colour variation between geographic populations of leopards (Kingdon *et al.* 2013). Individuals from arid regions are generally pale with dispersed and open-centred rosettes, in contrast to those residing in forests which are darker with clustered and small-centred rosettes. These patterns are thought to correspond with differing vegetation types and light levels in order to conceal the animal from prey and possibly other predators (Allen *et al.* 2010; Kingdon *et al.* 2013). This adaptive explanation is supported by the frequent occurrence of melanistic leopards in humid habitats such as the Malayan peninsula (Kawanishi *et al.* 2010; Schneider *et al*. 2012). The frequency of 'black panthers' dramatically decreases across more arid regions (Kawanishi et al. 2010). The release of eumelanin (black pigmentation) into mammalian pelage is known to be regulated by the *extension* gene and phaeomelanin (yellow-red pigmentation) by the *agouti* gene (Fontanesi *et al*. 2009). Mutations to either of these genes can produce melanism in felids; however it is a mutation in the *agouti* gene which results in melanism in leopards which is inherited as a recessive trait (Schneider *et al.* 2012).

In contrast, extreme pale (albino) colour morphs, which lack any pigmentation, or erythrism, which contain red pigmentation instead of black, are rarely documented in wild leopards (Divyabhanusinh 1993; Hartwell 2015; Sunquist & Sunquist 2014). Although the cause of erythrism in large felines is unknown, Peterschmitt *et al.* (2009) found evidence for a recessive mutation in the *extension* gene which produces more phaeomelanin, resulting in an amber colour in the domestic Norwegian Forest Cat (*Felis catus*). Similar mutations may also be responsible for the red colouration seen in dogs and humans and other mammals (Fontanesi *et al.* 2009; Majerus & Mundy 2003).

Reports of erythristic leopards (also informally known as strawberry or red leopards, or pink panthers; Anonymous 2013c, 2014b, 2015d; Dell'Amore 2012) are exceptionally rare. A detailed search of the literature found only one paper (Divyabhanusinh 1993), which reported that five pale leopards with light brown spots (one male, one female, and the rest undetermined) had been shot in India between 1905 and 1965. To our knowledge, no other records of wild erythristic leopards were documented until 2012 when a male was photographed by a guide at the Madikwe Game Reserve in the North West Province of South Africa (Figure 24). This was subsequently reported in the popular press (Dell'Amore 2012). Here, we report new sightings from Mpumalanga and the results of a survey of managers and section rangers of National Parks, wildlife reserves, and conservation organisations in South Africa, supplemented by press reports and social media, to understand the possible distribution and abundance of this leopard colour morph.

Figure 24: Map of South Africa with relative locations of erythristic leopard sightings (1) Madikwe Game Reserve, North West Province and (2) Thaba Tholo Wilderness Reserve, Mpumalanga (3) Lydenburg, Mpumalanga. Source: Google Street Map downloaded 02-07-2015 in QGIS 2015.

6.3. Methods

6.3.1. Our study

Original images were taken by camera traps as part of a wider study conducted at Thaba Tholo Wilderness Reserve (TTWR, Latitude: 24°57”404 S, Longitude: 30°21”105 E, Figure 24), Mpumalanga, South Africa, c. 20 km north-west of Lydenburg. TTWR is 5400 ha and is situated between the Steenkampsberg and Mauchsberg mountain ranges. The reserve lies on the boundary of two major biomes formally classified as savannah in the valleys and northern section of the reserve, and grassland on top of the mountains in the southern section of the reserve (Pirie *et al.* 2016a, Chapter 2). Altitudes range between 1100 m and 2000m and the reserve has an average annual summer rainfall of 700 mm – 900 mm falling mainly between October and February.

Leopard presence at TTWR was recorded using a network of more than 30 camera trap sites positioned less than 2.7 km apart, based on a grid system; sites were chosen to maximise the likelihood of recording leopards and covered all regions. Little Acorn 5210A (Ltl Acorn, Green Bay, Wisconsin, USA) camera units were used, which had three heat and motion sensors which could be triggered up to 15 m away. A series of three images were taken per trigger, with a 30-second interval between captures. The cameras had been in place for 3 years as of October 2012.

6.3.2. Wider survey

Twenty-five appropriate representatives from South Africa National Parks, the Endangered Wildlife Trust, Panthera, and similar organisations and reserves across South Africa were contacted via e-mail and asked if they have had reports of erythristic/strawberry leopards. A request was made to reply even if no animal had been witnessed. Other reports, including press, were located using Web of Science (http://www.wos.com), Google (http://www.google.co.uk), and references from Hartwell (2015). A general request was also posted on Twitter using the #mammalwatching hashtag, where it was seen 3053 times at the time of writing.

6.4. Results

From the Internet search and local reports, five individual erythristic leopards, identified through pelage patterns have been captured on camera trap, killed, or caught, in the Lydenburg area, Mpumalanga; and two animals in Madikwe Game Reserve and the surrounding area, North West Province (Figure 24, Table 22). Of the 28 individual leopards recorded at TTWR during this 3-year study two (7.14%) were erythristic Figure 25, Figure 26); one of which was born to a normal coloured female (Figure 26).

Of the 25 individuals approached we received replies from 19 managers, section rangers, and researchers from reserves and organisations from across South Africa. The skin of one other erythristic animal (Table 22: animal 1) had been identified. No other responses were received from the social media call for information on strawberry leopard sightings.

Figure 25: Image of erythristic individual 5 taken on a property on the R37 outside Lydenburg, Mpumalanga, Latitude: 24°93310 S Longitude: 30°33716 E., 01 May 2015. Source: Ingwe Leopard Research.

Table 22: All reports found of erythristic leopards in South Africa.

Ani	Date	Age and sex	Location	How recorded	Reference	Notes
1	Unk. ± 15 yrs	Unk. sex	Close to Botswanan border and Madikwe Game Reserve	Shot	Anonymous (pers. comm.15 Oct 2015)	Skin given to a farmer in Lydenburg Area
2	Aug-05	Adult female	R36, Lydenburg	Carcass; road death	Mr. B Van der Wal (pers. comm. 22 Oct 2015)	-
3	2012	Adult male	Madikwe Game Reserve Latitude: 24°8167 S Longitude: 26°2167 E	Photo.	Dell' Amore 2012	Photo. by Deon De Villiers
	Sept-15			Camera trap images	Samantha Sealie, Madikwe Conservancy Private Game Reserve; Gareth Mann, Panthera	Camera trap
4	Mar-13	Adult female	Sekhukhune road, Lydenburg	Carcass; road death	Anonymous 2013	Had recently weaned cubs
4 or 5	Jan-14	Unk.	Lydenburg area	Photo.	Anonymous (pers. comm. 08 Oct 2015)	Probably animal 4 or 5
5	Sept-14 (x3)	Adult female	TTWR and surrounding properties Latitude: 24°93310 S Longitude: 30°33716 E	Camera trap images (Figure 25)	This study	Pictured with known male
	Oct-14					
	Jan-15					
	Feb-15 (x2)					
	May-15					
6	Nov-14	Two-year-old male	Lydenburg area	Photographed; later captured and released	Anonymous 2014b	Satellite collared by Mpumalanga Parks and Tourism Authorities
	Jan-15			-	Anonymous 2015	
7	Mar-15	Un-weaned female cub	TTWR 24°98322 S Longitude: 30°35086 E	Camera trap images (Figure 26)	This study	With mother (normal coloured mother and grandmother)
	May-15					
	Jun-15					
	Jul-15			Observed by field worker		

Figure 26: (Left) First in a series of three images of an adult female leopard, FS44 left, and her erythristic cub (animal 7), middle, taken on 31 March 2015 at TTWR (right) last image in the series taken on 31 March 2015 at TTWR of FS44's erythristic cub (centre frame of image) and the second normal coloured cub (far right of image). Source: Ingwe Leopard Research.

6.5. Discussion

To our knowledge, only one previous paper has reported the presence of erythristic leopards (in India; Divyabhanusinh 1993). Here, we provide the first formal report of the presence of wild erythristic leopards outside of India. In total, there are seven records of wild erythristic leopards in South Africa, five in the Lydenburg area.

South Africa's first erythristic leopard report in 2012 was recorded in the North West Province, some 400 km from our Mpumalanga study site. Although such distances are likely to preclude dispersal of offspring of any given individual, it has been suggested that these widely separated leopard populations may be considered part of a single core population (Friedmann & Traylor-Holzer 2008).

General colour resemblance (where an animal resembles the general colour of their environment) may be the reason for the higher frequency of melanistic leopards in moist habitats sporting thick vegetation (Allen *et al.* 2010), but this is unlikely to provide an explanation for the presence of the erythristic forms recorded here, as this region does not exhibit a prolonged dry season and leopards in savannah habitats are thought to be predominantly nocturnal hunters (Bailey 1993), hence a pale pelage would not be beneficial.

It is worth considering other explanations for the recent sightings of erythristic leopards in Mpumalanga, and we posit three hypotheses. Firstly, this is simply a reflection of reporting bias. The area covered by the camera traps is limited and although our reports are unlikely to present a precise density of this colour morph, the numbers of observers and sightings shared though social media from large National Parks to small holdings across South Africa are a good indication of its rarity. Therefore we feel that reporting bias is unlikely (although because of the secretive nature of leopards, it is possible that unusual behaviours or forms are overlooked, e.g. Pirie *et al*. 2014). Secondly, and highly speculatively, this may reflect leopards released or escaping from captive breeding programmes, where animals are reared for trophy hunting. Some nine game ranches in South Africa breed leopard (Lindsey *et al.* 2011) and the captive breeding of colour morphs of other species for hunting, such as lion (*Panthera leo*), is known to occur (Crowley 2015). Indeed, there is a record of a captive bred male strawberry leopard born to parents which came from the same area as the wild individual seen in 2012 (Anon 2014c). This is possible, but unsubstantiated. Thirdly, that this reflects the result of population fragmentation and isolation and therefore a highly reduced effective population size, resulting in the expression of a *de novo* or previously rare allele at higher frequencies. Such inbreeding effects are thought to result in the presence of the very rare king cheetah *Acinonyx jubatus*, and white lion colour morphs in southern Africa (Sunquist & Sunquist 2014); it has also been documented with leopards in the Malaysian peninsula, where the rapid near fixation of melanism occurred following population fragmentation (Hedges *et al*. 2015; Kawanishi *et al*. 2010). Similarly, Haag *et al*. (2010) reported genetic drift within small fragmented jaguar populations over a relatively short time frame and McManus *et al.* (2015) showed that leopard populations can become isolated within a few generations. Perhaps this is the most reasonable explanation for observing the erythristic morph in relatively high numbers in a single area; however we can only speculate; future research is required to test this explanation.

The geographical range of the leopard has diminished by an estimated 37% which underpinned the need to reclassify the leopard on the IUCN Red data list from least concern to near-threatened in 2008 (Balme, *et al.* 2010b, new evidence states up to 75% and is now reclassified as vulnerable, Jacobson *et al.* 2016). Within South Africa, the destruction of suitable leopard habitat has produced highly fragmented areas with depleted prey densities, (Chase-Grey 2011; Swanepoel *et al.* 2013) which combined with persecution (Lindsey *et al*. 2011) has substantially reduced leopard numbers and caused populations to become isolated (Friedmann & Traylor-Holzer 2008). Until January 2016, 150 CITES (Convention for the International Trade in Endangered Species) trophy animal permits were allocated annually to South Africa (Balme *et al.* 2010b; Lindsey *et al*. 2011). Zero permits have been allocated for 2016; however, this is temporary and will be reassessed for 2017 (Anon 2016b). Documenting this rare leopard colour morph could result in negative outcomes (e.g. encouraging illegal capture for breeding); however, the expression of erythrism may be a visible indicator of potential population fragmentation.

6.5.1. Conclusion

We collated seven records of erythristic leopards in South Africa. Two of 28 individuals recorded at our study site (TTWR; Mpumalanga) were of this form, and we found five other records from Mpumalanga and North West provinces. The majority of records were recent, and the oldest was from the early 2000s; we were unable to find earlier records of erythristic leopards from South Africa. Although speculative, we suggest that this may reflect the consequences of population fragmentation and reduced genetic variation. However further research is needed in order to ascertain whether erythristic leopards are a visible sign of increasing threats to the viability of local leopard populations or just a random occurrence.

Chapter 7

Discussion

7.1. Importance of monitoring

Carnivores worldwide are under threat and their long term survival will depend on understanding these threats and implementing evidenced-based approaches to conservation. The declining trend for many large carnivores including cheetah, wild dog and lion, highlights the importance of population monitoring (Table 1). However, low densities, nocturnal behaviour, large home ranges and the hostile environments carnivores often inhabit can hinder collection of vital ecological and biological information required for their successful conservation. Within South Africa, lion, wild dog and cheetah are mainly restricted to protected fenced areas because of conflict and persecution, whereas leopard, brown hyena and many meso-carnivores are still free ranging, bringing them into conflict with humans. Although generally effective in protecting species, reserves can generate other issues such as population isolation and increased habitat fragmentation. Therefore understanding a species' ecology, biology and the cause of their decline is vital in order to inform their conservation.

7.2. Methods of monitoring elusive mammals (Chapter 2)

Field evidence including spoor and scat have been used historically to track and monitor a wide variety of mammals (e.g. dingo, Allen *et al.* 1996; Amur tiger, Hayward *et al.* 2002; tigers, Sharma *et al.* 2003; caracal, Melville *et al.* 2006; snow leopard Janečka *et al.* 2008; cougar, Sawaya *et al.* 2011), although this relies on field skill and expertise to locate and identify the evidence. Tiger censuses were based on spoor (or pug marks) which were recognized individually from track shape and unique features; however concerns were raised at the reliability of individual identification (Karanth 1995) which is paramount for reliable population estimates (Karanth & Nichols 1998).

Camera traps can overcome this problem as some species can be individually identified from their unique coat patterns (Jackson *et al.* 2006; Chapter 4 and 6). The fact they are easy to use, cost effective (Lyra-Jorge *et al.* 2008), are un-invasive and a wide variety of species can be identified (Yasuda 2004; Pettorelli *et al.* 2010; Liu *et al.* 2013, Chapter 4) is largely why they are becoming more commonly utilized (Trolliet *et al*. 2014; Brassine & Parker 2015). However there is a danger of relying too heavily on these methods while ignoring the benefits of traditional techniques which may help to enhance findings. This study shows field evidence collection by amateur trackers and experienced field ecologists alike can be utilized to calibrate and complement the data collected by camera traps (Chapter 2). Results also highlighted the limitations of spoor collection, as depending on the substrate conditions the print may not register completely, losing the information necessary for successful identification by amateur trackers (Chapter 2).

By directly comparing spoor with camera traps, the later was found to significantly under-record most of the large and meso-carnivores, which was inversely correlated with size (as was found by Lyra-Jorge *et al.* 2008), and to some extent the length of the species. However this contradicts Urlus *et al.* (2014), who found large Australian mammals were less likely to be detected than smaller species, although detections may have been higher for smaller species as they were baited and had restricted home ranges. Findings do support recommendations by Karanth & Nichols (1998) and Brassine & Parker (2015) that camera positioning can significantly affect the detection of focal species, confirming biasing cameras to increase detection of focus species is required and is more effective than baiting for large cats (Braczkowski *et al.* 2016). The success of camera traps in recording leopard compared to spoor located indicated the height and placement of the traps was optimum for this species, which was also corroborated by other research conducted on leopard using camera traps (Chase-Grey 2013; Braczkowski *et al.* 2016).

Direct measurements taken from spoor as a tool for trained field ecologists to confirm a broken or interrupted trail of an individual animal can be extremely beneficial. It can allow information missed by collar downloads, telemetry readings or between cameras to be gleaned and used to further understand the behaviour or the biology of a focus species. However data collected here suggests simple measurements are limited in terms of individual animal identification in situ due to the significant variation in measurements taken even by experienced data collectors. Nevertheless images taken of spoor have been found to be effective in individual tiger (Sharma *et al.* 2005) and rhino (Alibhai *et al.* 2008) identification when later analysed using complicated digital measurements a technique which could be applied to other species. This study shows that field evidence can be successfully located and utilised by amateur trackers.

7.3. Effects of fencing on mammal distribution (Chapter 3)

Fencing is the most common form of barrier for restricting animal movement for a variety of purposes (conservation), limiting the spread of disease (Andrews 1990, Vanak *et al*. 2010), protection from persecution (Hayward & Kerley 2009), and from predators (Rimmer & Deblinger 1992). However potential negative factors such as, population isolation, habitat fragmentation, resource overutilization and fatalities call into question the use of fences as an effective wildlife management tool (Hayward & Kerley 2009; Woodroffe *et al.* 2014). Alternative methods have been suggested, however they mainly focus on elephant deterrent (Sitati *et al.* 2006; King *et al.* 2011), leaving fences as the only viable option for restricting mammal movement, hence the widespread use of fences especially for the conservation of carnivores (Packer *et al.* 2011). Even though this may be true, little is really understood of the local effects of fences on the distribution of large mammals, particularly of non-target species, which is surprising considering the amount of research into the effects of roads and railway lines on a range of species (Adams & Geis 1983, Forman & Alexander 1998, Ng *et al.* 2004, Ito *et al.* 2005, Shepherd *et al.* 2008, Farig & Rytwinski 2009, Frantz *et al.* 2012).

This study compared the assemblages of larger mammals (using spoor and scat location, Chapter 2) and plants on either side of the TTWR fencing. A 76% overlap in mammal species was found either side of the fence and a 53% of plant species. The difference resulted from the effectiveness of the fence at separating livestock and large introduced grazers. This discrepancy in grazer composition was reflected in the difference in the percentage of non-woody cover, although at a crude level this supports the findings of Todd & Hoffman (1999) and Olofsson *et al.* (2001) which resulted from different grazing pressures. In contrast, the browsing community was similar on both sides of the fence, mirrored by similar proportions of woody cover either side, even though more animal evidence was located inside the fence. Augustine *et al.* (2011) also found browser presence was likely to reduce bush encroachment which could be facilitated by cattle. However the unrestricted movement of at least fifteen species, including members from the omnivore, browser and carnivore guilds highlights the potential benefit of maintaining holes along perimeter fences (Chapter 3) which could also be a relatively simple and economical solution in reducing the risk of genetic isolation within the wild mammal community especially for highly mobile species.

The presence of fencing, the introduction of some wild game and changed management practises has resulted in TTWR reverting from farmland to a habitat more typical of that found on the boundary between grassland and savannah biomes in South Africa. In allowing the movement of specific species while continuing to restrict others it may have avoided over utilization of resources within the fenced area (Cassidy *et al.* 2013) and limited the effects on vegetation caused by differing feeding pressures and therefore habitat fragmentation. However replication at other sites would be needed to determine if this is indeed due to the similarity of mammal community either side or just restricted to the study site.

7.4. Habitat and species interactions (Chapter 4)

Habitat and climate are important drivers for mammal diversity and general distribution (Andrews & O'Brian 2000), with local vegetation characteristics influencing species richness and abundance through bottom up processes (Sinclair 2003). Apex predators are also important in regulating ecosystems through top down processes, as they can affect other trophic levels directly through lethal removal or indirectly through inter-specific competition (Berger & Gese 2007; Gommper 2002; Ripple *et al.* 2006; Prugh *et al.* 2009). Systems have been found to collapse in the absence of apex predators (Terborgh *et al.* 2001; Myers *et al.* 2007). Understanding how both of these drivers contribute to the species composition and abundance in an area can increase our ability to manage a species more effectively.

Of the six members of the large carnivore guild in South Africa, lion, spotted hyena, cheetah, wild dog, are mainly restricted to game reserves with a small number of isolated pockets of wild populations in the north of the country (Stuart & Stuart 2015). Interactions have been well documented between these large carnivores (Durant 2000; Vanak *et al.* 2013) however interactions between the largest free-roaming carnivore in South Africa and meso-predators and habitat preference in the absence of the other large carnivores have not been well studied.

The leopard is the main apex predator throughout South Africa and indeed the African and Asian continents; however it has undergone rapid decline which has only recently been highlighted, having been reclassified on the IUCN red data list from least concern in 2008 to vulnerable in less than a decade (Jacobson *et al.* 2016). However the classifications and CITES permit allocations are based on recommendations rather than field data, which is severely lacking (Lindsey *et al.* 2011).Therefore it is critical to supply field data on the leopard, which is deemed tolerant to a wide variety of habitats to further understand why it might be undergoing such a rapid decline (Chapter 4, 5, and 6).

Density average based on the closed quarterly estimates, 3.04 (S.E.+/- 1.55) leopards per 100km^2, were similar to estimates taken outside Phinda private game reserve, Kwa-Zulu Natal 2.49 (S.E. +/- 0.87, Balme *et al.* 2009b). The slightly higher estimate based on the yearly data of 4.97 (S.E. +/- 2.14) leopards per 100km^2, was closer to estimates found for montane savannah inside Welgevonden private game reserve 4.56 (S.E. +/- 1.35), however both estimates were much lower than most other estimates based on adult animals within South African savannah inside and outside protected areas. However compared to other areas in Africa and Asia, estimates were average (Appendix 1). Although leopards move freely between both the reserve and farmland areas (Chapter 4), the evidence of leopards reproducing within TTWR suggests it is a source area. Density remained unchanged over the three years implying young animals moved away from the maternal area and that the study area was likely to be at carrying capacity for leopard at the transition zone between grassland and savannah.

As proposed by Maputla *et al.* (2013), Tobler *et al.* (2013) and Braczkowski *et al.* (2016), the year data may have produced more accurate density estimates compared to the quarterly estimates based on the average coefficient variation estimate of the density values of 0.46 and 0.52 respectively (Chapter 4). However the 0.07 difference between values may not warrant the time spent for a relatively small return in accuracy. The number of "best" models which included a positive learned behaviour towards the cameras by leopards supports findings by Trolle & Kery (2005) and Brassine & Parker (2015) who suggested dirt roads and trails are utilized frequently by animals, as was also shown by the variety of species captured throughout the duration of the study (Chapters 2 &4).

The study found there was a high diversity of carnivores (42% of the total terrestrial predators found in South Africa, Stuart & Stuart 2015) within the study site which incorporates an interface between two different eco-regions from the two major biomes grassland and savannah; the boundary between which is the longest of all the biomes crossing 18,800km of the country (Rutherford *et al.* 2006). Although both habitats were utilized by most carnivores, there was a significant preference for the mountainous grassland by the larger carnivores, brown hyena, caracal, and serval. Interestingly the smaller species showed preference for known favoured habitats. Relative abundance levels were higher for Cape fox in grassland, with the large-spotted genet and Meller's mongoose showing a preference for savannah, highlighting habitat could be a more significant factor influencing small predator abundance than for larger carnivores.

Interestingly relative leopard abundance only showed significant positive associations with African civet and large spotted genet even though leopard has been documented hunting both species (Bailey 1993, Hayward *et al.* 2006a) indeed evidence was found indicating a civet was killed by a leopard during the study (Pirie *pers. obs.*). Caro & Stoner (2003) proposed genet species were more likely to experience inter-specific competition due to overlap in diet and distribution. Both caracal and brown hyena relative abundance levels were negatively associated with Meller's mongoose and large spotted genet which is more in keeping with the theory larger predators could negatively impact smaller carnivores (Glen & Dickman 2005).

Nevertheless when carnivore relative abundances were tested as co-variants with habitat characteristics, habitat was found to be more important in influencing most carnivore abundances although abundance levels could ultimately be driven indirectly by carnivore abundance as vegetation can provide refuge from possible interactions (Janssen *et al.* 2007). Abundance levels are only a proxy method of looking at potential interactions, but the study does show there are possible positive and negative associations which may be of importance depending on habitat and abundance levels of each animal. However further research would be needed to tease apart the individual relationships and influences for each carnivore (Palomares *et al.* 1998) to fully understand how detrimental these relationships could become if apex carnivores are reintroduced into a reserve or if numbers exceed to a greater extent than they would naturally within an enclosed area.

Relative abundances for many carnivores significantly decreased in the wet season, which may be attributed to increased water availability and therefore wider dispersal of prey (Bailey 1993). However, fences are not impermeable barriers and the birthing of livestock, as well as some antelope including impala and wildebeest, occurs during the wet season which may account for reduced relative abundances recorded for species such as caracal and jackal, which are known to predate on livestock (Bergman *et al.* 2013), the latter of which are documented taking animals during the birthing process (Yom-Tov *et al.* 1995, Pirie *pers. obs*). Small protected areas, such as TTWR, can act as sources of predators that become a threat to livestock in the surrounding farmland. Understanding how increases in the local presence of predators effects landowner's attitudes is the first step in helping reduce human-wildlife conflict.

7.5. Negative behaviour towards carnivores (Chapter 5)

Attitudes are thought to be inaccurate when it comes to predicting the actions of a person due to other factors such as social influences, cultural background and possible repercussions (Wallace *et al.* 2005, Gross 2016), therefore by asking what action may be taken can avoid the ambiguity to a certain degree. Although there were fewer responses in 2015 and some farmers may not have provided completely accurate responses, results of the survey indicate negative actions have been taken towards members of the carnivore guild. Losses of livestock were not noticeably different, yet the use of any form of management to protect livestock had decreased. Game losses had increased in 2015, even though perceived carnivore attacks between the five years showed no significant change. The increase in protection and perceived greater losses of game could therefore be attributed to the rising cost of game over the years, as livestock prices have remained relatively stable (Chapter 5). In addition, a higher percentage of exotic game farmers (64%) responded they would take negative action against one or more species of carnivore compared to livestock farmers (41%) and there was a significant difference in actions taken between stock and non-stock farmers in 2015; with the former showing they were likely to remove certain carnivores more readily than the later; which is likely driven by the financial loss experienced when too many animals are killed (Thorn *et al.* 2013).

The dramatic rise in game prices coupled with the increase in game farming across the country has the potential to decrease tolerance shown towards carnivores and as a result could cause an increase in retaliatory killings (Chapter 5). These can be legal (DCA permits, Pitman *et al.* 2016) or illegal. Swanepoel *et al.* (2011) modelled the effects of retaliatory killings compared to regulated killings through trophy hunting on leopards, and found that the random removal of females and young animals was detrimental to local populations, while trophy hunting had much less of an effect. However the ripple effect of the removal of male animals from a system should not be overlooked especially in species like leopard that commit infanticide (Balme *et al.* 2013) and therefore could create the same problem as non-specific killings. If lethal removal occurs in areas where densities are already low, genetic diversity can be reduced (Hartl *et al.* 1991) which can decrease reproductive success and disease resistance (Kissui & Packer 2004). While it is clear that leopard numbers are rapidly declining in unprotected areas, we have almost no direct or indirect data on the consequences of this loss and fragmentation on leopard population structure.

7.6. Local leopard population (Chapter 5)

Over the last decade, sixteen trophy hunting permits (23% of the total potential permits for the province) were allocated between 2006 and 2013 to the area. Although there were no DCA permits requested, at least ten animals were illegally removed and an estimated 12-19 were killed on roads (Chapter 5), equating to an average of 4-5 animals removed by humans a year. Based on the average population estimates from animals over a year old from this study, 6.7 (S.E. +/- 2.3) leopards per 100km^2, this could have equated to 3-12% of the population removed within the 100km^2 area each year (Chapter 5). Although this is an extremely rough estimate considering age of animals killed was unknown, or if the animals were resident or vagrant and the consequential effects from the removal of each individual.

However, this loss may account for the exceptionally high numbers of an extremely rare erythristic colour form recorded in the local population. This is almost certainly a recessive inherited trait. Melanism is known to be recessively inherited in leopards (Schneider *et al.* 2012); a trait also been seen in leopards in the area (Anon 2013d). Erythrisism in other animals has been found to be determined genetically (Fontanesi *et al.* 2009; Majerus & Mundy 2003; Peterschmitt *et al.* 2009), and it is likely to be a similar trait in leopards. McManus *et al.* (2015) has shown genetic drift can occur relatively rapidly within the leopard and is thought in part to be the reason for a high density of melanistic leopards in the Malyasian peninsula (Kawanishi *et al*. 2010; Hedges *et al*. 2015). Therefore it is highly plausible this could have occurred within this population as densities are lower than in other areas within savannah (appendix 1, Chapter 4). The effects low numbers could be increased if long distance movement is restricted which could increase the loss of genetic variation which may have allowed the extremely rare colour morph to manifest within the local population in such high frequency (Kawanishi *et al*. 2010; Hedges *et al*. 2015). It is unlikely mesic highveld grassland is blocking movement (Chapter 4), however roads (Jensen *et al.* 2009) or a “landscape of fear” through persecution (Ciuti *et al.* 2012) could act as a barrier.

Since the paper on erythristic leopards was published, six more reports have been forthcoming (John Power, *pers. comms*); two more from the Lydenburg area, the rest from the North West Province, where the other two animals recorded in the Chapter were found. It is of concern that they are all located within one core leopard population thought to span Mpumalanga and the North West Province. So far no other reports have been found within the other ten core populations, including the closest neighbouring core population based in Limpopo. Such expression of rare colour morphs is highly suggestive of extensive population fragmentation and resultant inbreeding (Sunquist & Sunquist 2014). There could be two reasons for the lack of erythristic animals seen within the Limpopo population. First, leopard densities may be high enough to withstand losses combined with sufficient movement into the population from other core populations, so population fragmentation is countered. Second, the mutation is sufficiently rare that even if fragmentation was enough to increase inbreeding, it is not there to be expressed, however this is speculative and further research is needed to verify this theory.

7.7. Hunting verses tourism

Hunting can be divided into two categories: trophy and meat (termed biltong hunting, Taylor *et al.* 2016). It was reported trophy hunting broke the billion rand barrier in 2013 (Anon 2014d). It was further estimated to have generated R1.9 billion (US$ 132 million) in 2014 alone with the main species hunted as impala 18%, warthog 13%, springbok 12% and kudu 11%. Leopard was only mentioned as other (Taylor *et al.* 2016). Revenue generated through hunting for biltong was thought to generate R0.651 billion (US$ 45.5 million) in the same year, with springbok representing 27% and impala 23% (Taylor *et al.* 2016). Although large carnivores are highly prized for trophy hunting, exotic game and rare colour morphs are becoming increasingly popular to hunt (van Hoven 2015), which may place erythristic leopards or animals thought to carry the trait under threat. The financial return for farming trophy-worthy animals and colour variants from live auctions are considerable, which is likely to have been the cause of the increase in exotic game and rare colour forms farmed over recent years (Pitman *et al.* 2016).

South Africa had in region of 8.9 million tourists in 2015 (Anon 2015e). Large government protected reserves are likely to be supported through ecotourism alone due to the quantity of visitors they attract, e.g. 1.66 million foreign tourists visited Kruger national park in the 2014/2015 financial year, generating an estimated R321 billion (US$23 billion) in conservation fees alone (Anon 2015f). Unique selling points, such as birdlife or rock paintings can allow small reserves to attract specific clientele; however in order for reserves to compete for international tourists they often need to contain large carnivores, such as leopard and lion, to meet public demand (Hayward *et al.* 2007a). For private reserves carnivores can be costly not only to buy, if not already occurring naturally, but also to feed. With rising game prices this could continue to become more expensive. In addition, fenced areas have been shown to aid carnivores in reaching higher carry capacities (Packer *et al.* 2013; Welch *et al.* 2016) with some reserves containing a lion biomass density ratio which is three times higher than numbers for a stable lion to prey relationship (Tambling & Du Toit 2005). This combined with considerable expenses such as road, vehicle, and fence repairs as well as staff wages can directly impact the financial viability of privately owned properties. The hunting of certain species as an extra form of income may be utilized in order to subsidize the smaller reserves in the future, which could fuel further conflict. Although increasing negative attitudes towards carnivores will be likely to intensify, as well as the potential for retaliatory killings as prices of game continue to rise, smaller reserves could play an important role in conservation. This could be vital in South Africa as human disturbance increases and demands for food and other resources fragments the land further.

7.8. Habitat loss and fragmentation

Already 45% of grassland is thought to be damaged through human impacts (Fourie *et al.* 2015) which could have major implications for species such as the Cape fox which prefer grassland habitats compared to savannah (Chapter 4). Mineral richness is generally located where biodiversity is high, mainly in the west where the savannah biome occurs (Anon 2015b). Although private land may be owned, if minerals are located beneath the property mining can still occur, unless rare species are found in the proposed area (see Mineral and Petroleum Resources Development Act 28 of 2002, Anon 2014e). Farming and mining will continue to fragment suitable habitat which will increase the risk of isolating populations, and further urbanization could have implications especially considering leopards may be able to exist in highly urbanised areas (India; Athreya *et al.* 2013), although this is likely to be a last resort as leopards have been found to avoid human activity where possible (Steinmetz *et al.* 2013). Although controversial (Beier & Noss 1998), corridors as a means to connect wildlife populations may become more important to ensure genetic variation and species survival outside of formally protected areas.

Conservancies help to reduce the effect of fencing and allow movement between properties, there is still a risk of genetic isolation if species within the fenced areas are not managed properly. Animals may have to be relocated in order to maintain genetic variation, which may have serious implications on the resident population (Rabinowitz *et al.* 1986; Karanth & Sunquist 1995). Gaps for target species in fences may promote a more stable system outside of protected areas, especially as habitat loss and fragmentation will continue to increase as human populations expand and encroach further into wilderness areas. Hence there are plausible benefits, including allowing the dispersal of highly mobile species in order to reduce the risk of genetic isolation, while still providing access to protected areas and resources or through fencing designed to restrict people rather than animals (Hoyier 2000). However this could lead to increased levels of conflict. Unless the conflict between carnivores and humans can be resolved, carnivores will only thrive within the confines of fenced reserves needing to be managed to ensure genetic viability and maintenance of resources. Therefore solutions to resolve the conflict issue and promoting co-existence are paramount in the conservation of carnivores.

7.9. Solutions

The education of school children and communities alike to increase knowledge in order to encourage conservational action and behaviour (Jacobson 2010) has been implemented across many conservation projects (Jacobson 1999; Josiah 2001; Brewer 2002; Jacobson 2010). Engaging and involving the local community in conservation efforts may be the key to promote long term conservation success (Bjorkland &

Pringle 2001) and although measurements of the success of outreach programs are limited (Brooks *et al.* 2005), evaluations that have been conducted have shown a positive outcome (Leisher *et al.* 2012) and may possibly work in South Africa. One farmer surveyed suggested his attitude had improved by understanding how carnivores fit into the local ecosystem. Workshops that educate stock owners about behaviours of animals while promoting and encouraging the use of simple preventative measures and management strategies may help to reduce livestock depredation. For example, black backed jackal generally hold territories as a pair, but if either or both are removed the territory is left open which can result in an influx of jackals to take the vacant territory. If the alpha pair is left, jackal numbers are less likely to fluctuate in the area (Estes 1997).

Compensation payments for livestock losses to predators have been tried along the boundary of Kruger National Park. Farmers experienced payment delays due to uncertainty as to which authority should provide compensation (Anthony *et al.* 2010) causing traditional authorities to believe monies rightfully due were being corruptly withheld from them. In some circumstances providing proof of loss was also difficult and not all cases could be dealt with (Anthony *et al.* 2010). Nevertheless, compensation schemes should be explored further as a possible solution to encouraging co-existence with carnivores as the approach has shown potential elsewhere (Agarwala *et al.* 2010). If money is not a viable solution, a scheme whereby like for like is provided, where small losses occur (e.g. calf losses) or for large losses the loan of a prize bull with good blood lines to mate with heifers could be a form of compensation. Such schemes are used in Sweden, where farmers or communities are compensated for showing tolerance towards carnivores by receiving payments when carnivores successfully breed (Zabel *et al.* 2014). Farmers selling meat could have a regulated badge of honour (similar to honey badger-friendly honey in South Africa) showing that they protect carnivores, for which they might receive a higher price for the meat. Camera traps could assist with regulating the presence of animals on land, which could be incorporated into an outreach program to local school children who could help identify the animals recorded while making them aware of the important role of carnivores to the environment and importance of sustainability.

The issue of damage causing animals does need addressing as retaliatory killings are still evident (Chapter 5). Although relocation has been found to create problems for resident animals, problem animals could be relocated to re-stock areas of suitable habitat (Patton 2011). Alternatively provincial parks and tourism authorities have tendered permits to trophy hunter outfitters in the past to allow trophy hunters to shoot damage causing animals outside the Kruger National Park boundary; however this was not found to be viable due a small number of the DCAs that were of trophy standard (e.g. lions 20%), the time and money it took to trace the offending animal, the animal leaving the area or the evidence found was miss-identified as another animal (Anthony *et al.* 2010). There is the potential for a compromise in areas where losses are high (as long as regulations were met to ensure as much was done to limit the potential for an attack). Instead of targeting a damage causing animal which was killing (for example) high value game or livestock repeatedly, which could be a female or male in his prime; the removal of which could cause serious repercussions, it has been suggested targeting an old male past his prime instead (aged by features highlighted by Balme *et al.* 2012). It is argued a male past his prime is therefore likely to be killed or displaced by a new male, hence his removed could be used to generate money for compensation instead. A minimum age limit >7 years old has been suggested by Balme *et al.* (2012) to allow at least one set of cubs to be sired, but perhaps a higher age limit should be considered to allow for a longer periods of stability in the system. The argument for this solution being the animal would be acceptable to trophy hunters, he would have sired offspring and therefore the removal would mirror the natural cycle and affect the population dynamics to a less extent (Balme *et al.* 2012). This would need strict regulation to ensure the right animal was removed at the right time, but this may appease the financial losses of farmers while avoiding potentially catastrophic repercussions within a population. If the financial loss is converted into a financial gain there is less likely to be negative behaviour towards carnivores (Stander 1997c; Thorn *et al.* 2013; Blackburn *et al.* 2016) which may reduce the likelihood of retaliatory killings and increase co-existence (Chapron *et al.* 2016). If there are financial reasons for keeping animals in the area, this may help to promote co-existence, thereby allowing the carnivores to increase in number (Agarwala *et al.* 2010; Zabel *et al.* 2014).

In remote areas, schemes to promote wildlife have been tried with some success. Losses per village in Namibia were found to total N$55 per year ($4.06 USD), however when the villagers guided eco-tourists to see carnivores in the area they made an average of N$667 per village ($50 USD) per year (Stander 1997c). Similarly Blackburn *et al.* (2016) showed lions could live outside protected areas where community based conservancies were situated in Kenya. A similar scheme has also been tried in Madagascar to promote the sustainability of lemurs in the area by reducing harvesting and increasing eco-tourism (Schwitzer *et al.* 2014)

7.10. Further research

Further work should be undertaken to understand leopard ecology in the surrounding farmland and interior mesic highveld grassland, to fully understand the population dynamics. Further research is also needed to ascertain how closely related the leopards are in the local population (TTWR and surrounding areas) to determine if inbreeding has occurred. This could be conducted through DNA analysis of scat and hair samples taken at the site in conjunction with camera traps to provide detailed characteristics of individuals. It may be possible, as DNA sequencing techniques improve, to also analyse hair taken from pelts of the erythristic leopards in the area to determine if erythrism is a recessively inherited trait which could help to clarify if the rare colour morph occurred through genetic drift within the population.

Genetic samples could also be compared to those taken from animals in the north-west province, Limpopo and the other potential core populations to understand if migration has occurred or if they have indeed become isolated. The potential for dispersal and movement by leopard and other carnivores such as brown hyena should also be investigated to ascertain if there are barriers restricting movement, such as roads, between the study area or if a ‘landscape of fear’ has developed between the study area, north-west province and Limpopo. Areas where fatalities occur due to vehicle collisions should also be identified and assessed for the potential for assisted crossings to allow the safe passage of leopard and other animals. Developing approaches to allow individual privately owned reserves and land to become linked through dispersal corridors and data sharing would be a huge step forward in South African conservation. A part of this could be the development of appropriate fencing. Fencing provides a limited barrier to leopards and other cats, but the provision of fence gaps to allow some movement of prey species into surrounding farmland may help provide non-livestock resources to bridge the gap between reserves for large, mobile predators. Further investigation into leopard and other carnivore ecology residing outside formally protected areas is also needed to really understand the extent of the potential impact humans could have and may be having on these communities.

However the most important and urgent research needed should address the conflict between carnivores and humans. Indeed the potential conflict and threat of retaliatory killings from commercial game farmers should be investigated further as well as other reasons for direct removal of leopards and other carnivores (i.e. medicine and animal product trades). Until the threat of direct removal is removed, the issue is likely to escalate with population expansion which will impact greatly on the world's carnivores. Although various methods have been tried, there are mixed results. Compensation schemes are plausible and alternative methods instead of money should also be explored.

7.11. Implications

South Africa has experienced a loss of over 5,000 rhinos between 2008 and 2015 due to poaching (Anon 2016d). If poaching continues both black and white species are thought likely to become extinct in ten years (Winchester 2015), which will have huge repercussions for the tourism industry. Elephant poaching is increasing (Wittemyer *et al*. 2014) and the great white shark *Carcharodon carcharias* is thought to be facing local extinction in South Africa, with numbers reported to be as low as 300 (Maseko 2016). Although the leopard is unlikely to go extinct in the country, it may become so elusive tourists may decide to visit Kenya, Tanzania or other areas to see them rather than South Africa. This would impact the viability of smaller reserves, which may become ever more critical in the conservation of leopard and other carnivores as urbanisation, mining and livestock farming increases to satisfy the growing population increasing habitat fragmentation and further restricting movement of leopard and other species.

7.12. Conclusion

Improvements in technology and computer software are allowing researchers to provide data on more cryptic species. Camera traps are ideal for collecting data on a single target species for density estimates (Chapter 4), or mammal communities to provide further information about ecological process which will be important in the management and conservation of the species within the area. The data from this technology can be further supplemented by field evidence which can potentially be collected by amateur ecologists to aid in data collection or calibration of technology (Chapter 2 and 3).

Although small reserves may be important for the future conservation of leopard and other carnivore species (Swanepoel *et al.* 2014), there is a risk of species isolation and over utilization of resources as well as an increase in habitat fragmentation due to differing mammal communities either side of a fence. The effects of fencing may be reduced if movement of certain mammals is allowed to balance grazing and browsing effects on both sides which could limit habitat fragmentation (Chapter 3) and therefore may allow species to disperse and maintain genetic variation within the fenced area and local populations. It is evident small reserves can provide protection enough to become source areas for endangered species such as the leopard (Chapter 4) which are likely to become ever more important for species survival in the future (Swanepoel *et al.* 2014), however habitat and the potential interactions with lower trophic levels should be considered where species are introduced or allowed to propagate to large numbers in order to maintain a healthy ecosystem. The potential for conflict should also not be underestimated especially where small reserves are surrounded by farmland (Chapter 5) and therefore could increase conflict through species dispersal from the source reserves.

Although habitat loss is considered the largest threat to carnivores (Pullin 2002), the conflict with humans is no less a threat to carnivore survival. If there is little or no co-existence with predators, dispersal may be hindered and populations may become isolated. If local numbers drop to an extent where the population undergoes genetic drift (Chapter 6) an extinction vortex could occur (Pullin 2002). Small reserves have the potential to protect habitat and threatened species, however the threat from direct removal should not be underestimated. Trophy hunting accounted for a potential income of R1.9 billion, the majority of target animals were antelope, therefore the hunting industry can provide high revenue without carnivores such as brown hyena, leopard or lion being hunted which may allow densities to increase; nevertheless retaliatory killings are problematic and could increase with rising game prices in South Africa (Chapter 5). If left unaddressed this could contribute further to the declining trend in leopard distribution and densities and could potentially begin to affect other large carnivores in South Africa.

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