

Leopard diets and landowner perceptions of human wildlife conflict in the Soutpansberg Mountains, South Africa

Julia N. Chase Grey^{a,b,*}, Sandra Bell^a, Russell A. Hill^{a,b,c}

^a Department of Anthropology, Durham University, South Road, Durham DH1 3LE, UK

^b Primate & Predator Project, Lajuma Research Centre, P.O. Box 522, Louis Trichardt (Makhado) 0920, South Africa

^c Department of Zoology, University of Venda, Thohoyandou 0950, South Africa

ARTICLE INFO

Article history:

Received 31 January 2016

Received in revised form

22 December 2016

Accepted 3 March 2017

Keywords:

Carnivore conservation

Livestock predation

Human attitudes

Dietary analysis

Retaliatory killing

ABSTRACT

Human-wildlife conflict between carnivores and livestock and game owners is an issue of high conservation concern and has led to the global decline of many large carnivore species. Research has shown that carnivores are often blamed for higher levels of predation of livestock and game than actually occurs and this often leads to retaliatory killing. The aim of this study was to obtain information via scat analysis on the range of prey species taken by leopards in the Soutpansberg Mountains, South Africa, and combine these data with self-reported accounts of livestock predation from local landowners to examine differences between real and perceived leopard predation. Results showed that despite landowners reporting frequent events of leopard predation of livestock and introduced farmed game across the Soutpansberg farming community, no evidence of these species were found in leopard diets. The most frequently eaten species by relative biomass were bushbuck, hyrax and vervet monkeys; in contrast, the farmers reported cattle and impala as often being taken by leopards. Despite sharing the landscape with domestic cattle and introduced game, leopards in the Soutpansberg do not frequently utilise these species as prey and instead focus their diets on wild species. Human-carnivore conflict can be reduced by overcoming the mismatch between actual and perceived levels of predation via landowner education, effective anti-predation measures, an improved government response to reports of livestock predation and potentially giving economic value to problem animals via trophy hunting.

© 2017 Published by Elsevier GmbH.

1. Introduction

Conflict between humans and wildlife can be defined as a competition over resources or space and can take the form of threats to human life, economic livelihood, property or recreation (Treves & Karanth, 2003). Large predators such as the leopard (*Panthera pardus*), are obligate carnivores specialised for the predation of ungulate species (Loveridge, Wang, Frank, & Seidensticker, 2010). As a consequence they often come into conflict with farmers and pastoralists when they predate upon domesticated livestock or farmed game. Real or perceived predation of economically valuable species is an issue of high conservation concern and has led to the global decline of many large carnivore species (Woodroffe, Thirgood, & Rabinowitz, 2005). It often leads to negative attitudes

and retaliatory killing of large predators and can result in their extirpation from areas where it occurs (Sillero-Zubiri & Laurenson, 2001).

Incidences of human-carnivore conflict are increasing with the expansion of human populations and agricultural activity into the habitats of wild predators (Treves & Karanth, 2003). For example, real and perceived livestock predation by snow leopards (*Panthera uncia*) has led to their persecution by pastoralists in Nepal, India and Mongolia (Bagchi & Mishra, 2006; Johansson, McCarthy, & Samelius, 2015; Oli, Taylor, & Rogers, 1994), jaguars (*Panthera onca*) are frequently killed by ranchers in South America for reportedly taking cattle (Cavalcanti, Marchini, Zimmermann, Gese, & Macdonald, 2010) and cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*) and leopards are shot and poisoned in retaliation for actual and perceived game and livestock predation across Africa (Chase Grey 2011; Kissui, 2008; Ogada, Woodroffe, Ouge, & Frank, 2003; Woodroffe, Frank, & Lindsey, 2007). Similarly, grey wolves (*Canis lupus*) in North America have been subject to widespread eradication due to the threat they are believed to pose to livestock (Chavez, Gese, & Krannich, 2005) and wild dogs (*Lycaon pictus*) have been

* Corresponding author at: Department of Anthropology, Durham University, South Road, Durham, DH1 3LE, UK.

E-mail addresses: j.n.chase-grey@dur.ac.uk, chasegreyj@gmail.com (J.N. Chase Grey).

hunted extensively by cattle farmers throughout Africa due to perceived and real threats of livestock losses (Gusset et al., 2008).

Increases in human-carnivore conflict may be linked to perceptions of the extent of carnivore predation as much as actual losses. Research into actual versus perceived predation has shown that carnivores are often blamed by farmers and pastoralists for more losses than they actually cause (Boulhosa & Azevedo, 2014; Chavez et al., 2005; Mishra, 1997; Naughton-Treves, 1997; Rasmussen, 1999; Sillero-Zubri & Laurenson, 2001). In South America, cattle farmers claim that large felids such as jaguars and pumas (*Puma concolor*) have a significant impact on their cattle herds, even though studies have discovered that livestock predation rates by these carnivores are usually low (Boulhosa & Azevedo, 2014). Cattle farmers and rural residents have been found to hold negative attitudes towards grey wolves due to their perceived impact on livestock (Chavez et al., 2005) but dietary research has shown they prey predominantly on native prey species even when wild ungulate numbers are low and cattle are stocked at high densities (Chavez & Gese, 2005, 2006). In addition, despite being subject to retaliatory killing, snow leopards in Mongolia have been found to prey largely on wild ungulates and only kill livestock opportunistically even though livestock abundance is one order of magnitude higher than that of wild prey species (Johansson et al., 2015).

There are a number of reasons carnivores are often blamed for higher levels of predation of livestock and game than they actually cause; these include mistaken carnivore identity, misattribution of cause of death and the socio-cultural and economic context in which the human-carnivore conflict occurs (Kaczensky, Blazic, & Gossow, 2004; Kellert 1985; Naughton-Treves, Grossberg, & Treves, 2003). For example, Rasmussen (1999) found that cattle ranchers in Zimbabwe attributed losses of livestock to wild dogs when they had actually been caused by rustling and poaching. The presence of predators provided an excuse for herdsmen to explain missing livestock and hide cattle poaching. In a survey of livestock production in community group ranches, Mizutani (1995) found that herders were more likely to blame predators when livestock losses occurred due to theft or animals were missing, particularly if these losses were due to their own negligence. Mistaken carnivore identity is another reason for an observed difference between recorded and perceived livestock and game predation. For example, domestic predators such as feral dogs may exist in the same area as large carnivores and are capable of killing calves, goats and sheep. Deaths that have been attributed to wild carnivores may therefore be caused by domestic predators rather than wild carnivores (Ott, Kerley, & Boshoff, 2007).

Variation in attitudes toward large carnivores is partly based on the extent to which they conflict with human interests, but is also affected by inherent prejudices of landowners and farmers (Kellert, 1985). These prejudices are shaped by the socio-cultural and economic context in which farmers live. Quantitative research on attitudes towards carnivores has shown that the extent to which people tolerate wildlife damage is influenced by socio-economic factors such as education, age, sex and the financial impact of wildlife associated costs. Ranchers in Brazil with less education showed stronger negative attitudes towards jaguars and their attitudes were also negatively correlated with age (Cavalcanti et al., 2010). Similarly, Ericsson and Heberlein (2003) found that in Sweden older people, hunters, and those with less education and experience of wolf predation held the most negative attitudes towards wolves.

Gender has also been found to have a significant effect on attitudes towards wildlife in certain studies. Men expressed more positive attitudes towards wolverines (*Gulo gulo*), lynx (*Lynx lynx*), brown bears (*Ursus arctos*) and wolves (*Canis lupus*) than women in Norway (Røskaft, Handel, Bjerke, & Kaltenborn, 2007). In studying preferences for different wildlife species among a rural people

adjacent to Serengeti National Park, Tanzania, Kaltenborn et al. (2006) found gender to be the dominant variable in explaining preferences for non-carnivores with men showing more positive attitudes to most species than women. In contrast, gender differences were lacking for carnivores like leopards, possibly because the high perceived danger to livestock and human safety posed by these species resulted in more consistent perceptions. These studies show that people that tend to hold negative attitudes towards carnivores work in resource dependent professions such as farming, live in rural communities and carnivore ranges or have been affected by economic losses due to predators (Kaczensky et al., 2004). The socio-cultural effects of identity and occupation in rural communities also affects attitudes towards carnivores (Naughton-Treves et al., 2003). These attitudes are connected to individuals' lifestyles and once established become deep rooted. Within these specific social groups or professions, members share a social environment that reinforces their value laden attitudes towards wildlife and fosters a sense of shared values and goals (Naughton-Treves et al., 2003).

In addition, negative perceptions of carnivores may be due to inflated perceptions of risk that often outweigh economic damage and drive retaliatory behaviour (Knight, 2000; Naughton-Treves et al., 2003). These perceptions may relate to the highly charged beliefs associated with large carnivores that have the ability to cause significant damage that can have severe emotional, financial and political consequences for farmers (Kellert, Black, Rush, & Bath, 1996; Treves, Wallace, Naughton-Treves, & Morales, 2006). Such associations are shaped by catastrophic or costly events such as the predation of a large number of calves within one night (Treves et al., 2006). Research on farmer and landowner attitudes towards carnivores has also found that experiencing a lack of control over one's life (external locus of control) and a feeling of not being able to influence policies about resource management, or even comprehend them, can negatively affect rural perceptions of predators (Bjerke, Vitters, & Kaltenborn, 2000; Kleiven, Bjerke, & Kaltenborn, 2004).

The leopard is one of the most geographically widespread of the big cats and is found across Africa and tropical Asia (Hunter, Henschel, & Ray, 2013). Leopards can tolerate human activity and live in human-altered habitats and have an elusive nature which has enabled them to persist in places long devoid of other large predators (Hunter, 1999). The persistence of the leopard is partly due to its opportunistic hunting behaviour and varied diet (Hayward et al., 2006). However, although fairly abundant in comparison to other large cat species, leopard numbers have been significantly reduced over the last hundred years due to increasing human population expansion, large scale habitat loss and fragmentation, hunting for trade, poaching, and retaliation over real or perceived human wildlife conflict (Uphyrkina et al., 2001). This has resulted in a dramatic range loss in parts of Africa such as the Sahel belt, Nigeria and South Africa (Jacobson et al., 2016).

In rural areas in South Africa, where leopards co-exist with domestic livestock and commercial game on farm land, they frequently come into conflict with farmers due to real and perceived predation (Balme, Hunter, & Slotow, 2009; Chase Grey, 2011; Constant, Bell, & Hill, 2015; Daly et al., 2005; Miller, 2015). A few studies have examined the composition of leopard diets in sub-Saharan Africa via scat analysis and found that despite the fact that leopards can and do take livestock and game, either no evidence of livestock was found in leopard diets (Grobler & Wilson, 1972; Schwarz & Fischer, 2006; Stuart & Stuart, 1993), or leopards took much less livestock than would be expected in relation to their abundance (Mizutani, 1999; Norton, Lawson, Henley, & Avery, 1986; Ott et al., 2007). Livestock such as calves, sheep and goats fall within the preferred weight range of leopard prey of 10–40 kg (Hayward et al., 2006), so are certainly potential prey. Norton et al.

(1986) examined the contents of leopard scats in areas surrounded by intensive cattle farming but found that domestic livestock only made up a very small component of leopard diets (0.8%) despite the fact that high numbers of sheep were reportedly lost to leopards close to the areas where scats were collected. Similarly, leopards did not rely on livestock as an important food resource on cattle ranch land in Kenya even when both leopards and calves were found at high densities (Mizutani, 1999). Leopards may also predate upon commercial game species. Farmed game were found in 7.9% of leopard scats analysed from commercial game farms in South Africa, including expensive commercial species such as blue wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), ostrich (*Struthio camelus*), sable (*Hippotragus niger*) and waterbuck (*Kobus ellipsiprymnus*) (Power, 2002). Real or perceived leopard predation of commercial livestock and game is highly important as it negatively affects attitudes towards leopards and increases farmer willingness to take retaliatory action as a result (Sillero-Zubiri & Laurenson, 2001; Pitman et al., 2016).

The aim of this study was to examine if differences existed between landowner perceptions of leopard predation in the western Soutpansberg Mountains, South Africa, and actual leopard diets and if so, to explore the reasons for the mismatches in perceptions. The western Soutpansberg Mountains were home to the highest density of leopards recorded outside a state-protected area in sub-Saharan Africa (Chase Grey, Kent, & Hill, 2013), but the area has recently been identified as a zone where human-mediated leopard mortality exceeds the annual offtake rate considered sustainable (Pitman, Swanepoel, Hunter, Slotow, & Balme, 2015). Privately owned land is extremely important for the leopard in South Africa (Swanepoel, Lindsey, Somers, van Hoven, & Dalerum, 2013), and thus data on levels of human-leopard conflict in the Soutpansberg will provide valuable information to inform potential future conservation interventions (Chase Grey et al., 2013; Swanepoel et al., 2013).

Methodology

Study area

The study was conducted in the western part of the afro-montane forests of the Soutpansberg Mountains, Limpopo Province, South Africa which lie between 23° 05' S – 29° 17' E and 22° 25' S – 31° 20' E (Chase Grey et al., 2013). The mountains cover approximately 600 km² and range in height from 250 m above sea level to the highest peak Letjume (1748m) at the western extremity (Mostert et al., 2008). Temperatures vary in the wet season (December–February) from 16 to 40 °C and in the dry season (May–August) between 12 and 22 °C (Chase Grey et al., 2013). The western Soutpansberg is part of the Vhembe Biosphere Reserve and is recognised as a hotspot of South African biodiversity and endemism (UNESCO, 2009). The Soutpansberg Mountain Range is home to highly diverse animal communities (Chase Grey et al., 2013; Gaigher & Stuart, 2003). However, despite its high faunal diversity, uncontrolled colonial hunting during the 19th century and the destruction of habitat from farming practices has led to the decline and extinction of numerous animals (Chase Grey, 2011); African elephant (*Loxodonta africana*) and black rhino (*Dicero bicornis*) are now extinct in the mountain range (Chase Grey et al., 2013). In addition, cheetahs are no longer found on the mountain plateau and lions only remain in the far eastern part of the Soutpansberg (Gaigher & Stuart, 2003). The only large carnivores that remain are leopards, brown hyaenas (*Hyaena brunnea*) and spotted hyaenas (*Crocuta crocuta*) (Chase Grey et al., 2013). Twenty five ungulate species also inhabit the Soutpansberg including kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalo-*

pus natalensis) and common duiker (*Silvicapra grimmia*) (Gaigher & Stuart, 2003). Other bovid species present have recently been reintroduced by the game farming industry after being eliminated by overhunting such as impala (*Aepyceros melampus*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equines*) and nyala (*Tragelaphus angasii*) (Chase Grey, 2011). These species are utilised in the trophy hunting, eco-tourism and local meat industries. In addition, several domestic livestock species such as cattle, donkeys, goats and sheep are found on communal and private farmlands and used in commercial and subsistence farming (Chase Grey, 2011).

Land use of the farms surveyed in the Soutpansberg was made up of a patchwork of community, game and cattle farms, eco-tourism and conservancy areas with property ownership mainly divided across different cultural groupings. Afrikaners in the study area owned the majority of the land and were involved in cattle farming or holding recreational land; South Africans of British heritage managed game hunting and ecotourism properties and the Venda and Buys communities conducted either commercial or subsistence livestock farming (Chase Grey, 2011). In recent years the majority of cattle farms in the Soutpansberg have been converted into game farms for hunting or eco-tourism purposes with an 84% decline in cattle numbers in arid areas (Chase Grey, 2011). This shift in land use has come about due to the decreasing profitability of cattle farming and legislative changes allowing farmers ownership of wildlife on their land and the right to its consumptive use (Cousins, Sadler, & Evans, 2008; Lindsey, Frank, Alexander Mathieson, & Románach, 2006; Pitman et al., 2016).

Interviews and scat collection were conducted across twelve properties in the Soutpansberg Mountains covering an area of approximately 100 km². Five of these properties belonged to a conservancy, two conducted cattle farming, two were used for commercial game hunting, one for ecotourism and one conducted mixed game hunting and cattle farming. The final farm belonged to the conservancy but also had a subsistence small holding with cattle and donkeys. Land use on conservancy properties included personal recreation, scientific research or were left fallow (Chase Grey, 2011).

Dietary analysis

Faecal analysis is an effective method for determining predator diets (Hayward et al., 2006). To establish key prey species of leopards on the survey site, 100 leopard scats were collected opportunistically across the study area from May 2007 to December 2008 (Fig. 1). Leopard scats were identified from their characteristic elongated shape and size, which is often tapered at one end. The scats were generally found in several pieces between 6 and 13 cm in length and 2.5–4 cm in diameter. Although scats can be smaller than 2.5 cm in diameter, they were not identified positively unless they were found in close association with adult leopard tracks (Henschel & Ray, 2003). African civet and brown hyena scats may have similar proportions to those of leopards and may be mistaken for leopard scats (Henschel & Ray, 2003). However, civet scats contain arthropod exoskeletons, fruit and seeds and brown hyena scats are less elongated and often have a higher bone content giving them a chalky white colouration and therefore both could be differentiated from those of leopards (Henschel & Ray, 2003). Scats were not collected if there was any doubt regarding identification.

Once identified, each scat sample was placed in a plastic bag and the date, property on which it was collected and GPS location were noted on the bag. Scats were then washed in water using a sieve to remove soil, grass and leaves and were dried before all bones and hair were removed. Scat contents were then transferred to a plastic bag that was labelled with the sample's collection date, location and GPS coordinates. Any soft tissue found in the scat (e.g.

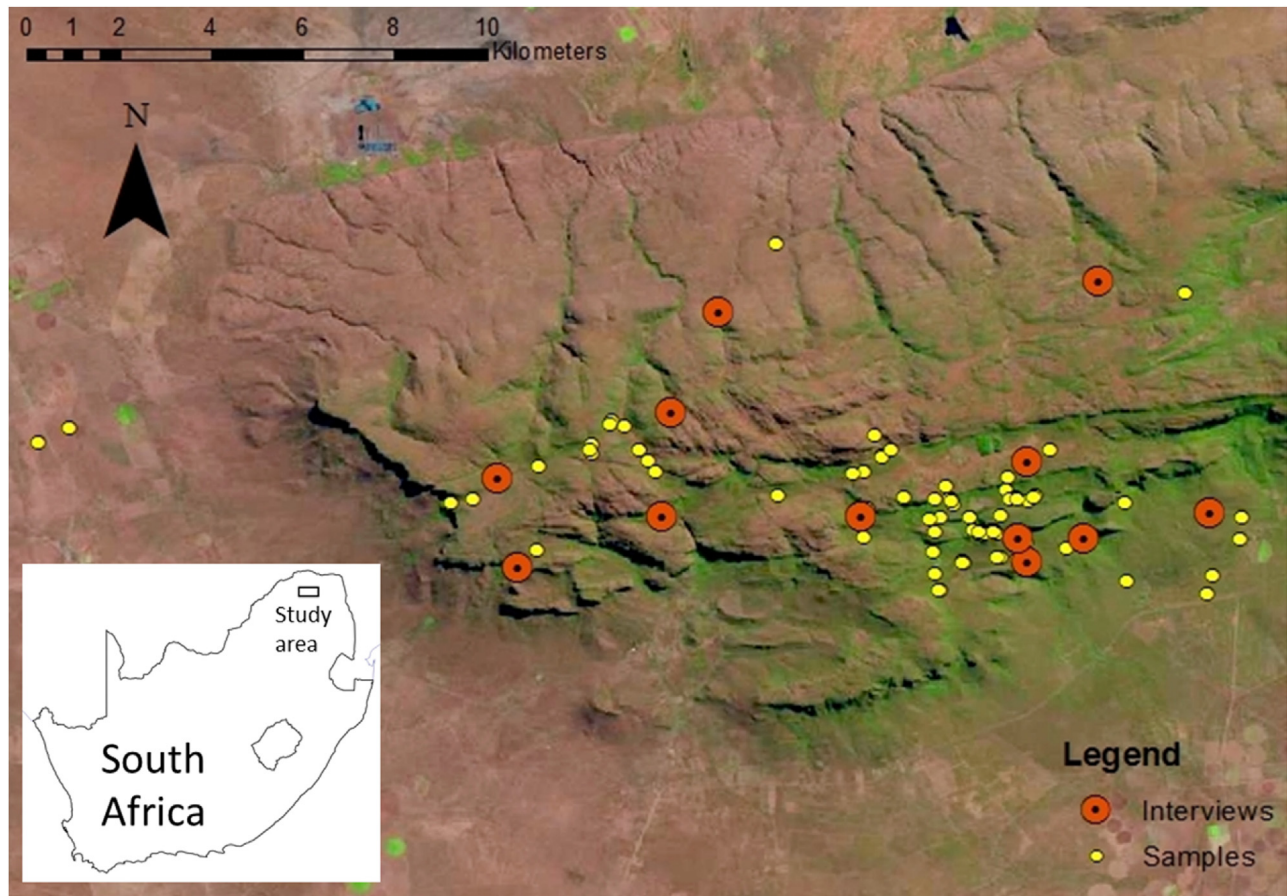


Fig. 1. Study area in the Soutpansberg Mountains, South Africa showing locations of interviews and scat collection.

flesh or cartilage) was placed in a vial of ethanol and included in the same bag.

The scats were examined for prey contents via microscopic analysis of cuticle scale imprints and cross-sections of hairs. Cuticle scale imprints were made from the extracted hair samples using a method adapted from Keogh (1983). Clean microscope slides were thinly coated with PVA wood glue and hairs were placed in position on the slide using fine forceps. Ten hairs were randomly selected from each scat and placed on a slide. The slides were allowed to dry for approximately 5 min before the hairs were removed and the scale imprints were then viewed under a light microscope under 100× and 200× magnifications.

Cross sections of hairs were made using a method adapted from Douglas (1989). Random selections of 10 hairs were made from each scat sample and were placed in a disposable plastic pipette. The bulb at the end of the pipette was depressed to remove air and the tube was filled with molten beeswax. Once filled, the tubes were cooled at room temperature. The pipette was then cut into thin sections of approximately 1–2 mm using a razor blade and 10–15 of these sections were fixed onto microscope slides using molten wax. Slides were examined under a 100× and 200× magnifications using a light microscope.

Reference slides for cross sections and cuticular scale patterns were made with hair samples obtained from local taxidermists from known prey animals. These were then compared to existing reference samples and published hair keys to identify prey species (Dreyer, 1966; Keogh, 1983; Perrin & Campbell, 1980). It was not possible to differentiate between the two hyrax species present at the study site, rock hyrax, (*Procavia capensis*) and yellow spotted

rock hyrax, (*Heterohyrax brucei*); therefore these two species were grouped together as hyrax following Stuart & Stuart (1993).

Prey contents were calculated as relative frequencies, i.e., the frequency at which a certain item is found in relation to the total number of items (relative frequency = number of items of one species/total number of items × 100). Correction factors for the body size of prey species have been devised to prevent the overestimation of small prey items in scats (Ackerman, Lindzey, & Hemker, 1984; Floyd, Mech, & Jordan, 1978). Ackerman's index was developed based on feeding trials with cougars (*Felis concolor*) and was used to compensate for the difference between overrepresented small prey and underestimated larger animals based on the assumption that the digestive system of leopards and cougars is similar. Ackerman's Index was calculated as: $Y = 1.98 + 0.035 X$, where X equals the mean weight of the prey animal and Y the intake of biomass in kg. Using Ackerman's Index the number of faecal samples containing particular prey items was then converted into relative biomass.

Perceptions of human-leopard conflict

Data on leopard predation of livestock and game were collected via semi-structured interviews and questionnaires with landowners from October to December 2008. Participants were selected to represent the full range of stakeholders present in the Soutpansberg and all farms on which dietary material were collected were included in the interview survey.

Semi-structured interviews are a widely used research methodology to obtain anthropological and social data (Bernard, 2006; Munn & Drever, 1995). With this methodology, the interview topic

Table 1
The number of leopard scats collected by season.

Season	N° of scats collected
Spring	35
Summer	9
Autumn	11
Winter	43

is chosen in advance but the interviewer is able to follow leads during the interview and change the way questions are asked if necessary. The questionnaire survey was conducted after 15 months of participant observation with landowners and farmers to ensure a rapport had been built with respondents before questioning and that they were comfortable with both the subject matter and the interviewer. Questionnaires took the form of personal, face to face interviews. Landowners were asked for information on their stock holdings, self-reported livestock and game predation events from 2007 to 2008, livestock management techniques (where animals were grazed, whether they were kraaled or watched at night), their attitudes towards the government process for dealing with problem leopards, the trophy hunting system in Limpopo Province, illegal leopard hunting and their attitudes towards leopards and their conservation.

Both quantitative and qualitative data were gathered during the interview survey. Quantitative data are useful for identifying broad trends in attitudes but qualitative data can be used for obtaining rich socio-cultural information from study participants. Qualitative data such as landowner perceptions of governmental processes for dealing with problem leopards were required to understand the attitudes and perceptions of respondents towards leopards in the complex socio-cultural mixture of communities that make up the Soutpansberg.

Before the interview, the participants were given information about the study and were informed that they would remain anonymous in any information gathered. All interviews were fully transcribed and where given permission were also recorded using an Olympus digital voice recorder (Olympus UK Ltd). Data from interviews were transcribed and coded to identify key reoccurring themes relating to the research area (Strauss & Corbin, 1990). In order to examine the difference between real versus perceived leopard predation of livestock and game, the relationship between the frequency of reported leopard predation events and the contents of leopard scats were analysed using a Spearman's rank order correlation. Statistical tests were conducted using SPSS for Windows 20.0.

2. Results

Dietary analysis

100 leopard scats were collected across all four seasons, with a peak of scat collection in winter and spring due to ease of access to certain properties and a lack of rainfall at this time improving scat preservation (Table 1). 43% of leopard scats were collected from conservancy properties, 20% from cattle farms, 16% from mixed land use farms, 7% from farms containing farmed game and 14% from properties with an unknown land use type due to (Table 2). Analyses were only conducted on scat samples from known land use types (n = 86).

Of the 86 leopard scats analysed for prey contents, nine contained unidentifiable prey remains. From the identifiable scats (n = 77), 10 mammal prey species were detected. Bushbuck proved to be the most frequently taken prey item by relative frequency (42.9%) followed by hyrax (26%) and vervet monkeys (10.4%) (Table 3). These three species made up 79.3% of the total prey items

Table 2
The number of leopard scats collected per land use type.

Land use type	Percentage of scats collected per land use type (%)
Cattle farm	20
Conservancy	43
Conservancy and cattle mixed	3
Ecotourism	2
Game	5
Game and cattle mixed	13
Unknown	14
	100

consumed by leopards by relative frequency. Mountain reedbuck, thick tailed bush baby and kudu calf were only found in single scats. No remains of members of the Lagomorph family, birds, reptiles or carnivores were found in the scats analysed and no livestock or farmed game species were detected. Converting the results of the dietary analysis from relative frequency to relative biomass, increased the importance of larger prey items such as the bushbuck from 42.9% to 49.6% and reduced the importance of smaller species such as hyrax from 26.0% to 21.3%.

In scats found on cattle farms, the majority came from bushbuck (37.5%) and hyrax (31.25%); on the cattle/conservancy mixed land use property hyrax formed the highest relative frequency of prey items (66.7%), whereas on conservancy properties hyrax and bushbuck were the major items found in leopard scats (74.35%) (Table 4). On the ecotourism farm leopard scats were formed equally of common duiker and hyrax (100%), whereas leopard scats from game farms contained a mixture of bushbuck, duiker, hyrax and porcupine (100%). Bushbuck showed the highest relative frequency in the game and cattle mix farm (41.7%).

Perceived leopard predation events

Predation events were pooled via land use and grouped into reports of cattle losses, other livestock (dogs, sheep and donkeys), naturally occurring game (bushbuck and kudu), and fenced farmed game (blue wildebeest, eland, impala, ostrich, sable and waterbuck) (Table 5). In total there were 125 reports of leopard predation. Of the 27 cattle predation events, cattle farmers reported more cattle losses than any other land use type (37%), followed by conservancy properties (29.6%). There were six reports of leopard predation of other livestock with conservancy properties reporting the largest perceived losses (50%). Of the reports of predation of free ranging and fenced game, game farmers claimed the bulk of losses at 85.6% and 84.6% of predation events.

Data from interviews showed that many respondents perceived the levels of loss to leopards to be extensive, and this was particularly true of ecotourism operators. One stated that leopards caused expensive losses on her property as they annually killed most of her sable and wildebeest calves. Another ecotourism property manager said that 65–70% of all zebra and blue wildebeest calves were killed by leopards per year. Impala were also commonly reported as being eaten by leopards. One cattle farmer stated that of his herd of 400 impala, leopards had taken 350 individuals over the last few years and a hunting game farm manager said that leopards eat 1–2 impala per week on his property. Other introduced farmed game species such as eland and waterbuck were also reported as being killed by leopards. Landowners and farmers perceived high levels of livestock and commercial game predation by leopards but no evidence of livestock and farmed game species were found in the scats analysed. As a consequence a significant negative correlation was found between the frequency of reports of leopard predation by species and the frequency of species observed in scats but this

Table 3

Relative frequency of occurrence and biomass of prey in leopard scat in the western Soutpansberg Mountains, South Africa (unidentified prey items not included).

Species	Relative Frequency of occurrence (%)	Relative biomass consumed (%)
Bushbuck (<i>Tragelaphus scriptus</i>)	42.9	49.6
Hyrax (<i>Procavia capensis</i>)	26.0	21.3
Vervet Monkey (<i>Chlorocebus pygerythrus</i>)	10.4	8.63
Porcupine (<i>Hystrix cristata</i>)	5.2	5.12
Common Duiker (<i>Sylvicapra grimmia</i>)	5.2	5.49
Chacma Baboon (<i>Papio ursinus</i>)	4.2	4.14
Red Duiker (<i>Cephalopus natalensis</i>)	3.1	2.91
Mountain Reedbuck (<i>Redunca fulvorufula</i>)	1	1.16
Kudu calf (<i>Tragelaphus strepsiceros</i>)	1	0.86
Thick tailed Bushbaby (<i>Otolemur crassicaudatus</i>)	1	0.79

Table 4

Relative frequency of occurrence of prey in leopard scat in the western Soutpansberg Mountains, South Africa via land use type.

Land use type	N	Scat contents (Relative frequency %)									
		Baboon	Bushbuck	Common duiker	Hyrax	Kudu	Porcupine	Mt reedbuck	Red duiker	Bushbaby	Vervet
Cattle farms	20	6.25	37.5	6.25	31.25	0	6.25	0	0	0	12.5
Cattle conservancy mix	3	0	0	0	66.7	0	0	0	0	0	33.3
Conservancy properties	43	5.12	43.55	0	30.8	1.3	5.12	0	2.56	1.3	10.25
Ecotourism	2	0	0	50	50	0	0	0	0	0	0
Game	5	0	40	20	20	0	20	0	0	0	0
Game cattle mix	13	8.33	41.68	8.33	8.33	0	0	8.33	0	0	25

was not statistically significant (Spearman Rho, $rs = -0.229$, $N = 8$, $P = 0.293$).

Attitudes towards leopards were split across the different land uses (Table 6). Landowners with farmed game (both the ecotourism operator and the game farmers) felt that leopards were economically valuable although for differing reasons; either because they brought in money from tourists paying to view them (the ecotourism operator) or because paying clients came to shoot them on legal hunts (the game farmers). It is because of this view of leopards as bringing in money to their properties that members of both of these landowner groups were willing to sustain what they perceived to be as high game losses.

2.1. Cattle farmer attitudes towards leopards

The cattle farmers interviewed in the survey showed marked negative attitudes towards leopards and perceived them to be problem animals. Every cattle farmer interviewed stated that they had lost calves to leopards. One landowner said when asked about predation events on his cattle farm:

“I’ve had a lot of trouble with leopards.”

Cattle farmers were all also very clear in describing how they dealt with these perceived losses:

“Most of the farmers kill the leopard when it is a problem, catch it with snares, if it is a problem just kill the bloody thing.”

The detail with which some cattle farmers illustrated their killing methods during their interviews demonstrates the strength of feeling they have against leopards as pest species:

“With a gin trap the leopard can turn its leg and take its own leg off and walk without it. Let me tell you how to kill them. I could shoot five leopards per year. I try to shoot them but if the damage is too big I use poison. It is against the law but I don’t compromise with losses.”

Some of cattle farmers interviewed perceived that losses to wild animals could totally destroy their source of income. One farmer stated:

“Older generation farmers will pay anything to kill a leopard, if there are no calves how can they carry on?”

As a result of the high perception of risk they felt leopards posed to their livelihoods, some cattle farmers displayed an embattled attitude towards dealing with them. One cattle farmer stated:

“I shot a leopard that took a calf, I have a constitutional right to kill them” and “I am trying to make a living and have to fight animals.”

Cattle farmer attitudes towards the government process for dealing with livestock losses

The interview survey showed that cattle farmers felt a lack of control over the official process of dealing with livestock losses and that this frequently drove them to retaliatory killing in order to sort out the problem as quickly as possible. If a cattle farmer suspects that they have a problem animal and has supporting evidence, such as a kill, they are supposed to call a local government officer who will send out a team to investigate (Chase Grey, 2011). If the investigators find a problem animal, they will translocate it or the farmer

Table 5

Frequency of leopard predation reports by land use type.

Land use (N° of properties)	Predation reports (%)			
	Cattle	Other livestock	Free-ranging game	Farmed game
Cattle farms (2)	37	16.7	7.2	0
Cattle conservancy mix (1)	22.3	16.7	0	0
Conservancy properties (5)	29.6	50	0	0
Ecotourism (1)	0	0	7.2	14.1
Game (2)	0	0	85.6	84.6
Game cattle mix (1)	11.1	16.7	0	1.3

Table 6
Landowner attitudes towards leopards via land use type.

Land use (N° farms)	Attitude to leopards	Actions
Cattle farms (2)	Pest species	Illegal hunting/poisoning
Cattle and game (1)	Pest species	Illegal hunting/poisoning
Conservancy land (5)	Should be conserved	Conserve leopards
Conservancy and Cattle mix (1)	Should be conserved	Conserve or kill illegally
Ecotourism (1)	Economically valuable as it brings in money from tourism	Conserve
Game farms (2)	Economically valuable as it brings in money from commercial hunting	Commercial leopard hunting

will be given a destruction permit to shoot the leopard. However due to staff shortages it can take weeks for an investigation team to check a property. This time lapse means that when investigators finally arrive, any animal carcasses which could be used as evidence of leopard predation may have disappeared or decomposed or the leopard could have killed again. A farmer who had worked in the cattle farming industry said:

“If you have a problem leopard . . . by the time you get the permit that same leopard has either left or has done so much damage and that’s why some farmers resort to trapping and poisoning and just keeping quiet about it.”

Another cattle farmer stated:

“Yes, if you are a farmer with a leopard, you have to deal with it. I have never run to the government about it.”

Part of the motivation for this response appears to emerge from the fact that Government regulations state that cattle farmers in Limpopo Province cannot trophy hunt damage causing leopards (Chase Grey, 2011). While the law is in place to avoid false claims of leopard predation and illegal hunting, one cattle farmer stated:

“People would not care about the damage leopards caused if they could hunt them. If the system was so that if I report I lost cattle to a leopard they could be here within a day or two at least to see if it was a leopard and say ok on the grounds of what we’ve seen we can give you a permit and you can find a guy that wants to shoot a leopard, I’d say ok let’s do this.”

This frustration also extended to the potential for trophy hunting. None of the cattle farmers interviewed undertook trophy hunting and many said that they found the permit system to be complex and confusing. As one cattle farmer explained:

“I am not into (trophy) hunting as there are too many regulations.”

2.2. Game farmer attitudes towards leopards

Game farmers also reported losses to leopard predation but showed positive views towards leopards and did not view them as problem animals. One game farmer who used her property for ecotourism purposes said:

“Leopard predation has caused a reduction in the wildebeest population, no young survive because of the leopards.”

She also perceived leopards to be frequently feeding on her valuable sable antelope herd:

“Leopards also antagonise sable and have taken out most of them.”

However despite these losses, when asked whether she viewed the leopard as a pest species she stated:

“Tourists see leopards and that is a big advantage, that is why leopards are not considered to be a problem animal. I see the

leopard as an economic resource. It is part of what we are selling, we sell two of the Big Five. I don’t mind losses because of this.”

All game farmers shared this more positive and accepting view of having leopards on their properties. This attitude was encapsulated by one game farmer when he said:

“If it’s a game farm there must be leopards on there, that’s the risk you take with a game farm” and “I think (game farmers) just have to roll with those punches, it’s part of the industry.”

A game farmer that conducted licensed trophy hunting explained why he did not see leopards as problem animals:

“(Hunting) is a way of utilising a resource and it brings in foreign currency and creates jobs. If people cannot hunt leopard it will have no value for some people.”

3. Discussion

Ten mammalian prey species were identified in the scats analysed in this study. Bushbuck were the most frequently taken prey item by frequency, followed by hyrax, and vervet monkeys. In the same region, Schwarz and Fischer (2006) also found bushbuck to be the most commonly occurring prey species in leopard scats (relative frequency of occurrence 45.3%), but Power (2002) and Stuart and Stuart (1993) found hyrax to be the most frequently taken prey species representing 41.3% and 43% of the relative frequency of occurrence, respectively. The prey spectrum of species consumed by leopards here is thus similar to that found by other studies on leopard diets in the Soutpansberg Mountains.

Nine scats contained hair that was unidentifiable but were checked against reference material from livestock and farmed game and did not contain any of these species. This was despite being collected from properties that hold livestock and economically valuable game species such as sable, zebra, blue wildebeest and nyala. This suggests that livestock and farmed game are not important prey species for leopards in the Soutpansberg Mountains and may reflect the high abundance of preferred prey species such as bushbuck and common duiker (Chase Grey et al., 2013). These results also agree with research on diets of leopards living on African rangelands, ranches or areas close to cattle farms (Mizutani, 1999; Norton et al., 1986; Ott et al., 2007) which found that leopards either did not predate on livestock or livestock made up a much lower proportion of the diet than would be expected on the basis of their availability as potential prey.

Amongst perceived leopard predation events, cattle farmers reported more cattle losses than any other land use type despite the fact that no livestock were found in the scats analysed on those, or any other of the properties. On cattle farms the bulk of prey items came from bushbuck and hyrax. Conservancy properties also reported high losses of cattle and other livestock (sheep and dogs). The main prey items on these properties were hyrax and bushbuck. Of the reports of predation of free ranging and fenced game, game farmers claimed the majority of losses despite no evidence of these species being found in the scats.

The wide discrepancy between reports of livestock and expensive game predation and the lack of presence of these species in

leopard scats may be due to a number of factors. Some methodological considerations may have contributed to the difference between actual and perceived predation of livestock and game. For example, misidentification of certain scats may have occurred and this could have caused a bias in the results. However, all scats were examined thoroughly against reference material and checked for errors by a number of researchers. It is known that problem animals do exist in the study area (unpublished data) and their scats may also have been missed in the survey. In addition, leopard predation on livestock will not necessarily produce a scat on that particular farm due to the time taken for food passage in the gut. This is especially true given the large home ranges of leopards in relation to the size of properties. Some properties in the study area were as small as 4 km² and a female leopard home range in the Soutpansberg has been measured at 13.9 km² (95% MCP) (Chase Grey, 2011).

Nevertheless the fact that livestock and farmed game only make up a very small percentage of leopard diets in the Soutpansberg is supported by the results of other dietary studies (Schwarz & Fischer, 2006; Stuart & Stuart, 1993). One of the main reasons for the gap between actual and perceived leopard predation may relate to the perceptions of the landowners themselves. Landowners may only notice the loss of species on their land that hold economic value for them such as livestock or expensive introduced game. Leopards in the Soutpansberg predate mainly upon bushbuck and hyrax which naturally occur in the area and hold little or no economic value in the trophy hunting or ecotourism industry. The loss of a bushbuck on a farm may therefore go unnoticed by a landowner unless a carcass was found. Sable and blue wildebeest, however, are located frequently on game properties for trophy hunting or eco-tourism purposes and therefore losses of these species are quickly noticed (Chase Grey, 2011).

Some livestock and game deaths attributed by landowners to leopards may have also been caused by other predators (Ott et al., 2007). Domestic hunting dogs used to poach wildlife and sympatric predators such as caracals, brown hyena and black-backed jackal are all present in the study site and these species are capable of killing calves, goats and sheep. The gap in perceived predation of livestock and game may therefore also be in part due to mistaken predator identity. Similarly, farmers may use the presence of carnivores to provide an excuse for explaining livestock losses that have actually been caused by theft or negligence (Mizutani, 1995; Rasmussen, 1999). Farmers may blame leopards for livestock losses as it may be easier to hold a predator responsible rather than admit their own negligence and improve their livestock protection or husbandry measures; drought, lack of food, unequal sex ratios in prey species or a low reproduction rate due to infertile males may all be causes of loss. In addition, some of the livestock and game losses that occur in the Soutpansberg that landowners attribute to leopard predation may actually have been caused by poaching. Poaching of game species by local communities does occur on private farmland and is undertaken to supplement income from rural manual labour or subsistence farming with the meat or skins obtained (Chase Grey, 2011). Snaring for consumable bush meat or for leisure may also contribute to game losses.

The socio-cultural and economic context in which the landowners live may also prejudice their views of predators and so further explain the gap between actual and perceived leopard predation. Studies on farmers' attitudes towards predators have found that experiencing a lack of control over one's life and a feeling of not being able to influence policies about resource management can negatively affect their perception of carnivores (Bjerke et al., 2000; Kleiven et al., 2004). Data from the interview survey showed that cattle farmers felt that the official process of dealing with suspected livestock killing leopards in Limpopo Province is inefficient. It can often take days for the local authorities to come out to a property and verify that livestock has been killed by a leopard by which time

further kills may have taken place. Cattle farmers expressed a lack of faith in the ability of local authorities to effectively handle livestock raiding leopards and they instead preferred to deal with the situation themselves by poisoning livestock carcasses or shooting the suspected individual. The lack of control cattle farmers felt over the official process of dealing with livestock losses drove them to retaliatory killing in order to sort out the problem as quickly as possible.

Research has shown that social identity and occupation in rural communities also affects attitudes towards carnivores (Naughton-Treves et al., 2003). Members of rural farming communities share a social environment within these specific social groups that reinforces their value laden attitudes towards wildlife and fosters a sense of shared values and goals (Naughton-Treves et al., 2003). The majority of private cattle farmers in the Soutpansberg belong to the culturally distinct Afrikaner group. Many are older farmers whose families have lived in the area for generations and their attitudes towards carnivores have been passed down from the Europeans that settled in the area over 150 years ago. Afrikaner cattle farmers' attitudes towards carnivores were found to be highly negative and they frequently admitted to killing leopards via illegal means such as using poison or the 'shoot, shovel and shut up method' without informing the authorities they had killed a suspected livestock killer. The strength of negative feeling against leopards as a widespread problem animal is in part to do with membership of this distinct social group whose deeply ingrained negative attitudes towards wild animals have been handed down for generations. Afrikaner livestock farmers also work in rural, resource dependent professions, live in carnivore ranges and may have been affected by economic losses due to predators. People that belong to these categories have been found to hold the most negative attitudes towards carnivores (Kaczensky et al., 2004).

In contrast to cattle farmers, all game farm owners interviewed showed much more positive attitudes towards leopards and even if they reported losses of expensive commercial game on their properties, this did not drive retaliatory action towards them. The reason for this difference in attitudes towards leopards relates to the value each type of landowner places on them. Leopards hold economic value for game farm owners as they can utilise them for trophy hunting or eco-tourism purposes. Therefore any losses that they perceive leopards may cause can be offset by money obtained from hunters killing leopards for trophies or tourists coming to see leopards on their properties. They are therefore willing to accept a certain level of loss of commercial game. Cattle farmers on the other hand are not able to commercially hunt problem leopards and therefore only see leopards as problem animals that cause an economic drain on their resources due to their perceived predation of livestock.

Finding conservation solutions for leopard human conflict in the Soutpansberg

The large gap between real and perceived predation of livestock and to a lesser extent game is a problem of high conservation concern as negative attitudes towards leopards can affect landowner actions and lead to retaliatory killing. In the case of cattle farmers in the Soutpansberg, the majority of landowners interviewed admitted to illegally killing leopards on a regular basis over many years (Chase Grey, 2011).

A number of solutions may help to close the gap between actual and perceived predation of cattle and therefore foster more positive attitudes towards leopards. Education can improve tolerance towards carnivores (Lindsey, du Toit, & Mills, 2005; Woodroffe et al., 2005). However a focus on ways in which cattle farmers' feelings of loss of control over their resources and environment can be improved may yield the greatest benefits. For example, an

improved government response to reports of livestock predation by cattle farmers may create an increased sense of control over their resources. This could include faster response times from local authorities when livestock farmers perceive that they have a damage causing animal and more local government staff on the ground to verify reports of leopard predation (Chase Grey, 2011). Trophy hunting of verified problem animals could also be instituted in Limpopo Province in order to compensate livestock owners for losses caused by leopards (Balme et al., 2010). This could improve attitudes towards leopards, foster the perception of them as economically valuable rather than as a pest species and therefore reduce retaliatory killing. However, the Department of Environmental Affairs, South Africa, has set a zero quota for the hunting of leopards in 2016 and 2017 following evidence that they were over-harvested in South Africa prior to that point (Pitman et al., 2015). Nevertheless, a sense of economic value is critically important across the range of stakeholders in this multi-use landscape. If significant populations of carnivores are to persist outside of state protected areas then such value is critical to the landowners. In addition, farmers with livestock and expensive fenced game could improve their anti-predation measures to minimize predation risks. Effective methods to reduce carnivore predation include corralling animals at night in predator proof enclosures close to human habitation, grazing in open habitat and using methods such as livestock guarding dogs to deter predators (Gehring, VerCauteren, Provost, & Cellar, 2010; Woodroffe et al., 2007).

Acknowledgements

We are very grateful to Dr Ian Gaigher for permission to work at the Lajuma Research Centre and to Dr Graham Avery of Iziko Museum, Cape Town for assistance with the identification of prey remains. We thank the Natural Environment Research Council (NERC) and the Economic and Social Research Council (ESRC) for their generous funding of this research. All fieldwork was approved by the Life Sciences Ethical Review Process Committee and the Department of Anthropology Ethics Committee at Durham University, UK and was conducted with approved permits from Limpopo Province Department of Economic Development and Tourism (LEDET).

References

- Ackerman, B. B., Lindzey, F. G., & Hemker, T. P. (1984). *Cougar food habits in southern Utah*. *Journal of Wildlife Management*, 48, 147–155.
- Bagchi, S., & Mishra, C. (2006). Living with large carnivores: Predation on livestock by the snow leopard (*Uncia uncia*). *Journal of Zoology*, 268, 217–224.
- Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, 142, 2681–2690.
- Balme, G. A., Hunter, L. T. B., Goodman, P., Ferguson, H., Craigie, J., & Slotow, R. (2010). An adaptive management approach to trophy hunting of leopards (*Panthera pardus*): a case study from KwaZulu-Natal, South Africa. In D. W. Macdonald, & A. J. Loveridge (Eds.), *Biology and conservation of wild felids* (pp. 341–352). Oxford: Oxford University Press.
- Bernard, H. R. (2006). *Research methods in anthropology: Qualitative and quantitative methods*. [California: Walnut Creek, US].
- Bjerke, T., Vitters, J., & Kaltenborn, B. P. (2000). Locus of control and attitudes toward large carnivores. *Psychology Reports*, 86, 37–46.
- Boulhosa, R. L. P., & Azevedo, F. C. C. (2014). Perceptions of ranchers towards livestock predation by large felids in the Brazilian Pantanal. *Wildlife Research*, 41, 356–365.
- Cavalcanti, S., Marchini, S., Zimmermann, A., Gese, E. M., & Macdonald, D. W. (2010). Jaguars, livestock, and people in Brazil: realities and perceptions behind the conflict. In D. W. Macdonald, & A. J. Loveridge (Eds.), *Biology and conservation of wild felids* (pp. 383–402). Oxford: Oxford University Press.
- Chase Grey, J. N., Kent, V. T., & Hill, R. A. (2013). Evidence of a high density population of harvested leopards in a montane environment. *PLOS ONE*, 8(12), e82832. <http://dx.doi.org/10.1371/journal.pone.0082832>
- Chase Grey, J. N. (2011). *Leopard population dynamics, trophy hunting and conservation in the Soutpansberg Mountains, South Africa*. PhD thesis. Durham: Durham University.
- Chavez, A. S., & Gese, E. M. (2005). Food habits of wolves in relation to livestock depredations in northwestern Minnesota. *American Midland Naturalist*, 154, 253–263.
- Chavez, A. S., & Gese, E. M. (2006). Landscape use and movements of wolves in relation to livestock in a wildland–agriculture matrix. *Journal of Wildlife Management*, 70, 1079–1086.
- Chavez, A. S., Gese, E. M., & Krannich, R. S. (2005). Attitudes of rural landowners toward wolves in northwestern Minnesota. *Wildlife Society Bulletin*, 33, 517–527.
- Constant, N. L., Bell, S., & Hill, R. A. (2015). The impacts, characterisation and management of human-leopard conflict in a multi-use land system in South Africa. *Biodiversity and Conservation*, 24(12), 2967–2989.
- Cousins, J. A., Sadler, J. P., & Evans, J. (2008). Exploring the role of private wildlife ranching as a conservation tool in South Africa: Stakeholder perspectives. *Ecology and Society*, 13, 43.
- Daly, B., Power, J., Chamacho, G., Taylorholzer, K., Barber, S., Catterall, S., et al. (2005). *Leopard (Panthera pardus) PHVA workshop report*. Johannesburg: Endangered Wildlife Trust, Conservation Breeding Specialist Group (SSC/IUCN)/CSBG South Africa.
- Douglas, R. M. (1989). A new method of cross-sectioning hair of larger mammals. *South African Journal of Wildlife Research*, 19, 73–76.
- Dreyer, J. H. (1966). A study of hair morphology in the family Bovidae. *Onderstepoort Journal of Veterinary Research*, 379–472.
- Ericsson, G., & Heberlein, T. A. (2003). Attitudes of hunters, locals: and the general public in Sweden now that the wolves are back. *Biological Conservation*, 111, 149–159.
- Floyd, T. J., Mech, D. L., & Jordan, P. A. (1978). Relating wolf scat content to prey consumed. *Journal of Wildlife Management*, 42, 528–532.
- Gaigher, I. G., & Stuart, C. T. (2003). Mammals. In K. Berger, J. Crafford, I. Gaigher, M. J. Gaigher, N. Hahn, & I. Macdonald (Eds.), *A first synthesis of the environmental, biological and cultural assets of the Soutpansberg*. South Africa: Leach Printers & Signs, Louis Trichardt.
- Gehring, T. M., VerCauteren, K. C., Provost, M. L., & Cellar, A. C. (2010). Utility of livestock protection dogs for deterring wildlife from cattle farms. *Wildlife Research*, 37, 715–721. <http://dx.doi.org/10.1071/WR10023>
- Grobler, J. H., & Wilson, V. J. (1972). Food of the leopard *Panthera pardus* (Linn.) in the Rhodes Matopos National Park, Rhodesia: As determined by faecal analysis. *Arnoldia*, 5, 1–10.
- Gusset, M., Maddock, A. H., Gunther, G. J., Szykman, M., Slotow, R., Walters, M., et al. (2008). Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity and Conservation*, 17, 83–101.
- Hayward, M. W., Henschel, P., O'Brien, P., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, 270, 298–313.
- Henschel, P., & Ray, J. (2003). *Leopards in african rainforests: survey and monitoring techniques*. New York: Wildlife Conservation Society.
- Hunter, L., Henschel, P., & Ray, J. C. (2013). *Panthera pardus* leopard. In J. Kingdon, & M. Hoffmann (Eds.), *Mammals of Africa, Vol. V: carnivores, pangolins, equids and rhinoceroses* (pp. 159–168). London (England): Bloomsbury.
- Hunter, L. (1999). The quintessential cat. *Africa: Environment & Wildlife*, 7, 32–41.
- Jacobson, A. P., Gerngross, P., Lemeris Jr, J. R., Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., et al. (2016). Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ*, 4, e1974 [p].
- Johansson, O., McCarthy, T., Samelius, G., et al. (2015). Snow leopard predation in a livestock dominated landscape Mongolia. *Biological Conservation*, 184, 251–258.
- Kaczensky, P., Blazic, M., & Gossow, H. (2004). Public attitudes towards brown bears (*Ursus arctos*) in Slovenia. *Biological Conservation*, 118, 661–674.
- Kaltenborn, B. P., Bjerke, T., Nyahongo, J. W., & Williams, D. R. (2006). Animal preferences and acceptability of wildlife management actions around Serengeti National Park, Tanzania. *Biodiversity and Conservation*, 15, 4633–4649.
- Kellert, S. R., Black, M., Rush, C. R., & Bath, A. J. (1996). Human culture and large carnivore conservation in North America. *Conservation Biology*, 10, 977–990.
- Kellert, S. R. (1985). Public perceptions of predators, particularly the wolf and coyote. *Biological Conservation*, 31, 167–189.
- Keogh, H. J. (1983). A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research*, 13, 89–132.
- Kissui, B. M. (2008). Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation*, 11, 422–432.
- Kleiven, J., Bjerke, T., & Kaltenborn, B. P. (2004). Factors influencing the social acceptability of large carnivore behaviours. *Biodiversity and Conservation*, 13, 1647–1658.
- Knight, J. (2000). *Natural enemies: people-wildlife conflicts in anthropological perspective*. London: Routledge.
- Lindsey, P. A., du Toit, J. T., & Mills, M. G. L. (2005). Attitudes of ranchers towards African wild dogs *Lycaon pictus*: Conservation implications on private land. *Biological Conservation*, 125, 113–121.
- Lindsey, P. A., Frank, L. G., Alexander Mathieson, R. A., & Romañach, S. S. (2006). Trophy hunting and conservation in Africa: Problems and one potential solution. *Conservation Biology*, 21, 880–883.
- Loveridge, A. J., Wang, S. W., Frank, L. G., & Seidensticker, J. (2010). People and wild felids: conservation of cats and management of conflicts. In D. W. Macdonald, & A. J. Loveridge (Eds.), *Biology and conservation of wild felids* (pp. 383–402). Oxford: Oxford University Press.

- Miller, J. R. B. (2015). Mapping attack hotspots to mitigate human-carnivore conflict: approaches and applications of spatial predation risk modelling. *Biodiversity and Conservation*, 24(12), 2887–2911.
- Mishra, C. (1997). Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation*, 24, 338–343.
- Mizutani, F. (1995). *The ecology of leopards and their impact on livestock ranches in Kenya*. Ph.D. Thesis. Cambridge: University of Cambridge.
- Mizutani, F. (1999). Impacts of leopards on a working ranch in Laikipia, Kenya. *African Journal of Zoology*, 37, 211–225.
- Mostert, T. H. C., Bredenkamp, G. J., Klopper, H. L., Verwey, C., Mostert, R. E., & Hahn, N. (2008). Major vegetation types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *Koedoe*, 50, 32–48.
- Munn, P., & Drever, E. (1995). *Using questionnaires in small-scale research* (revised ed.). Edinburgh: Scottish Council for Research in Education.
- Naughton-Treves, L., Grossberg, R., & Treves, A. (2003). Paying for tolerance: Rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, 17, 1500–1511.
- Naughton-Treves, L. (1997). Farming the forest edge: vulnerable places and people around Kibale National Park. *Uganda Geographical Review*, 87, 27–46.
- Norton, P. M., Lawson, A. B., Henley, S. R., & Avery, G. (1986). Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Journal of Wildlife Research*, 16, 47–52.
- Ogada, M. O., Woodroffe, R., Ouge, N. O., & Frank, L. G. (2003). Limiting depredation by African carnivores: The role of livestock husbandry. *Conservation Biology*, 17, 1521–1530.
- Oli, M. K., Taylor, I. R., & Rogers, M. E. (1994). Snow leopard *Panthera uncia* predation of livestock: an assessment of local perceptions in the Annapurna conservation area Nepal. *Biological Conservation*, 68, 63–68.
- Ott, T., Kerley, G. I. H., & Boshoff, A. F. (2007). Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region. *South Africa African Zoology*, 42, 31–37.
- Perrin, M. R., & Campbell, B. S. (1980). Key to the mammals of the Andries Vosloo Kudu Reserve (Eastern Cape), based on their morphology, for use in predator scat analysis. *South African Journal of Wildlife Research*, 10, 1–14.
- Pitman, R. T., Swanepoel, L. H., Hunter, L., Slotow, R., & Balme, G. A. (2015). The importance of refugia: ecological traps and scale for large carnivore management. *Biodiversity and Conservation*, 24, 1975–1987.
- Pitman, R. T., Fattebert, J., Williams, S. T., Williams, K. S., Hill, R. A., Hunter, L., et al. (2016). The conservation costs of game ranching. *Conservation Letters*, <http://dx.doi.org/10.1111/conl.12276>
- Power, R. J. (2002). *Prey selection by leopard (Panthera pardus) in the Soutpansberg, Limpopo Province, and utilisation recommendation*. In *Dissertation*. Pretoria University of Pretoria.
- Røskaft, E., Handel, B., Bjerke, T., & Kaltenborn, B. P. (2007). Human attitudes towards large carnivores in Norway. *Wildlife Biology*, 13, 172–185.
- Rasmussen, G. S. A. (1999). Livestock predation by the painted hunting dog (*Lycan pictus*) in a cattle ranching region of Zimbabwe: A case study. *Biological Conservation*, 88, 133–139.
- Schwarz, S., & Fischer, F. (2006). Feeding ecology of leopards (*Panthera pardus*) in the western Soutpansberg, Republic of South Africa, as revealed by scat analyses. *Ecotropica*, 12, 35–42.
- Sillero-Zubiri, C., & Laurenson, M. K. (2001). Interactions between carnivores and local communities: conflict or co-existence? In J. L. Gittleman, S. M. Funk, D. W. Macdonald, & R. K. Wayne (Eds.), *Carnivore conservation* (pp. 282–312). Cambridge: Cambridge University Press.
- Strauss, A., & Corbin, J. (1990). *Basics of qualitative research: grounded theory procedures and techniques*. London: Sage.
- Stuart, C. T., & Stuart, T. D. (1993). Prey of leopards in the western Soutpansberg: south Africa. *Journal of African Zoology*, 107, 135–137.
- Swanepoel, L. H., Lindsey, P., Somers, M. J., van Hoven, W., & Dalerum, F. (2013). Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation*, 16, 41–50. <http://dx.doi.org/10.1111/j.1469-1795.2012.00566.x>
- Treves, A., & Karanth, U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491–1499.
- Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human-wildlife conflicts — A review. *Human Dimensions of Wildlife*, 11, 383–396.
- UNESCO. (2009). *UNESCO MAB biosphere reserves directory*. [Accessed March 1 st 2010]. <http://www.unesco.org/mabdb/br/brdir/directory/biores.asp?code=SAF+06&mode=al>
- Uphyrkina, O., Johnson, W., Quigley Miquelle, D., Marker, L., Bush, M., & O'Brien, S. (2001). Phylogenetics, genome diversity and origin of modern leopard, (*Panthera pardus*). *Molecular Ecology*, 10, 2617–2633.
- Woodroffe, R., Thirgood, S., & Rabinowitz, A. (2005). The impact of human-wildlife conflict on natural systems. In R. Woodroffe, S. Thirgood, & A. Rabinowitz (Eds.), *People and wildlife: conflict or coexistence?* (pp. 1–12). Cambridge: Cambridge University Press.
- Woodroffe, R., Frank, L. G., Lindsey, P. A., et al. (2007). Tools for conserving large carnivores in Africa's community rangelands: A case-control study of livestock husbandry. *Biodiversity and Conservation*, 16, 1245–1260.