

Characteristics and determinants of human-carnivore conflict in South African farmland

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Abstract Reducing human-carnivore conflict may provide conservation, social and economic benefits, but designing suitable mitigation activities requires information regarding underlying anthropogenic and environmental determinants. To obtain those data, we interviewed game and livestock farmers in Limpopo province, South Africa from March to August 2011. We quantified (1) human-carnivore conflict characteristics; (2) determinants of perceived carnivore predation levels and; (3) determinants of retaliatory persecution of carnivores. Carnivores reportedly killed 1.4 % of total game and domestic livestock holdings and the median annual rate of loss was ZAR 1.23 ha⁻¹, which is generally not sufficient to threaten farming livelihoods or the provincial economy. Farmers reportedly killed 303 carnivores in the year prior to the interview, 44 of which were threatened species. African wild dogs were the least tolerated species, followed by cheetahs, although these species were only blamed for 6 and 3 % of reported kills respectively. The main determinants of human-carnivore conflict were high elevation, mixed purpose farming (i.e., stocking both game and livestock), dense vegetation cover and high perceived financial losses. The results suggest a number of potential conflict-mitigation strategies which include addressing predation problems in areas with a high proportion of vulnerable farms, improving tolerance of carnivores among low-tolerance social groups and correcting misconceptions about the provenance and financial impact of local carnivore populations. This information has already lead to the implementation of several suitably tailored mitigation activities.

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Introduction

In the last century, many carnivore species have undergone declines in distribution and population size (Woodroffe and Ginsberg 2000). This is often due to human-carnivore conflict in non-protected areas (especially those bordering reserves), where the interests of co-existing people and carnivores clash (Stein et al. 2010; Woodroffe and Ginsberg 1998). In agricultural landscapes, human-carnivore conflict most often arises when carnivores prey upon domestic livestock or game. For example wolves (*Canis lupus*) and bears (*Ursus* spp.) prey upon sheep in North America and Europe (Prugh et al. 2009; Treves and Karanth 2003; Rigg et al. 2011), tigers (*Panthera tigris*) and leopards (*Panthera pardus*) kill livestock in Asia (Treves and Karanth 2003) and species such as lions (*P. pardus*), cheetahs (*Acinonyx jubatus*), leopards, caracals (*Caracal caracal*) and black-backed jackals (*Canis mesomelas*) feed on cattle, sheep, goats and game in Africa (Woodroffe and Frank 2005; Thorn et al. 2012; Marker et al. 2003). People frequently respond by killing suspected predators and such persecution is now among the leading world-wide threats to large carnivores (Graham et al. 2005; Inskip and Zimmermann 2009; Treves and Karanth 2003; Stein et al. 2010). At the same time, predation of human-owned animals can cause loss of income or food, which can have serious adverse impacts on individual farmers, agricultural production, food security and rural development (Graham et al. 2005; Treves and Karanth 2003; Woodroffe et al. 2007). Thus, in areas where animal production is prevalent, mitigating human-carnivore conflict may be of conservation, social and economic concern.

Here, we investigate conflict between co-existing carnivores and people in Limpopo, South Africa. The agricultural sector is Limpopo's second largest source of employment (Limpopo DFED 2003) and our study area has the highest proportion of grazing land in the province (de Klerk 2003), further accentuating the local economic importance of animal production. We focused on non-protected areas, where intensive and extensive commercial animal production, stud breeding, sport hunting, and wildlife-based tourism on privately-owned farms are the predominant land uses. Anecdotal information from local researchers, conservation workers and the Limpopo Department of Economic Development, Environment and Tourism suggests that carnivore predation of human-owned animals and retaliatory persecution of carnivores is common.

Several South African carnivore species, e.g. cheetahs, leopards, brown hyaenas (*Hyaena brunnea*) and African wild dogs (*Lycaon pictus*) are protected under the National Environmental Management: Biodiversity Act (NEMA 2004), which also prescribes permissible methods of lethal control for non-protected wildlife. However, the institutions charged with managing human-wildlife conflict and enforcing biodiversity legislation in Limpopo are hampered by corruption, overlapping responsibilities and a fundamental lack of financial and human resource capacity (Anthony et al. 2010). Hence, compliance with governmental policy cannot simply be compelled, especially in remote rural areas. Sustainable human-wildlife conflict-mitigation strategies must therefore foster voluntary implementation by balancing human interests with carnivore conservation objectives. This requires a clear understanding of the characteristics and determinants of conflict.

Conflict determinants are relatively well researched in Europe and North America and there have been a number of prior African studies (Graham et al. 2005; Inskip and

Zimmermann 2009). Findings therein identify several potentially useful mitigation options but also suggest that conflict arises from a range of inter-related social, economic, environmental and ecological factors whose effects vary spatially and temporally (Graham et al. 2005; Inskip and Zimmermann 2009; Woodroffe et al. 2007). For example, determinants of conflict in Tanzania included education, predation rates and the use of effective anti-predation measures (Holmern et al. 2007). Factors affecting attitudes to wolves in America included social group and occupation (Naughton-Treves et al. 2003) and in Slovakia, husbandry methods and occupation accounted for most of the variation in attitudes to wolves and bears in farmland (Rigg et al. 2011). Selection and successful application of conflict-mitigation strategies therefore depends upon accurate knowledge of the local context and circumstances.

Few prior publications (see Anthony et al. 2010; Balme et al. 2009; Blaum et al. 2009; Lindsey et al. 2005; St John et al. 2011) have addressed human-carnivore conflict in South Africa and only one study in the North West Province of South Africa (Thorn et al. 2012) has evaluated the relative contribution of social, economic and environmental drivers. By comparison with the North West Province, our study area supports relatively high occupancy of large carnivores (Lindsey et al. 2004; Daly et al. 2005; Friedmann and Daly 2004; Thorn et al. 2011b). We expect this difference to affect carnivore dietary niches, which in turn influence the predator–prey interactions that are at the heart of human-carnivore conflict in farmland. Our aim was therefore to assess the characteristics and determinants of conflict in Limpopo, thereby informing the development of suitably tailored conflict-mitigation options. Accordingly, we interviewed game and livestock farmers throughout the study area to obtain baseline measures of (1) human-carnivore conflict characteristics; (2) determinants of perceived carnivore predation levels and; (3) factors determining human persecution of carnivores.

Methods

Study area

The study was conducted in the UNESCO Waterberg Biosphere Reserve and surrounding areas of the Waterberg District Municipality (hereafter collectively termed ‘the Waterberg’) in Limpopo Province, South Africa (Fig. 1). The terrain within the 4,174 km² Biosphere Reserve consists mainly of rolling hills, but includes the Waterberg Mountain range. Elevation is from 808 to 2,100 m and annual rainfall is between 600 and 900 mm (de Klerk 2003). The Waterberg is within the savanna biome and sour and mixed bushveld vegetation types predominate (de Klerk 2003).

The most common agricultural enterprise in the study area is game farming, which involves extensive management of plains game (de Klerk 2003). Game farming income is derived mainly from sport hunting for meat or trophies, sale of live animals, stud breeding and tourism (Bothma 2005). Game farming is increasingly prevalent in South Africa because it is often more profitable than livestock production (Bothma 2005). In recent years, breeding of intensively managed high-value game (e.g., rare antelope colour morphs or sub-species) has also become popular due to rapidly escalating sale prices. For example, the average 2011 auction price for a standard impala (*Aepyceros melampus*) male was ZAR 1344, compared with ZAR 131 667 (9697 % higher) for a black colour morph of the same species (Vleissentraal 2011).

Domestic livestock production is also a common land use. Livestock is sometimes managed extensively, but is usually intensively farmed in pastures. Income from livestock

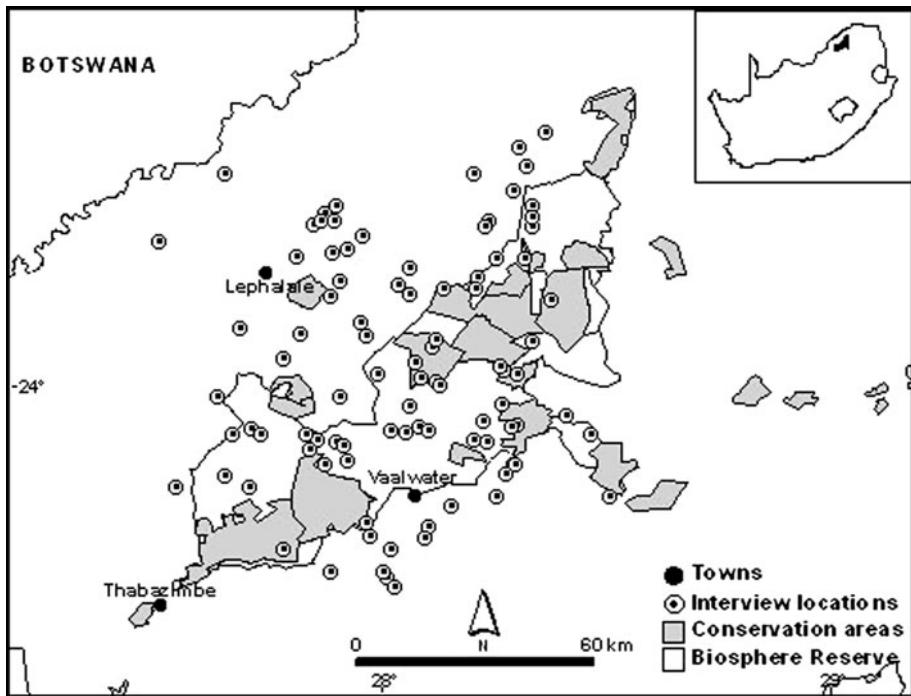


Fig. 1 Study area and interview locations ($n = 92$). The *black patch* on the *inset* indicates the position of the study area in South Africa

farming comprises mainly meat, dairy and wool sales from cattle and small-stock (pigs, sheep and goats) (Department of Agriculture Forestry and Fisheries 2010). Stud breeding is also common and although such high-value animals are often intensively managed, this is not always the case. Many farmers combine game and livestock farming or stud breeding (mixed farming).

Several carnivore species that may prey upon game and livestock are resident in Waterberg farmland. These include caracals, black-backed jackals (hereafter referred to as jackals), leopards, cheetahs, brown hyaenas and African wild dogs. Transient spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) occasionally occur in our study area, but are resident only inside reserves with predator-proof fencing (Friedmann and Daly 2004).

Interview methods and questionnaire design

To obtain information on human-carnivore conflict, we visited farmers throughout the Waterberg between March 2011 and August 2011. We interviewed 92 people who were responsible for the management of 95 farms (Fig. 1). Initial respondents were recruited at local farming forums and further contacts were supplied by each participant. With a refusal rate of 8 %, non-response bias was assumed to be minimal. All but one of our respondents were white, reflecting typical land tenure patterns in South African commercial farms (Tladi et al. 2002). As in Marker et al. 2003, we considered white farmers to be a homogeneous group and therefore assumed our respondents to be approximately representative of the wider population of farmers in the study area. While not inherently

unrealistic, this assumption could not be verified as there are no available reference statistics for land ownership by ethnic group. Our interpretation of the wider effects of conflict therefore remains tentative.

Interviews were administered in person by M.T. Each lasted approximately 40 min and was based on a semi-structured socio-economic questionnaire (available from M.T.) adapted from a previous study in a neighbouring province (Thorn et al. 2012). The questionnaire contained four sections concerning (1) characteristics of respondents and their farms; (2) carnivore presence, predator–prey interactions and the perceived cost of predation; (3) use of anti-predation measures and lethal control of carnivores and; (4) degree of tolerance toward carnivores. All respondents were assured of anonymity and confidentiality.

The characteristics we recorded about respondents included age and cultural group, which was inferred from the respondent's first language. Recorded characteristics of farms included elevation, measured with a hand-held GPS at the entrance to the farm. Respondents estimated the proportion of grassland and crop areas (open cover habitats) on their land, compared with scrub and woodland areas (dense cover habitats). From this, we determined the predominant category of vegetative cover at each farm (open, dense or heterogeneous). This method of allocating cover categories was ground-truthed and validated in a subset of 36 farms where extensive scat searches were completed in addition to questionnaire surveys.

Game and livestock abundance and losses were also based on land owner estimates. Livestock abundance estimates are considered likely to be accurate as these species are usually intensively managed and frequently counted. The accuracy of game estimates may be more variable as these species are often extensively managed and abundance is usually estimated annually/bi-annually. Furthermore, the survey methods employed during game counts vary widely in their suitability and reliability. Many land owners cited lack of population growth in game species as indirect evidence of predation, but as such losses were unquantifiable and could be caused by factors other than carnivore predation, they were not recorded.

To assess whether reported financial losses were congruent with market values, we compared sale prices estimated by respondents with independent data such as sale prices at game and livestock auctions in 2011. Although we cannot corroborate the number of animals reportedly lost, we found that in general, respondents did not over-estimate predated game and livestock values. We were not able to verify the estimated values given for stud animals because prices vary according to the breed, sex, size and genetic properties of individual animals.

Analysis

We summarised human-carnivore conflict characteristics using standard descriptive statistics. We then calculated financial rates of loss (cumulative Q1, median and Q3 ZAR losses/cumulative area surveyed) and extrapolated them over the total area of commercial grazing land in Limpopo province to give a coarse estimate of the order of magnitude of the wider impact of current levels of predation. Similarly, we calculated persecution rates for each carnivore species (total number killed/total area surveyed), but limited our extrapolation to the survey area as several of the focal species have restricted ranges, i.e. do not occur throughout the province (Friedmann and Daly 2004).

We evaluated the effect of potential conflict determinants using two sets of generalised linear regression models. Prior to analysis, we excluded any variables that were inter-

correlated by Spearman's $\rho(r_s) > 0.7$ (Kolowski and Holekamp 2006). The first set of models evaluated the effect of farm-specific and environmental predictors (Table 1) on the number of game and livestock reportedly preyed upon at each farm, using a negative binomial error distribution and a log link function. Secondly, we modelled the effects of social, economic and environmental predictors (Table 1) on the probability of carnivore persecution using the binary response variable 'use or non-use of lethal control', a binomial error distribution and a logit link function.

For each response variable, we evaluated a set of candidate models containing all additive combinations of predictors as well as all two-way interactions. We then used standard information-theoretic multi-model inference techniques to interpret the results (Burnham and Anderson 2002; Dochterman and Jenkins 2011) based on Akaike's

Table 1 Predictor variables and their anticipated effect on response variables that indicate human-carnivore conflict

Predictor variable	Predicted effect
<i>Response variable: no. of game and livestock reportedly killed by carnivores at each farm</i>	
Anti-predation measures (lethal control, non-lethal methods, both or neither)	Indiscriminate lethal control is unlikely to reduce predation because it does not necessarily remove habitual livestock predators ^a and has little long-term effect on large carnivore density ^{b,c} . Non-lethal measures such as protective enclosures have been shown to reduce predation losses in a number of studies world-wide ^d
Land use (livestock, game or mixed farming)	Intensive management and associated anti-predation measures on livestock farms should reduce predation levels compared with extensively managed game or mixed farms
Total prey density (individuals/km ²)	High stocking densities should increase the frequency with which carnivores encounter prey, leading to higher levels of predation
Cover (open, dense, or equal proportions of open and dense cover, i.e. heterogeneous)	Dense vegetation increases the cover available to carnivores, which has been shown to increase predation ^{d,e}
<i>Response variable: use (1) or non-use (0) of lethal control</i>	
Predation losses (ZAR)	High financial losses are expected to increase the use of lethal control ^b
Land use (livestock, game or mixed farming)	Predation of intensively managed livestock is easier to detect and quantify than loss of extensively managed game. We therefore suspect that greater awareness of losses coupled with lower profitability of livestock farming ^f may provoke increased use of lethal control among livestock farmers
Farmer age (years)	Previous studies found that younger farmers tend to be more tolerant of carnivores ^c and should, therefore, be less likely to use lethal control
Farmer cultural group (Afrikaans or English)	We expect tolerance toward large carnivores and thus, prevalence of lethal control to differ among cultural groups ^e

Sources: ^a Inskip and Zimmermann (2009), ^b Woodroffe and Frank (2005), ^c Prugh et al. (2009), ^d Woodroffe et al. (2007), ^e Thorn et al. (2012), ^f Bothma (2005)

Information Criterion adjusted for small sample size (AIC_c) (see Thorn et al. 2012 for a more detailed description of the procedure).

Analysis was conducted using SPSS v17 (SPSS Inc., Chicago, USA). Financial values throughout are given in South African Rand (ZAR 1 = GBP 0.08 = USD 0.13).

Results

Characteristics of the sample

Most respondents (73 %) were members of the Afrikaans or Afrikaans and German-speaking cultural group. The remainder were English-speaking (23 %) and 4 % were from Bantu-speaking or non-South African cultural groups. Most (92 %) were full time residents at their farm with mean tenure of 16 years (\pm SE 1.5). The total area of the farms surveyed was 231,549 ha (median = 1,300 ha, range = 6.2–16,000 ha). This represents 23 % of farmland within the whole study area, which we calculated as the area within the minimum convex polygon formed from the outermost interview locations. Forty three percent of farms were used mainly for game farming, 35 % for cattle or small-stock and 22 % for mixed farming (a roughly equal area used for game and domestic livestock). Total estimated stock holdings (66,520 animals) consisted of 1031 sheep, 1242 goats, 1575 pigs, 11,467 cattle (including 3,861 stud animals) and 51,205 game, 3,020 of which were high-value antelopes. High-value animals (stud livestock or rare antelope) were present in 37 % of the farms surveyed, but were stocked in (67 %) of mixed farms. Median elevation was 1077 m (range 822–1,600 m). Farms with predominantly dense cover accounted for 74 % of the sample, compared with 17 % farms with open cover and 9 % farms with heterogeneous cover.

Lethal control of carnivores was reportedly practiced at 45 farms (47 %), where 92 % of the carnivores that were destroyed were shot. Non-lethal anti-predation methods were reportedly used by 79 % of respondents, the most popular being enclosures with fencing intended to exclude predators ($n = 61$), moving potential prey animals to open areas with a lower risk of predation ($n = 29$) and natural anti-predator adaptations (stocking native, predator-adapted breeds and not dehorning livestock) ($n = 17$). Neither lethal nor non-lethal methods were reportedly used by 15 % of respondents, all of whom were extensive game farmers. We presume that they were unconcerned about predation or did not consider anti-predation efforts practical. Thirty five percent of respondents reportedly used both lethal and non-lethal measures.

Human-carnivore conflict characteristics

Perceived predation losses

Eighty six percent of respondents reported perceived predation losses totalling 934 animals (1.4 % of total stock holdings used for commercial purposes) in the year preceding interviews (Table 2). Perceived losses as a function of elevation, land use, cover and anti-predation methods are illustrated in Fig. 2.

The median annual number of animals reportedly preyed in game farms was 3 ($Q_1 = 1$, $Q_3 = 8.5$), compared with 5 ($Q_1 = 0.5$, $Q_3 = 7.5$) in livestock farms and 12 ($Q_1 = 3.5$, $Q_3 = 25$) in mixed farms. Reported median financial losses were ZAR 6000 ($Q_1 =$ ZAR 800, $Q_3 =$ ZAR 26500) in game farms, compared with ZAR 11450 ($Q_1 =$ ZAR 0, $Q_3 =$ ZAR 34100) in livestock farms and ZAR 15800 ($Q_1 =$ ZAR 8000

Table 2 Kills attributed to carnivores (predation) and carnivores killed by respondents (persecution) in the year preceding interviews ($n = 92$)

Carnivore species	Predation				Persecution		
	Small-stock	Cattle	Game	Total	ψ	No. killed	Persecution rate/100 km ²
Jackal	62	24	33	119	0.98	229	9.89
Caracal	39	2	103	144	0.89	14	0.60
Leopard	18	95	155	268	0.87	16	0.69
Cheetah	0	1	26	27	0.39	0	–
African wild dog	0	7	51	58	0.42	15	0.65
Brown hyaena	0	8	13	21	0.97	27	1.17
Serval	2	0	0	2	0.46	1	0.04
Honey badger	0	0	3	3	0.59	1	0.04
Unknown	44	45	203	292			
Total	165	182	587	934		303	13.09

ψ = proportion of farms occupied by carnivore species, persecution rate = number of carnivores killed/total farm area surveyed

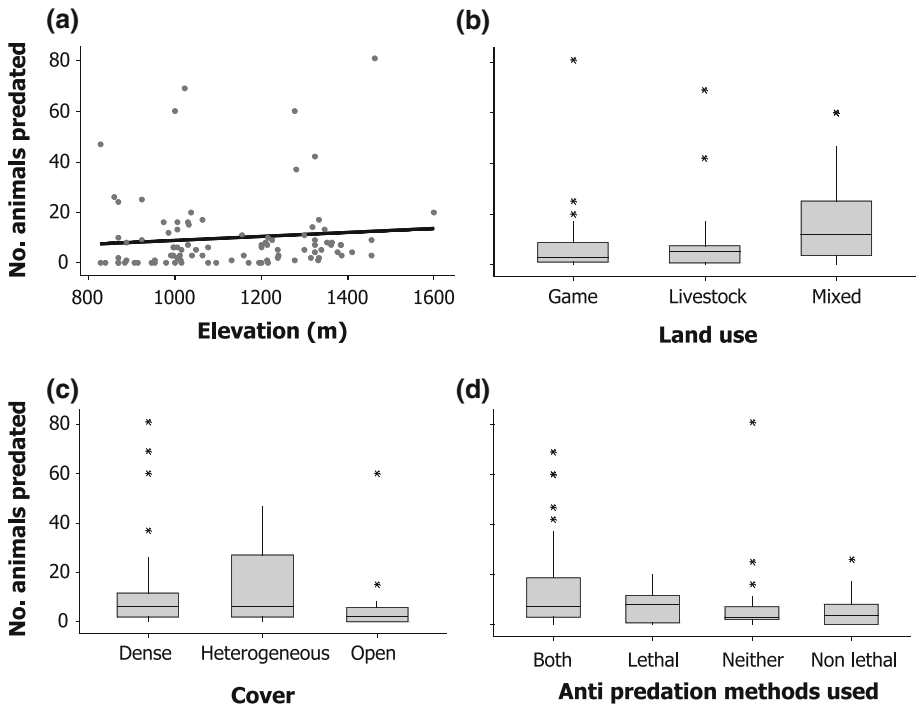


Fig. 2 The number of animals per farm ($n = 95$) reportedly preyed upon by carnivores, in relation to elevation (a), land use (b), cover (c) and anti-predation methods used (d). Box plots display median, 25 and 75 % quartiles, maximum, minimum and outliers (asterisks)

Q3 = ZAR 66500) in mixed farms. High-value animals comprised 11 % of reportedly predated animals in mixed farms, which means that the financial losses perceived by these respondents arose mainly from frequent predation of relatively low-value animals. Perceived losses as a function of land use and use of lethal control are illustrated in Fig. 3.

Overall, the majority of animals perceived to have been predated were game species (63 %), followed by cattle (19 %) and small-stock (18 %) (Table 2). Animals ≤ 1 year old accounted for 54 % of predated animals.

The estimated total value of reportedly predated animals was ZAR 2792873, with a median annual loss per farm of ZAR 12000 (Q1 = ZAR 1000, Q3 = ZAR 30000). Extremely high losses were reported by seven respondents, who each lost sums between ZAR 105800 and ZAR 392500. Four of the seven were stud or high-value game breeders who lost a relatively small number of very expensive animals.

Perceived cumulative financial losses at the median, divided by the cumulative area of the farms surveyed, gives a median annual rate of loss of ZAR 1.23 ha⁻¹ (Q1 = ZAR 0.03 ha⁻¹, Q3 = ZAR 3.98 ha⁻¹). Extrapolating that rate of loss across all commercial grazing land in Limpopo produces a perceived annual predation loss of ZAR 7385509, which equates to 0.15 % of Limpopo agricultural GDP in 2010 (Statistics South Africa 2011).

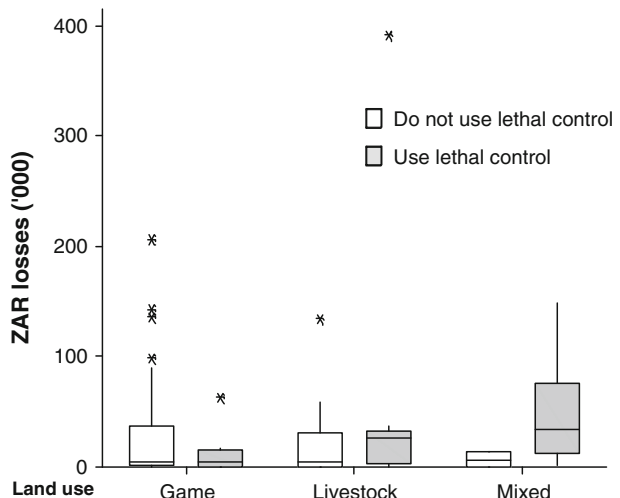
Perceived culpability, persecution and tolerance of carnivores

The majority of predation losses were attributed to leopards, followed by caracals and jackals (Table 2). Most respondents (67 %) inferred culpability from indirect evidence like spoor, bite marks and feeding patterns, 20 % witnessed attacks or photographed carnivores assumed to be returning to a kill, and 13 % offered no supporting evidence.

Forty two respondents reportedly killed a total of 303 carnivores in the year preceding the interviews (Table 2). These included a serval (*Leptailurus serval*) and a honey badger (*Mellivora capensis*) thought to have been preying on poultry. Annual species persecution rates (Table 2) extrapolated over the whole study area equate to 1096 jackals, 129 brown hyaenas, 77 leopards, 72 African wild dogs and 67 caracals.

Surprisingly, the species most often blamed for predation (Table 2) were not the ones that were least tolerated. Only 23 % of respondents said that they would tolerate African

Fig. 3 Reported financial losses (median, 25 % and 75 % quartiles, maximum, minimum and outliers (*asterisks*)), in relation to land use and lethal control of carnivores



wild dogs if they were regularly present at their farm, compared with 58 % for cheetahs, 73 % for leopards, 78 % for jackals, 79 % for caracals, and 92 % for brown hyaenas. Of 78 people who answered the question, 42 % said that they would cross the threshold from tolerance of carnivores to intolerance if ≤ 1 % of their stock were preyed upon. Another 23 % reached that point after losing between 1 and 5 % of their stock and 17 % gave a tolerance threshold of between 5 and 35 % of stock holdings. A further 18 % felt that predation losses were a natural and acceptable hazard no matter how many animals were preyed upon. The median percent loss that farmers with high-value stud or game animals were willing to tolerate was 83 % lower than farmers without high-value animals ($W = 2103.5$, $P < 0.001$, $n = 78$) and two thirds of respondents who said they were willing to tolerate losing ≤ 1 % of their stock were farming high-value animals.

There was no correlation ($r_s = 0.467$, $P = 0.243$, $n = 8$) between the stock losses attributed to each carnivore species and species-specific persecution levels (Table 2). However, there was a strong positive correlation between carnivore occupancy (the proportion of farms where the species was reportedly present) and species-specific persecution levels ($r_s = 0.802$, $P = 0.017$, $n = 8$). The implication is that carnivores were persecuted according to their availability and not in relation to their perceived culpability for predation. Indeed, when asked why they had killed carnivores, only 35 % of people who used lethal control said they were trying to remove a specific animal suspected of attacking their game or livestock. Another 37 % killed carnivores as a general precaution against future predation, 21 % earned income from carnivore sport or trophy hunting, and 7 % killed carnivores to control their population numbers.

Determinants of predation

The global additive model showed no evidence of a lack of fit ($\chi^2_{80} = 94.913$, $\hat{c} = 1.186$, $n = 94$). Seven of 78 candidate models were within 7 Akaike units of the top ranked model (Table 3). Elevation (summed Akaike weight 0.86) and land use (summed Akaike weight 0.83) were the most influential variables, followed by cover (summed Akaike weight 0.79) and anti-predation methods (summed Akaike weight 0.65). Prey density (summed Akaike weight 0.12) and terrain (summed Akaike weight 0.01) had little effect.

Beta coefficients from regression models (Table 4) indicate that after controlling for the effect of other variables, predicted predation frequency in farms at high elevation (1,600 m) was almost five times that of farms at low elevation (822 m). Predicted predation frequency in mixed farms was three times greater than in game farms. Predicted predation frequency in farms with predominantly dense or heterogeneous cover was more than twice that of farms with open cover. Unsurprisingly, farms that did not use any anti-predation measures were associated with the highest predation losses. Predicted losses in those farms were over twice as high as in farms using non-lethal measures. The same is true of farms using both lethal and non-lethal anti-predation techniques, but in this case, cause and effect are confounded: the increased probability of persecution may be a reaction to high predation levels or alternatively, lethal control may increase predation levels (e.g. by triggering compensatory responses such as increased natality or immigration) (Prugh et al. 2009).

Determinants of persecution

There was no evidence of a lack of fit in the global additive model ($\chi^2_{88} = 91.487$, $\hat{c} = 1.04$, $n = 94$). Three of the 22 candidate models were within 7 Akaike units of the top

Table 3 Generalised linear models that were within 7 AIC_c units of the model with the lowest AIC_c, with associated degrees of freedom (df), number of parameters in the model (*k*), AIC_c, ΔAIC_c and Akaike model weights

Model	df	<i>k</i>	AIC _c	ΔAIC _c	Weight
<i>Response variable: no. of game and livestock reportedly killed by carnivores at each farm</i>					
1. Land use + cover + elevation + anti-predation	8	9	607.831	0.00	0.5206
2. Land use + cover + elevation	5	6	609.340	1.51	0.2448
3. Prey density × anti-predation	4	5	611.365	3.53	0.0880
4. Land use × elevation	3	4	613.136	5.31	0.0367
5. Elevation × anti-predation	4	5	613.224	5.39	0.0351
6. Land use	2	3	613.613	5.78	0.0289
7. Prey density × elevation	1	2	614.608	6.78	0.0176
<i>Response variable: use (1) or non-use of lethal control (0)</i>					
8. Land use × ZAR losses	3	4	112.521	0.00	0.7941
9. Language + age + land use	4	5	117.175	4.65	0.0775
10. Language + land use	3	4	117.973	5.45	0.0520
11. Age + land use	3	4	119.025	6.50	0.0307

ranked model (Table 3). Land use was by far the most influential determinant (summed Akaike weight 0.99), followed by financial losses (summed Akaike weight 0.79). Cultural group (summed Akaike weight 0.16) and age (summed Akaike weight 0.12) had little effect.

Regression coefficients were taken from model 8 (Table 3), which received considerably greater support than any other model (0.79 Akaike weight). After controlling for the effect of other variables, a mixed farmer with losses at the 75th percentile (ZAR 30 000) would be over 43 times more likely to kill carnivores than a mixed farmer with losses at the 25th percentile (ZAR 1000).

Discussion

Data from interviews comprise reported information, some of which may be subject to bias. Declared predation rates may be negatively biased if stock abundance is poorly monitored and if owners fail to find or report all predated carcasses. Positive bias may arise if respondents incorrectly assume predation to be the cause of death, or deliberately inflate losses in pursuit of ulterior motives (Rasmussen 1999). Similarly, reported persecution rates may be negatively biased if fear of prosecution or censure inhibits respondents who use illegal methods of lethal control or kill legally protected carnivores (St John et al. 2011). Nevertheless, capturing and incorporating information from affected communities provides essential contextual data that are not available from any other source and this is essential in designing effective human-wildlife conflict solutions (Anthony et al. 2010). Furthermore, exploratory analyses such as ours are vital for the identification of key parameters in complex systems where there is little or no pre-existing information (Dochterman and Jenkins 2011).

Our modelling results indicate that the probability of predation was greatest in farms at high elevation, those with predominantly dense or heterogeneous cover and those used for mixed farming. Hence, areas with a high proportion of farms possessing these

Table 4 Estimated regression coefficients ($\hat{\beta}$), standard errors (\pm SE) and odds from generalised linear models that were within 7 AIC_c units of the model with the lowest AIC_c

Parameter	$\hat{\beta}$	\pm SE($\hat{\beta}$)	Exp($\hat{\beta}$)
<i>Response variable: no. of game and livestock reportedly killed by carnivores at each farm Reference categories: cover = open, land use = game, anti-predation = non lethal</i>			
Elevation (model average)	0.002	0.0007	1.002
Land use = livestock (model average)	0.290	0.3122	1.337
Land use = mixed (model average)	1.102	0.4475	3.010
Cover = heterogeneous (model average)	0.855	0.4322	2.352
Cover = dense (model average)	0.856	0.3377	2.355
Anti predation = neither (model 1)	0.931	0.4163	2.537
Anti-predation = lethal (model 1)	0.776	0.4655	2.173
Anti-predation = both (model 1)	0.848	0.3908	2.335
Prey density \times (anti-predation = non lethal) (model 3)	-0.006	0.0047	0.994
Prey density \times (anti-predation = lethal) (model 3)	0.004	0.0044	1.004
Prey density \times (anti-predation = both) (model 3)	0.017	0.0049	1.017
Prey density \times (anti-predation = neither) (model 3)	0.016	0.0162	1.016
(Land use = livestock) \times elevation (model 4)	0.001	0.0009	1.001
(Land use = mixed) \times elevation (model 4)	0.002	0.001	1.002
(Land use = game) \times elevation (model 4)	0.001	0.0009	1.001
Elevation \times (anti-predation = non lethal) (model 5)	0.001	0.0007	1.001
Elevation \times (anti-predation = lethal) (model 5)	0.001	0.0008	1.001
Elevation \times (anti-predation = both) (model 5)	0.002	0.0008	1.002
Elevation \times (anti-predation = neither) (model 5)	0.001	0.0009	1.001
Prey density \times elevation (model 7)	9.13E-06	3.63E-06	1.000
<i>Response variable: use (1) or non-use of lethal control (0)</i>			
(Land use = livestock) \times ZAR losses (model 8)	0.005	0.0038	1.005
(Land use = mixed) \times ZAR losses (model 8)	0.130	0.0538	1.139
(Land use = game) \times ZAR losses (model 8)	-0.012	0.0770	0.988

Bold $\hat{\beta}$ values differed significantly from zero

characteristics will be obvious focal points for future mitigation activities. The same can be said of the large group of respondents (42 %) who considered losses in excess of 1 % of stock holdings intolerable. That threshold seems unrealistically low, given that the perceived annual predation rate for the Waterberg (1.4 % of total stock holdings) is at the bottom of the 1.4–4.5 % range reported in other recent African studies (Holmern et al. 2007; Kolowski and Holekamp 2006; Marker et al. 2003; Schiess-Meier et al. 2007; Thorn et al. 2012; Stein et al. 2010).

Most of those who expressed low tolerance were stud or rare game breeders and even low predation levels in farms that stock such high-value animals can be extremely expensive. Contextual information about the turnover and profit of affected farmers is rarely available, making it impossible for others to assess whether losses with large absolute values seriously affect net profit or are balanced by correspondingly high turnover and assets. This may engender a heightened sense of financial vulnerability among high-value stock farmers, particularly as their animals are usually intensively managed (personal observation, M.T.), making losses relatively easy to detect (Table 1), thereby increasing

awareness of predation risk. Those factors may explain why financial losses were an important trigger for carnivore persecution in the group most likely to stock high-value animals (mixed farmers), especially as they were also associated with the highest predicted predation frequencies. If that interpretation is correct, recent increases in sale prices for high-value game may have triggered an accompanying decrease in tolerance toward carnivores, which may be ameliorated or compounded by future movements in rare game prices.

Despite a widespread perception that carnivores are economically damaging, financial losses within the inter-quartile range were relatively low. For example, the reported median rate of financial loss (ZAR 1.23 ha⁻¹) represents approximately 1.5 % of net earnings in agriculture (approximately ZAR 80 ha⁻¹) (ABSA 2003) and would result in annual losses of ZAR 1605 on an average-sized farm. Such losses seem insufficient to threaten commercial farming livelihoods in general. Our extrapolation of the results to grazing areas elsewhere in Limpopo gives only a coarse estimate of the wider impact of predation losses, but provides an economic context for the results and identifies the order of magnitude of the economic effect. The actual impact may differ from our estimate because elevation, land use, vegetation cover (the three most influential variables) and consequent predation rates in other areas of Limpopo may differ from those in the Waterberg. For this reason and in view of the complex links between agriculture and other important economic factors (e.g. employment), our interpretation of the wider economic impact of predation losses is tentative. Nevertheless, at 0.15 % of Limpopo agricultural GDP, the wider economic effect of predation losses appear negligible, particularly as agriculture, forestry and fishing constituted only 2.3 and 2.5 % of South African and Limpopo GDP, respectively in 2010 (Statistics South Africa 2011).

The only directly comparable information about predation comes from the North West Province, which borders Limpopo. Land use, farm management and animal husbandry practices in the North West Province and the Waterberg are very similar (personal observation, M.T.), yet the proportion of stock holdings preyed in the North West (2.8 %) was double that in the Waterberg. In the North West, which appears to be affected by meso-predator release, 61 % of reported predation incidents were attributed to jackals and caracals (Thorn et al. 2012). By comparison, jackals and caracals were blamed for just 28 % of reported predation losses in the Waterberg, where apex carnivores like leopards and African wild dogs are still widespread (Friedmann and Daly 2004). This contrast may exemplify the functional benefits of apex carnivores and possibly, the negative financial consequences of removing them.

The median annual rate of loss in the North West was just (ZAR 0.22 ha⁻¹) (Thorn et al. 2012), indicating that although Waterberg farmers lost a smaller proportion of their stock holdings, prey animals were considerably more valuable. This probably reflects higher occupancy of large carnivores (Friedmann and Daly 2004) that are able to kill large prey, combined with greater prevalence of stud and high-value antelope breeding in the Waterberg (personal observation). These factors may explain why financial losses were a key determinant of conflict in the Waterberg, but not in the North West Province.

Counter intuitively, our results indicated that the species reported to be the main cause of predation losses (leopard) is not among those that are least tolerated (African wild dogs and cheetahs) or most persecuted (jackals). There are several possible reasons for this. Jackals have long been considered vermin in South African farmland and receive no legal protection. They are common and abundant despite intense long-term persecution (Sillero-Zubiri et al. 2004), which seems to have spawned a widespread belief that lethal control of jackals (and caracals) is necessary to prevent over-population and predation (personal

observation). Leopards also have high occupancy in the Waterberg (Daly et al. 2005), but although they pose a threat to stock holdings, hunting leopards under CITES quota permits provides local people with a source of income, as does wildlife-based tourism. This may explain why leopards were better tolerated than meso-carnivores that are less likely to attract hunters or tourists or species like African wild dogs and cheetahs that cannot be legally hunted.

However, there are alternative explanations arising from rapid growth in the area committed to game farming over the last two decades (Bothma 2005). Historically, African wild dogs and cheetahs were extirpated across much of their South African range (Marnewick et al. 2007; Sillero-Zubiri et al. 2004). Together with our occupancy results, anecdotal information regarding the frequency of sightings suggests that both species are re-colonising the Waterberg, probably because of the increased availability of habitat, prey and refuge that are offered by game farms (Thorn et al. 2011a). This appears to be a relatively recent phenomenon so low tolerance may stem from fear of unfamiliar species. Furthermore, as they were absent from the area for a prolonged period, there is a widespread belief that African wild dogs and cheetahs are not naturally-occurring in the Waterberg (personal observation). Their reappearance has stimulated resentment of ‘foreign’ damage-causing animals and the organisations (conservation NGO’s and local reserves) incorrectly blamed for introducing them into farmland (personal observation).

The estimated global population of African wild dogs (Endangered) is <5,500 with approximately 450 mature individuals in South Africa (personal communication, Endangered Wildlife Trust, South Africa), 42–106 of which are resident outside of protected areas (Lindsey et al. 2004). The Waterberg is considered a prime target for range expansion (Lindsey et al. 2004) and the population in northern Limpopo is thought to provide important genetic connectivity to nearby populations in other parts of Southern Africa (Davies-Mostert et al. 2012). Our persecution rates do not account for road kills, natural mortality, poisoning/snare by-catch or illegal trade, which undoubtedly take a further toll on the size and structure of the local population. It is therefore likely that persecution constitutes a serious threat to the conservation status of African wild dogs in the Waterberg.

The only available abundance estimates for brown hyaenas (Near Threatened) and leopards (nationally Least Concern, globally Near Threatened) are tenuous, but suggest that both species have much higher population numbers than African wild dogs (Mills and Hofer 1998; Daly et al. 2005). However, as the majority of individuals occur outside protected areas (Mills and Hofer 1998; Mackinnon and Mackinnon 1986), further research is required to quantify local abundance and evaluate the importance of persecution-related threats. This is true of all three species and is particularly important because changes in the status of carnivore populations in the Waterberg may affect the stability of the wider regional meta-population by virtue of spatial and genetic linkages with populations in adjoining areas of southern Africa.

The results of this initial research have suggested several avenues for developing conflict-mitigation strategies in the Waterberg. These include addressing predation problems in areas with a high proportion of vulnerable farms, improving tolerance of carnivores among low-tolerance social groups and correcting misconceptions about the provenance and financial impact of local carnivore populations. In each case, the literature suggests a range of suitable initiatives. Examples include improving the physical security of enclosures (Woodroffe et al. 2007), using livestock guarding dogs (Woodroffe et al. 2007; Rigg et al. 2011) selective lethal control of habitual livestock predators (Woodroffe and Frank 2005), education and awareness raising activities (Marker et al. 2003) and constructive

dialogue with affected communities (Anthony et al. 2010). Many such activities have already been implemented in the study area to address the most pressing priorities revealed by our exploratory analysis. The intention is to quantify and refine their effectiveness before recommending them for wider use in other conflict situations with similar characteristics.

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