A socio-ecological landscape approach to human-wildlife conflict in Northern Botswana

Jeffrey A. Dunnink[1*], Robyn Hartley[2], Lucas Rutina[3,4], Joana Alves[5], Aldina M.A. Franco[1]

[1]School of Environmental Sciences, University of East Anglia Norwich Research Park, Norwich NR4 7TJ, UK,

[2]WildlifeACT, Maun Botswana,

[3]Okavango Research Institute, University of Botswana, Maun Botswana,

[4]Ecosystem conservation Foundation, Maun, Botswana

[5]CFE - Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, 3004-517 Coimbra, Portugal.

[*]Current address: African Wildlife Foundation, Ngong road, Karen Nairobi, Kenya

Corresponding author: Jeffrey Dunnink, jeffdunnink@gmail.com

Mailing address: African Wildlife Foundation Headquarters, P.O. Box 310, 00502

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Abstract

Human-wildlife conflict (HWC) is considered one of the most pressing issues facing conservation today, with negative impacts being felt disproportionately by the rural poor leading to the persecution of large predators. To overcome this, socio-ecological studies that merge existing knowledge of large predator ecology with long term livestock depredation monitoring are required. This study examined key patterns and drivers of livestock depredation in northern Botswana, using a mixed effects model of the government's long term HWC monitoring data to identify depredation reduction measures at key spatial and temporal scales. The results were contrasted to farmers' understanding of their personal risk within the landscape. The location of 342 depredation events occurring between 2008 and 2016 were influenced by distance to protected area and predator and herbivore density, with increased depredation in the wet season using variables measured at a 2km scale. Herbivore density was not significant at the 1km scale but all other variables were unchanged. The 4km scale model was influenced by livestock and herbivore density with increased depredation in the wet season. An 8km livestock free buffer along the protected area boundary, if established, could reduce livestock depredation. There was a clear disparity between government HWC monitoring, interview depredation monitoring and farmers risk awareness. Farmers across the community would benefit from workshops providing appropriate tools to make evidence-based decisions to minimize their risk to HWC. This will ultimately contribute to conservation of wildlife in the Kavango-Zambezi Transfrontier Conservation Area.

Key words: human-wildlife conflict, socio-ecology, landscape ecology, livestock depredation, large African predators.

Introduction

Human-Wildlife-Conflict (HWC) is a problem of global conservation concern (Gusset et al. 2009; Seoraj-pillai & Pillay 2017). Characterized as either crop raiding by herbivores or livestock depredation by carnivores, HWC results in substantial damage to both wildlife assemblages and the livelihoods of human communities living near them (Mbaiwa, 2005; Scheiss-Meier et al. 2007; Hemson et al. 2009; Seoraj-pillai & Pillay 2017). Livestock depredation alone threatens up to 18% of sub-Saharan African households costing up to 50% of their per capita income, preventing their emancipation from poverty (Kissui, 2008; Loveridge et al. 2017).

The retaliatory killing of apex predators, limits the ecosystem resilience and functioning promoted by these keystone species (Ripple et al. 2014; Loveridge et al. 2017). In extreme examples such as East Africa, indiscriminate killing is the greatest threat to lion *Panthera leo* populations (IUCN, 2014). Globally, predator persecution by farmers drove the Falklands *Dusicyon australis* and marsupial wolves *Thylacinus cynocephalus* to extinction and is a key threat to 85% of existing large carnivores (Woodroffe, 2000; Suryawanshi et al. 2017). Despite being protected species, almost all large sub-Saharan African predators are threatened due to historical range shifts and population declines (Ripple et al. 2014). Lions, cheetah *Acinonyx jubatus* and leopard *Panthera pardus* are listed as 'vulnerable' (IUCN, 2017), wild dog *Lycaon pictus* are 'endangered' and spotted hyena *Crocuta crocuta* face severe persecution on agricultural land (IUCN, 2017; Loveridge et al. 2017).

Numerous strategies are available to reduce the impact of depredation on human livelihoods and wildlife populations; including: compensation schemes, problem animal removal, improved livestock husbandry and wildlife monitoring (Gusset et al. 2009; Hemson et al. 2009; Hazzah et al. 2014; Seoraj-pillai & Pillay 2017). These interventions, however, are often financially unsustainable or occur post-conflict. Adopting a landscape ecological approach to identify important drivers and patterns of HWC so that preventive interventions at key spatial and temporal scales can be identified, may provide a more sustainable solution (Treves et al. 2004; Valeix et al. 2012; Loveridge et al. 2017). This requires merging existing knowledge on large predator spatial, foraging and behavioural ecology with long term depredation monitoring (Loveridge et al. 2017). Known landscape variables influencing livestock kill site include: distance from a protected area, surrounding herbivore, predator density and habitat type, and season (Gusset et al. 2009; Inskip & Zimmermann 2009; Davidson et al. 2012; Valeix et al. 2012; Suryawanshi et al. 2017). Scale also influences predator habitat selection in response to environmental characteristics, specifically the allocation of time budgets to areas within a territory (third order) and kill site selection (fourth order; Johnson 1980). Different landscape features, then, may induce different behavioural responses at different scales.

HWC is often the physical expression of socio-political human-human conflict and is influenced by existing social systems (Matema & Andersson 2015; Pooley et al. 2017). Conservation initiatives can be drawn into such human-human conflicts by focusing on protecting animals as opposed to human settlements (Pooley et al. 2017). Any attempt to understand livestock depredation must, therefore, adopt a socio-ecological angle by identifying the interactive influence of livestock husbandry and ecological factors (Ogada et al. 2003; Hemson et al. 2009; Pooley et al. 2017). Community and individual risk awareness needs to be contrasted with robust depredation records to promote evidence-based decision making and potentially reduce depredation (Ogada et al. 2003; Hemson et al. 2009; Rutina et al. 2017).

There is, however, an absence of long term HWC monitoring data, limiting the capacity to identify effective threat reduction measures (Loveridge et al. 2017). In countries such as Botswana, which compensate farmers for livestock depredation, the absence of depredation monitoring data is overcome through investigations into the veracity of compensation claims

(Scheiss-Meier et al. 2007; Rutina et al. 2017). This study adopts a socio-ecological, landscape approach to livestock depredation, potentially contributing to the Kavango-Zambezi (KAZA) Trans-Frontier Conservation Areas (TFCA) stated objective of HWC mitigation to promote the integration of conservation and human well-being (Loveridge et al. 2017; Rutina et al. 2017).

The overarching objective is to determine the landscape ecological features influencing livestock depredation in northern Botswana. The second objective is to determine which livestock husbandry practices best mitigate depredation by large carnivores. The third objective is to evaluate farmer's awareness of the risk of livestock depredation.

Study Site

The Chobe Enclave (CH1), Northern Botswana (Fig. 1), has a mixed land use pattern incorporating agriculture, human settlement and wildlife management (Jones, 2002). This roughly 2000 km^2 communal enclave is surrounded by protected areas on three sides (Chobe National Park and Chobe Forest Reserve, IUCN category Ib and II respectively; CH2) and the Namibian border (Chobe and Linyati River) on the fourth. The area is considered semi-arid receiving 650 mm average annual rainfall, predominantly in the wet season (October to April; Scheiss-Meier et al. 2007) and hosts wild herbivores such as Burchell's zebra, *Equus quagga,* blue wildebeest *Connohaetes taurinus,* impala *Aepyceros melampus* and buffalo *Syncerus caffer.* The dominant economic activities are small-scale agro-pastoralism and employment in the civil service and tourism industries (Jones, 2002). The human population has been stable since 2002 with roughly 7500 people inhabiting the five main villages of Kachikau, Parakarungu, Kavimba, Satau and Mabele (Statistics Botswana 2011). Cattle, the most common livestock, are kept in "cattle posts" located throughout the enclave, grazed on communal land during the day and kept in "bomas" overnight. Bomas are made from natural materials such as thorn shrubs and occasionally modern fencing. Cattle are rarely raised commercially, acting as an investment and indicating wealth and social standing in a cultural sense (Jones, 2002; Mbaiwa, 2005).

Methods

Density estimates

A predator spoor survey was conducted using the available sandy road network over three years (2014-2016). 7 transects (16.2±0.65km; Fig. 1), representative of the dominant habitat types (short grass, forest and riverine) were driven at an average speed of 10km/h between October and March and June and September (wet and dry season respectively) of each year covering a total of 777.5km. Only spoor from the previous 24 hours were counted with transects never driven on consecutive days. Spoor found within 1km of each other were considered the same animal unless otherwise identified by the tracker. Large predator spoor (lion, leopard, spotted hyena, cheetah and wild dog) were identified by an expert tracker to calculate predator density using the equation: predator density= track density/100km ÷ 3.26 following Funston et al. (2010) and Winterbach et al. (2016). ANOVA's were conducted to determine differences in predator density between season and habitat type.

Prey counts were conducted separately from spoor surveys using line transect with distance sampling focusing on medium to large herbivores. Species, number of individuals, distance from the transect and GPS position were recorded. The same transects were driven at an average speed of 20km/h covering 933.4km during the same time period (as described above), counting animals encountered within 400m on either side. Herbivore density in wet and dry seasons was estimated using multiple covariate distance sampling on Distance 7.0 (Thomas et al. 2010). Herbivore species, year and habitat were included in the detection probability model as covariates. Herbivore density was estimated globally and per stratum (post-stratify by habitat). Model selection was based on the smallest Akaike Information Criteria (AIC), and variance and tested with χ^2 goodness-of-fit (Buckland et al. 1993). Chi-squared analysis was used to determine differences in the spatial (habitat) and temporal (season) distribution of herbivores.

Landscape ecological variables

The location of livestock depredation incidents is collected in the Problem Animal Control registry (PAC) since 2008, by the Department of Wildlife and National Parks (DWNP). This includes: GPS location of the cattle post attacked (GPS position of attack not recorded), date, season, number of livestock killed and predator responsible. Attacks by hyena are often not recorded, receiving no compensation, and were excluded from this analysis (Scheiss-Meier et al. 2007; Gusset et al. 2009; Loveridge et al. 2017).

Distance of each cattle post to the protected area boundary was calculated in ArcMap 10.3 (ESRI, 2011) using the global network of protected areas (Gusset et al. 2009; UNEP-WCMC 2016). Lion habitat selection has shown kill site selection to occur in densely vegetated habitats and within 2km of a water hole in semi-arid areas similar to the current study site (Valeix et al. 2010; Davidson et al. 2012; Davidson et al. 2013). Dominant habitat type surrounding each cattle post and distance to the nearest wet flood plain was calculated using previously generated habitat maps (Sianga & Fynn 2017). Average annual rainfall was collected in ArcMap 10.3 at a 30-arc second spatial resolution following Hijmans et al. (2005). Season was included as predators in semi-arid systems commonly select wild prey during their increased abundance of the wet season and livestock during the dry season (Valeix et al. 2012; Davidson et al. 2013).

Social methodology

103 questionnaires were administered to respondents evenly sampled across the five main villages of the Enclave between June and October 2014 with shortened follow up questionnaires administered to 84 respondents between June and August 2016. Questionnaires were designed following the British sociological association's ethical guidelines. Questionnaires were translated to Tswana and administered in person, at each cattle post, to participants ≥18 years of age selected by chance encounter. Respondents were asked to divulge number of livestock owned, husbandry techniques used, total depredation incidents over the preceding 12 months and household demographic data. Respondents were also asked about their awareness of personal risk to depredation relative to other areas of the Enclave.

Statistical analysis

All statistical analyses were conducted in R (R core team 2016). A repeated measure mixed effects logistic regression model was developed using the PAC registry. The dependent variable was the location of cattle posts attacked by large predators. Each incident was coded as a binary indicating whether a cattle post was attacked in each season of each year from 2008 to 2016 (excluding 2014 due to a lack of data). Independent variables were: distance of cattle post to protected area; distance to flood plains; average annual rainfall at each cattle post; dominant surrounding habitat type and diversity; surrounding livestock and human counts; surrounding herbivore and predator density and season of attack. Explanatory variables were analysed for collinearity prior to model selection. Habitat type and human density were removed as they were collinear with herbivore and livestock density, respectively. Random effects were year of attack and cattle post location. 20% of the data was randomly removed to test the predictive strength of the final model by calculating the Area Under the Curve (AUC) of the Receiver Operating Characteristics (ROC) with a threshold of 0.7 (Brooker et al. 2002).

Predator, herbivore and livestock density, and average annual rainfall were calculated within 2km of each cattle post, based on the restricted area foraging demonstrated by lions in similar systems (Valeix et al. 2010; Davidson et al. 2012). The modelling procedure was rerun using a 1km and 4km buffer to determine the influence of scale. Predator density was replaced by lion, leopard and hyena density and models rerun independently.

A general linear model was developed to determine the influence of livestock husbandry and household demographics on depredation recorded in interviews. With the exception of active herding, all husbandry techniques (boma, fire at the boma and borehole presence) were visually inspected by interviewers. Demographic variables included: age, level of education and number of people living in the household.

Results

Predator density (lion, leopard, hyena, cheetah and wild dog combined) remained stable across seasons (Dry: 2.98±0.47 predators/100 km^2, Wet: 2.61±0.62 predators/100 km^2, $F= 0.22$, df= 1 $p= 0.64$) and between habitats (Forest: 2.27±0.73 predators/100km^2, riverine: 2.1±0.68 predators/100km^2, short grass: 3.31±0.52 predators/100km^2; $F= 1.14$, df= 2 $p= 0.32$). There was, however, significantly more hyena (11.5±1.11 hyena/100km^2) than both lion (1.4±0.41 lion/100km^2, $F= 73.71$, df= 2 $p < 0.001$) and leopard (0.8±0.24 leopard/100km^2, $F= 73.71$, df= 2 $p <0.001$). Limited cheetah and wild dog observations made comparisons with these species unreliable.

Herbivore density increased significantly in the wet (39.1±6.4 herbivores/km^2) compared to the dry (13.3±2.5 herbivores/km^2) season ($\chi^2= 6.76$, df= 1, $p= 0.009$). Both the short grass

(33.8±4.5 herbivores/km^2; χ^2= 7.10, df= 1, p= 0.007) and riverine habitats (26.6±9.3 herbivores/km^2; χ^2=4.08, df= 1, p= 0.04) held significantly higher density than the forest habitat (9.9±3.5 herbivores/km^2) across all seasons. Zebra occurred at the highest density (12.75±2.42 herbivores/km^2), while kudu occurred at 0.4±0.11 herbivores/km^2 across all seasons.

Using a total of 342 livestock depredation incidents across 22 cattle posts recorded by the DWNP, the repeated measures mixed model, found distance from the protected area (Fig. 2a), herbivore density (Fig. 2c) and predator density (Fig. 2d) were significant negative predictors of livestock depredation. Depredation also significantly increased during the wet season (Fig. 2b). The interaction between protected area distance and predator density indicated that depredation increased in close proximity to the protected area even in areas with low predator density (Table 1).

Model validation returned an AUC of 0.751, indicating good performance. When considering individual predator models, as opposed an agglomeration of all predators, only lion (coefficient= -12.64±4.69, z= -2.70, p= 0.003; Fig. 3a) and leopard density (coefficient= 1.31±0.36, z= 3.59, p <0.0003; Fig. 3b) significantly influenced livestock depredation.

Scale significantly influenced the results obtained. Similar to the 2km scale model, significant variables at the 1km scale included: protected area distance, predator density, season and the interaction between predator density and distance to the protected area. At the 4km scale significant variables included: season and livestock and herbivore density (Table 1).

None of the reportedly used livestock husbandry techniques significantly influenced livestock depredation (boma: F= 0.28, df= 1, p= 0.59; fire: F= 0.44, df= 1, p= 0.51; herder: F= 0.02, df= 1, p= 0.89, borehole: F= 1.18, df= 1, p= 0.28). 60% of interview respondents considered there to be no difference in depredation with changing proximity to the protected area. 40% of respondents were unaware of seasonal differences in depredation. 81% of respondents claimed to report all depredation incidents to the DWNP but 35% claim the DWNP response time is between 24-hours and 2-weeks. 9% claim they do not investigate at all (Table 2). Hyena were reported by 35% of farmers as the most common predator in their area followed by lion (28% of respondents) and leopard (14% of respondents).

There is an average of 52 cattle per cattle post with annual average depredation of 52 livestock (range 27-103; DWNP data) across the Enclave. Interviews captured significantly more depredation (293 cattle) than DWNP data (52 animals; χ^2: 95.9, p <0.001; Fig. 4), and significantly more lion depredation (160 cattle) than DWNP data (44 animals; χ^2: 35.9, p <0.001) between 2015 and 2016. In total, the DWNP recorded 280 cattle, 54 goats and 8 donkeys (342 animals combined) depredated from 2008 to 2016. Interview respondents claim a total of 616 cattle were depredated from 2013 to 2016.

Discussion

The Chobe Enclave experiences a slightly higher rate of depredation (0.7% of available cattle in 2016) compared to Kweneng community area, Botswana (0.34% of available cattle in 2002; Scheiss-Meier et al. 2007). Depredation recorded in interviews, however, indicated that 1.5% of available cattle were depredated in 2016. For comparison, interviews indicated that 3.9% of available cattle were depredated in 2014 while 1% and 3.2% were lost to theft and disease respectively. Interview records were inflated by depredation caused by hyena, not captured by the DWNP, but lion still accounted for significantly more depredation recorded in interviews than DWNP data. It is possible that the 81% of respondents that claimed to report all depredation to the DWNP provide inaccurate reports due to their demonstrated inability to identify predators by kill site evidence (Rutina et al. 2017). Additionally, depredation was potentially artificially inflated in interviews as respondents were asked to recall all incidents that occurred a year prior. A true depiction of the severity of livestock depredation likely falls somewhere between the DWNP and interview records.

Hyena occurred at the highest density of 11.5 animals/100km^2 and were reported most common by 35% of respondents. In Ethiopian community areas, hyena can occur at 52 animals/100km^2 (Yirga et al. 2013). Interestingly, hyena were considered the most problematic predator but lion were responsible for the most depredation in interview and DWNP data. Lion occurred at the second highest density of 1.4 animals/100km^2, similar to grazing areas surrounding Khutse Game Reserve (1.21 lions/100km^2; Bauer et al. 2014) and were reported most common by 28% of respondents. Leopard occurred at the third highest density of 0.8 animals/100km^2, similar to community areas in South Africa (0.87 leopards/100km^2; Balme et al. 2010) and were reported most common by 14% of respondents. Chobe Enclave farmers, then, are aware of predator abundance relative to other predators but do not base negative associations solely on depredation (Hazzah et al. 2017). Hyena persecution is likely dependent on the interaction between density, lack of compensation and socio-cultural norms and fears. Community perceptions and predator populations need to be actively managed in the KAZA TFCA to ensure community areas do not become ecological traps (Yirga et al. 2013; Rutina et al. 2017).

Lions undergo hierarchical habitat selection (Johnson, 1980), spending most of their time in open acacia or short grass habitats (third order) while kill site selection (fourth order) occurs in dense thicket or forested habitats due to increased prey catchability (Hopcraft et al. 2005; Davidson et al. 2012; Davidson et al. 2013). This theory, coupled with the non-significant increase in predator density in the short grass habitat, may explain why increased predator density surrounding a cattle post decreased the probability of livestock depredation, contrary to Inskip & Zimmermann (2009). Leopard, however, prefer the same habitat type for third and fourth order habitat selection (Balme et al. 2007) explaining why increased lion density decreased the probability of livestock depredation but increased leopard density increased the risk of depredation. An opportunity exists for human-predator coexistence as the presence of lions does not cause the presumption of livestock depredation but the presence of livestock in areas ecologically suitable for predatory behaviour, does. Livestock husbandry systems should be strategically placed away from thicket and forested habitats to reflect this.

Husbandry systems should likewise be moved a greater distance from the protected area boundary as increased distance from the protected area decreased the probability of livestock depredation (Inskip & Zimmermann 2009; Loveridge et al. 2017). 60% of interview respondents, however, stated that livestock depredation is not influenced by proximity to the protected area. At low predator densities, the interaction between distance from the protected area and predator density indicated that the probability of depredation dramatically decreased after 8km from the protected area boundary, but remained stable at high predator densities. Providing farmers with this information and encouraging a livestock free buffer along the protected area (recommended elsewhere; Beale et al. 2013) may reduce depredation and improve protected area management.

Contrary to previous studies (Ogada et al. 2003; Hemson et al. 2009), none of the reportedly used husbandry techniques (herding, boma, fire at the boma and borehole present) significantly influenced livestock depredation in the Chobe Enclave. Bulte & Rondeau (2005) hypothesise that compensation schemes reduce farmer vigilance, limiting the impact of livestock husbandry. Fear of predators and the loss of Indigenous Ecological Knowledge (IEK) among younger generations may complimentarily reduce farmer's capacity for effective depredation mitigation, especially if compensation is expected (Packer et al. 2011; Rutina et al. 2017). It must be noted that respondents potentially inflated herding effort as interviewers were unable to confirm active herder presence. Additionally, only 6% of respondents used a "Predator Proof Boma" (PPB) supplied by the DWNP (2m high steel and wire boma). PBBs should be supplied to farmers across the Enclave with training on effective depredation mitigation (Hazzah et al. 2014; Lichtenfeld et al. 2015).

The short grass habitat and the wet season held the highest herbivore density due to increased forage quality and seasonal migrations of zebra and wildebeest from central regions of Botswana (Fynn et al 2014). The management of livestock grazing systems to conserve functional landscape heterogeneity may allow for increased herbivore populations and a concomitant reduction in livestock depredation, as increased herbivore density decreased depredation probability (Fynn et al. 2014; Suryawanshi et al. 2017). This intervention must be closely monitored ensuring increasing herbivore populations do not increase predator abundance and, ultimately, livestock depredation (Suryawanshi et al. 2017).

Despite the increased herbivore density and contrary to previous studies (Valeix et al. 2012; Davidson et al. 2013), livestock depredation increased during the wet season. One hypothesis is that lion spatial time allocation shifts seasonally, with prolonged presence in the Enclave and the protected area in the wet and dry seasons, respectively. This is supported by Makgadikgadi lions altering home range size and time allocation in response to wild herbivore migrations (Valeix et al. 2012). This would not change seasonal predator density but could increase depredation in the wet season. Only 40% of respondents were aware of this temporal change in risk, further highlighting the need for effective depredation mitigation training. It must be noted that socio-ecological variables included in the model were assumed not to change when back-cast from 2014/2016 to 2008. It is possible but unlikely (given the stable human, predator and herbivore densities) that these variables did change, potentially impacting the results of this study.

The influence of scale is vital when considering habitat selection (Davidson et al. 2012). Prey make *a priori* assessments of risk based on surrounding landscape characteristics while predators select habitat features at different scales to increase prey abundance, encounter rates and catchability (Davidson et al. 2012; Courbin et al. 2015). Predator density significantly influenced depredation at the 1km and 2km scales but not the 4km scale. This indicates that 4km is too large to influence large predator third order habitat selection. Herbivore density significantly influenced depredation at the 2km scale (in accordance with lion habitat selection and restricted area foraging; Valeix et al. 2010; Davidson et al. 2012) and the 4km scale, indicating the possibility of large predator fourth order habitat selection occurring at multiple scales. Interestingly, livestock density significantly influenced depredation at the 4km scale, indicating the possibility of different prey types influencing kill site selection at different scales. Further research is needed to test this theory.

If implemented, the research and recommendations presented here can potentially promote human carnivore coexistence in the Chobe Enclave, contributing to the conservation management of the KAZA TFCA. Farmers should be trained in appropriate livestock husbandry techniques, promoting IEK and overcoming fears of large predators to make evidence-based decisions and reduce the gap between awareness of and actual depredation risk.

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Author contributions

JD: Principal researcher, RH: Data collection, JA: Distance analysis, LR: Study design, AF: Data analysis and discussion.

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Table 1: Livestock depredation models at 1km, 2km and 4km scales, including the coefficient, standard error, z-value and p-value for all significant variables.

1 kilometre	**Coefficient**	**Standard Error**	**Z**	**P**
Protected area distance	-4.31	1.23	-3.51	0.0004
Predator density	-31.61	9.54	-3.31	0.0009
Season of attack	1.24	0.27	4.56	<0.0001
PredDens*PAdist[1]	3.47	1.06	3.27	0.001
2 kilometres				
Protected area distance	-5.15	1.41	-3.67	0.0002
Predator density	-39.88	11.42	-3.49	0.0004
Herbivore density	-0.98	0.36	-2.71	0.006
Season of attack	1.23	0.27	4.54	<0.0001
PredDens*PAdist[1]	4.35	1.21	3.59	0.0003
4 kilometres				
Herbivore density	-0.93	0.43	-2.14	0.03
Season of attack	1.24	0.27	4.57	<0.0001
Livestock density	0.4	0.15	2.28	0.02

[1]PredDens*PAdist is the interaction between predator density and distance to the protected area.

Table 2: Perception of risk based on interview results.

Perception of risk			
Question	**Percentage of respondents**		
	Closer	**Further**	**No Difference**
Where do most attacks occur in relation to the protected area?	24%	16%	60%
	Wet	**Dry**	**No Difference**
Which season do most attacks occur?	40%	20%	40%
	1 Day	**2 Weeks**	**Do not show**
How long does it take DWNP to investigate attacks?	59%	32%	9%
	Track and kill	**DWNP report**	**Nothing**
Action taken after depredation	4%	81%	15%

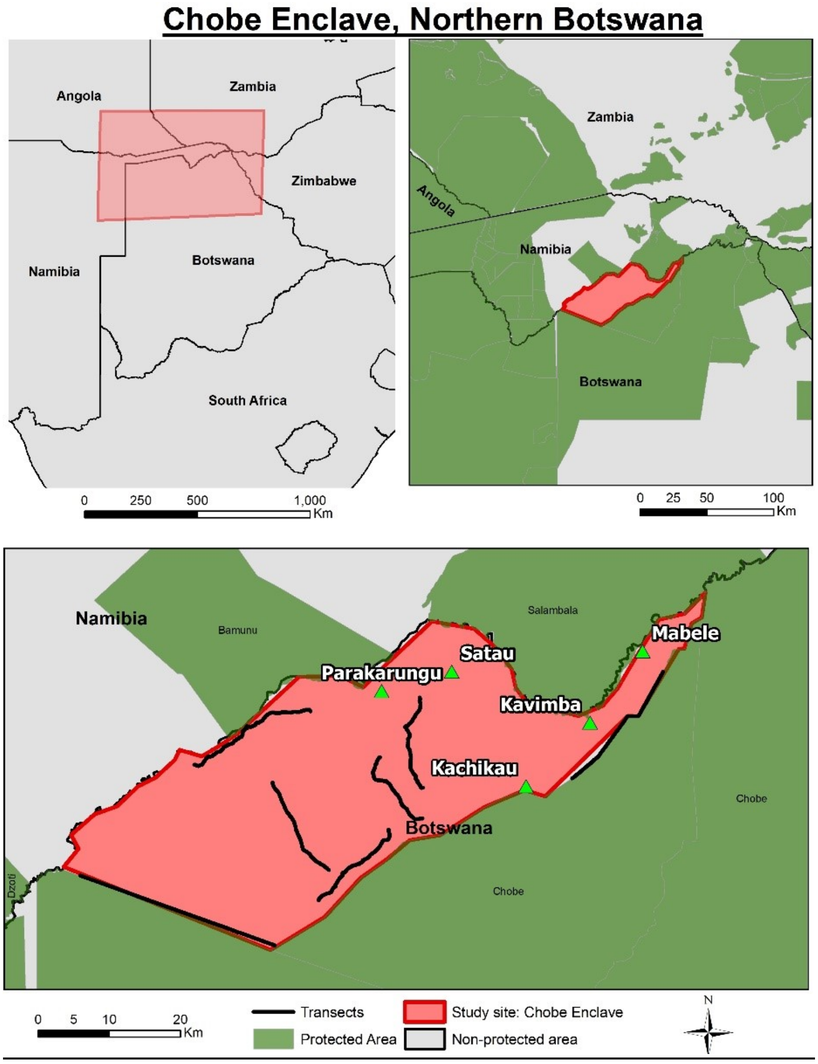
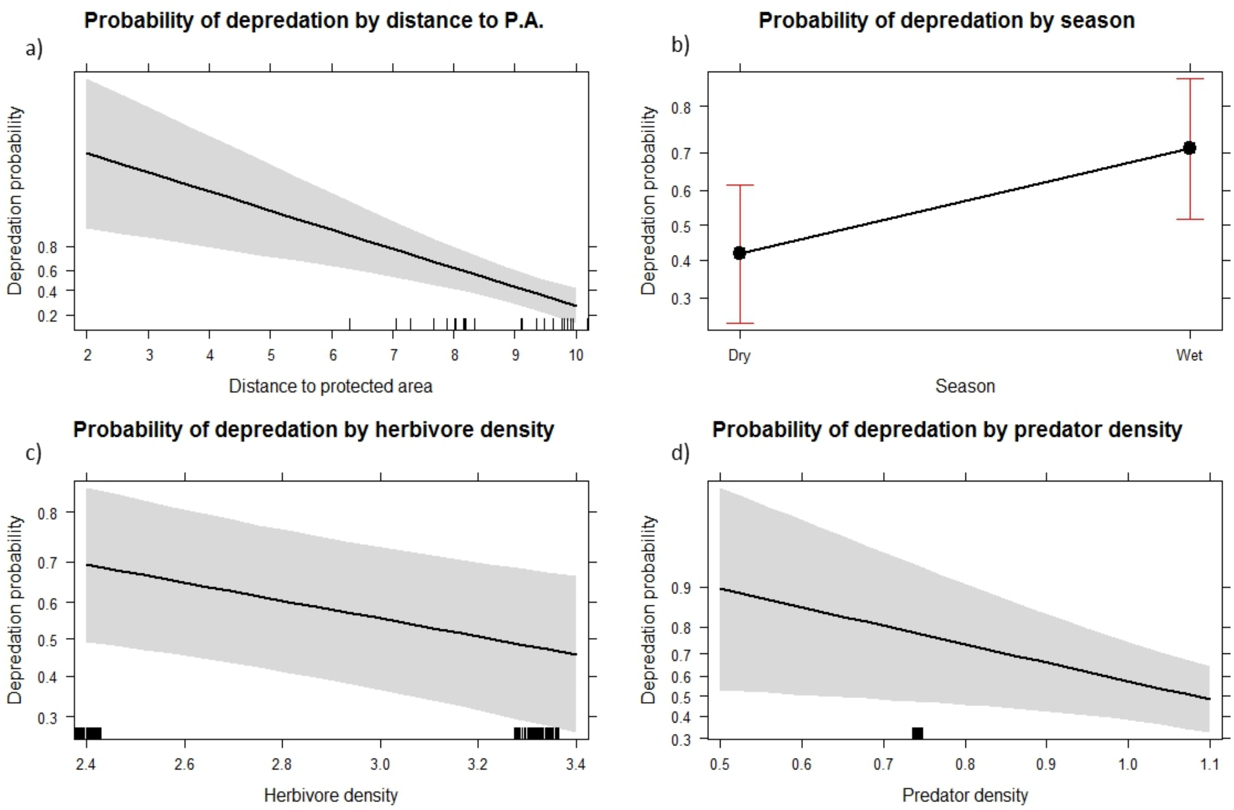


Figure 1: Location of the Chobe enclave, northern Botswana, including the five main villages, the border with Namibia and the location of transects used.



<u>Figure 2:</u> Predicted probability of livestock depredation a) with increasing distance to the protected area, b) by season c) with herbivore density and d) predator density.

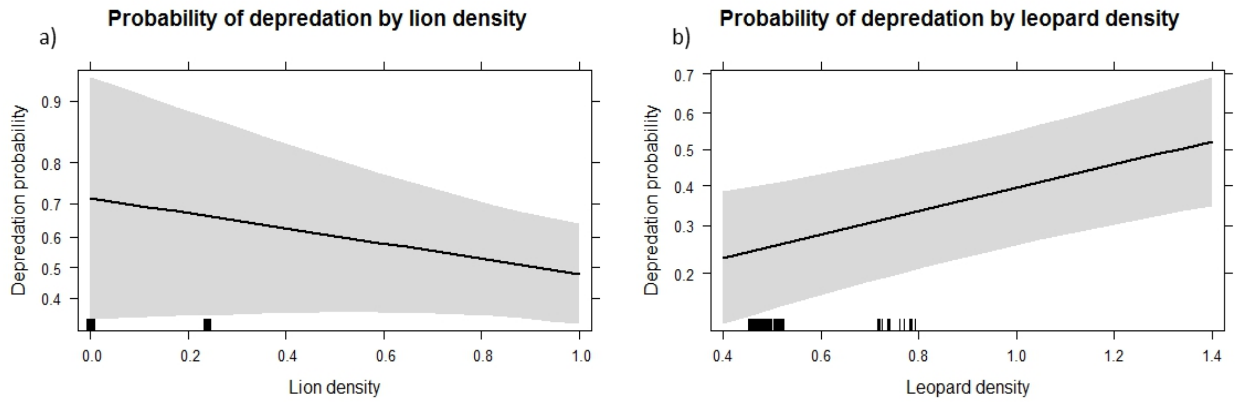


Figure 3: Predicted probability of livestock depredation as a function of a) lion density and b) leopard density.

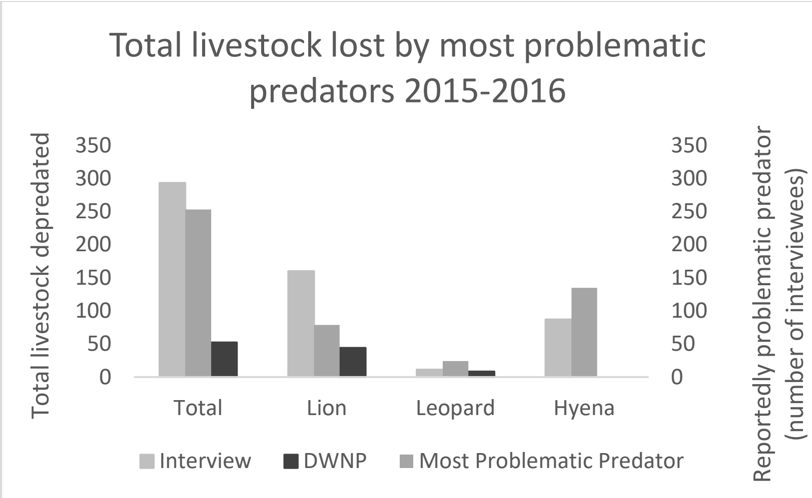


Figure 4: Total counts of cattle lost to predators as reported by the Department of Wildlife and National Parks (DWNP; black) and by farmers directly in interviews (light grey) for the years 2015 and 2016. The total counts of farmers who reported each predator as most problematic in interviews is shown in grey.