Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores

A.J. Loveridge[a],[*], L.L. Sousa[a], J. Seymour-Smith[a], J. Hunt[a], P. Coals[a], H. O'Donnell[a], P.A. Lindsey[b], R. Mandisodza-Chikerema[c], D.W. Macdonald[a]

[a] *Wildlife Conservation Research Unit, Recanati-Kaplan Centre, Oxford University, OX13 5QL, UK*
[b] *Wildlife Conservation Network, 209 Mississippi Street, San Francisco 94107, USA*
[c] *Zimbabwe Parks and Wildlife Management Authority, PO Box CY140, Causeway, Harare, Zimbabwe*

ABSTRACT

The bush-meat poaching crisis is a significant threat to biodiversity in tropical forest and savannah biomes, however its impacts on wild animal populations are often difficult to quantify across large spatial scales. Using data from 17 camera trap survey sites in southern Africa, within the Kavango-Zambezi (KAZA) Transfrontier Conservation Area, we show it is possible to assess the demographic impact of wire-snare bush-meat poaching on large carnivore populations, distribution of snaring hotspots and drivers of bush-meat poaching prevalence across this landscape. Results suggest that mortalities in snares may have significant demographic effects on lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) with evidence for population declines and extirpation of large carnivores in the most heavily affected areas. Spatial drivers of bush-meat poaching were found to be a composite of anthropogenic threat scores, environmental resource extraction, protected area size and land-use type. Incidences of snared large carnivores were more prevalent in trophy hunting areas than national parks. Across our study sites, bush-meat poaching has the potential to cause severe declines in populations of large carnivores, particularly in small isolated protected areas surrounded by areas of high human population growth, with resulting loss of regional connectivity and increasing fragmentation of the KAZA landscape.

1. Introduction

The bush-meat poaching crisis is a significant threat to biodiversity in tropical forest and savannah biomes (Lindsey et al., 2013; Ripple et al., 2016). As well as threatening vertebrate biodiversity and posing an extinction risk for some target and non-target species (Ripple et al., 2016), extraction of bush-meat can have cascading effects on ecosystem function, for example seed dispersal and forest regeneration (Effiom et al., 2013) and trophic relationships (Dirzo et al., 2014; Effiom et al., 2014; Estes et al., 2011). Additionally, handling, consumption and trade of bush-meat poses a threat to human health through spread of zoonotic disease (Smith et al., 2012; Wolfe et al., 2005). Whilst there is some evidence that bush-meat extraction of rapidly reproducing species can be sustainable (Fa et al., 2002), many species are severely affected by high levels of exploitation (Noss, 1998b; Wilkie and Carpenter, 1999).

The motivational drivers of bush-meat extraction are complex (Luiselli et al., 2019) and can vary widely between regions. Examples include rural subsistence livelihoods and food security (Cavendish, 1995), sale in urban commercial markets (Wilkie and Carpenter, 1999), and intercontinental trade as a luxury commodity (Chaber et al., 2010; Lindsey et al., 2013). Bush-meat extraction in Southern African savannahs is severely understudied (van Velden et al., 2018). Despite the potential severity of the threat, the demographic impacts on animal populations and spatial distribution of bush-meat extraction are extremely difficult to quantify, not least because traders and poachers conceal illegal activities and poaching often takes place in regions where law enforcement is weak and monitoring of biodiversity lacking.

Geographic extent and intensity of bush-meat extraction have often been assessed through indirect surveys of extraction, trade, consumption of bush-meat products (Fa et al., 2004; Martin et al., 2013; Mgawe et al., 2012) or analysis of law enforcement data (Lindsey et al., 2011; Watson et al., 2013). However, because interpretation of spatial and temporal intensity of poaching is dependent on consistent data collection effort between sites and time periods it is often difficult to compare poaching levels across studies.

The demographic impacts of bush-meat extraction on hunted populations are even more challenging to determine because this requires

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data not only on numbers of individuals killed but also an assessment of other population characteristics such as demographic groups affected and overall population size and structure. Furthermore, most illegal anthropogenic mortality is cryptic in that it is either concealed by the perpetrators or goes unrecorded (Liberg et al., 2012). Impacts on populations have often been assessed indirectly through market (Albrechtsen et al., 2007; Fa et al., 2004) or consumer surveys (Kiffner et al., 2015; Mgawe et al., 2012), surveys of rates of extraction by bush-meat hunters (Martin et al., 2013; Rist et al., 2010; Rogan et al., 2017), or, directly assessed by researchers accompanying bush-meat hunters in the field (Noss, 1998a) or detailed demographic field studies of affected species (Becker et al., 2013; Loveridge et al., 2016a). There are obvious biases inherent in using indirect methods to quantify impacts, particularly when users or hunters of bush-meat are asked to self-assess their involvement in potentially illegal activity. Detailed field studies of hunter behaviour and intensive species demographic studies that can be used to assess population impacts of poaching activities are often lacking. These limitations hamper a clear understanding of the effects of bush-meat poaching on biodiversity.

To overcome these challenges, we used systematically collected camera trap survey data across multiple sites within the Zimbabwean component of the Kavango-Zambezi Transfrontier Conservation Area (KAZA) to assess the spatial distribution and impacts of bush-meat poaching on large carnivore populations in a Southern African wooded savannah ecosystem. In order to assess the potential impact on predator populations we used data on survival rates of snared lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) to estimate the impacts on these predator populations based on snaring occurrence observed in our camera trap datasets. We model the spatial variation and predictors of bush-meat poaching activity across this multi-use landscape from detections of snared large predator species in order to evaluate its impacts and potential to affect predator biodiversity.

2. Methods

2.1. Study sites

Camera trap surveys were undertaken between 2013 and 2018 at 17 sites (Table S1, Fig. 1), across the Zimbabwean component of KAZA, which encompasses 16 protected areas (5 National Parks, 5 Safari Areas and 6 Forest Areas), making up 14% of the protected area network within KAZA (KAZA, 2019). The surveys covered all the major Zimbabwean protected areas within KAZA and one major national park (Mana Pools) immediately outside KAZA that has been shown to be functionally linked to the KAZA landscape (Cushman et al., 2018). Survey sites fell into three distinct regions: Hwange-Matetsi Protected Area Complex (11 sites), Sebungwe Region (4 sites) and the Zambezi Valley (2 sites). Eleven survey sites were situated in National Parks (NPs), and managed by Zimbabwe Parks and Wildlife Management Authority (ZPWMA), primarily used for photographic tourism. Six surveys were sited in Safari Areas (SAs), managed by ZPWMA, and Forest Areas (FAs), managed by the Forestry Commission, where trophy hunting was the primary use of wildlife resources. Annual hunting quotas were set by ZPWMA and hunted in areas leased out to private concessionaires. Human settlement was absent from all survey sites. Habitats were predominantly wooded savannah within the drier Zambezian woodland and South-west arid biotic zones (White, 1983).

2.2. Camera trap surveys

Surveys were undertaken during the dry season each year (April-early November). Each survey consisted of a mean of 42 (range 35–55) camera trap stations, with stations spaced in a predetermined grid approximately 4–5 km apart, set where possible on trails and roads to optimise the set-up for detection of large carnivores (duPreez et al., 2014). Each station consisted of paired trail cameras (Cuddeback

models 1125, 1149 and C1, Non-Typical, WI, USA; Panthera V4, Panthera, NY, USA; Stealthcam G42NG, Grand Prairie, TX, USA). Surveys were deployed for a mean of 46 ± 13 days and camera batteries and memory cards were checked regularly throughout the survey and replaced when required. Images were downloaded, catalogued and archived at the end of each survey.

Images of the three most commonly detected large carnivores (lion, spotted hyaena, leopard; *P. pardus*) were extracted from the database and animals were individually identified based on pelage patterns, whisker spots, unique scars and other physical features (Miththapala et al., 1989; Pennycuick and Rudnai, 1970). We also noted whether animals had injuries typical of having been trapped in snares (scars or open wounds on neck, body or legs sustained while struggling to escape a snare) or were carrying the remains of wire snares (either loosely or embedded in snare wounds, Fig. 2). In addition, we noted the presence of the other rarer large carnivore species: cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*). We used a Chi-Square test to compare the occurrence of snared individuals across land-use types and tested for a relationship between snaring hotspots (using hotspot bin categories, see below) and number of large carnivore species present, using a Spearman's Rank correlation.

2.3. Estimating demographic impacts of snaring

In order to assess the potential impacts of snaring, we used long term demographic records of lions radio-collared as part of a 20 year study in Hwange National Park, (see Loveridge et al., 2016a for details) to estimate the proportion of animals that survive being caught in snares and calculate survival rates of snared animals. Because the risk of dying once trapped in a snare is independent of the length of time an animal has been monitored (Heisey and Fuller, 1985) we simply calculated survival rates as the number of collared animals known to have escaped snares divided by sum of individuals escaping snares and individuals dying in snares. For spotted hyaenas we used existing estimates of snare survival calculated from long term demographic data from the Serengeti National Park, Tanzania, which provides three rates of survival of snared hyaenas a) 0.25 from survival of intensively monitored individuals; b) 0.5 from the death of two of four radio-collared study animals and c) 0.62 from all confirmed deaths in snares compared to the number of recorded snare survivors (Hofer et al., 1993). The later estimate is acknowledged by Hofer et al. (1993) as likely to be a significant overestimate of survival in that many snares deaths went unrecorded or could not be confirmed. We used the maximum and minimum estimates in our analysis.

Using the rationale that snared individuals observed in camera trap images represent the proportion of animals that have survived being snared, we used survival rates of snared animals to calculate the number of animals that could have potentially died as an estimate of the hidden impact of snare related mortality on large predator populations. As visual evidence of snares or snare injury decays relatively fast (as loose snares fall off, injuries heal or animals succumb to their injuries) our estimates represent loss of animals to the population over a relatively short time period. This time period is comparable to the time period over which populations were estimated using data generated by the surveys.

2.4. Modelling hotspots of snare poaching

The camera station location at which each snared individual was first detected was recorded, with subsequent detections of the same individual omitted from the analysis. Number of snared individuals per survey was divided by the total number of recorded individuals of each species in that survey to generate a weighted index of snare risk per survey. To examine the spatial distribution of snaring events this index was used to, a) calculate the Kernel Density Estimation (KDE) to highlight the relative probability of snaring occurrence based on where
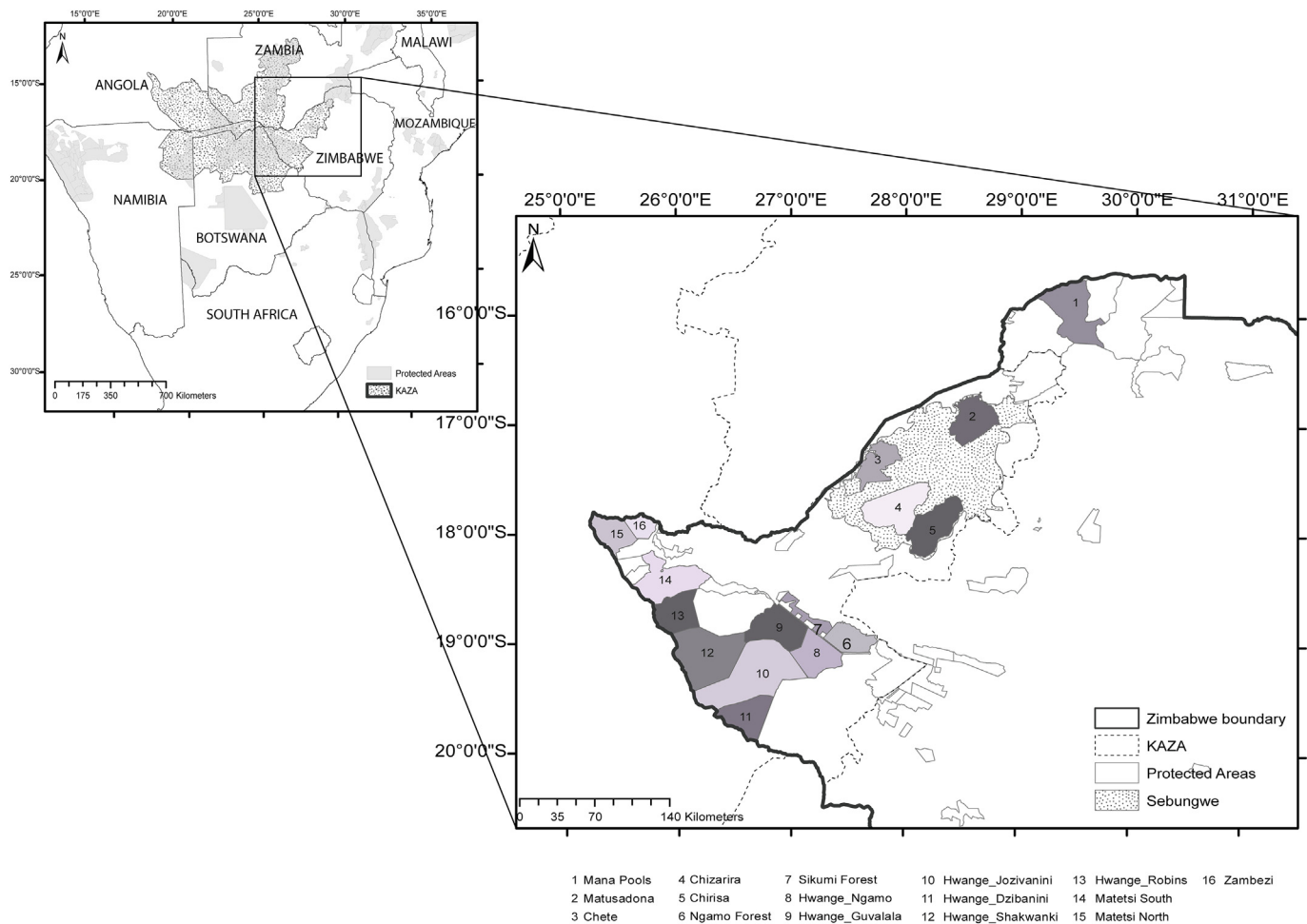
Fig. 1. Map showing location of Kavango-Zambezi (KAZA) Trans-frontier Conservation Area (top left) and location of individual survey sites within Zimbabwe.
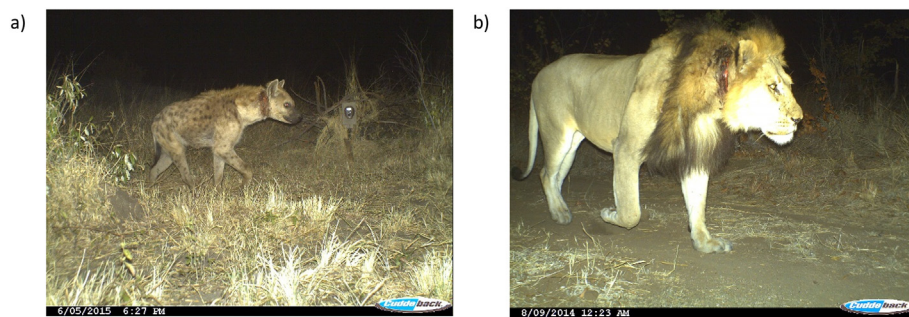
1 Mana Pools	4 Chizarira	7 Sikumi Forest	10 Hwange_Jozivanini	13 Hwange_Robins	16 Zambezi
2 Matusadona	5 Chirisa	8 Hwange_Ngamo	11 Hwange_Dzibanini	14 Matetsi South	
3 Chete	6 Ngamo Forest	9 Hwange_Guvalala	12 Hwange_Shakwanki	15 Matetsi North	

Fig. 2. Camera trap images of a) spotted hyaena and b) lion showing evidence of having been caught in a wire snares.

these individual events occurred; and b) a Hotspot Analysis using the Getis Ord GI* Algorithm with False Discovery Rate (FDR) Correction (ArcGIS 10.4.1ESRI Inc., Redlands CA, USA), accounting for multiple testing and spatial dependency, was used to detect significant clustering of snaring events, and thus patterns in spatial distribution of poaching events. The Hotspot analysis takes into account the spatial clustering of the records and reveals statistically significant high (hot) and low (cold) areas of clustering. A distance band from neighbour count (ArcGIS, $N = 8$) was calculated and twice the maximum of 20,000 m (40 km) was selected for both the KDE threshold and the Getis Ord GI* fixed band value.

To assess the predictors of snaring intensity, each survey area was assigned the maximum Gi-Bin for that site, which varies between -3 and 3 and identifies statistically significant hot and cold spots, corrected for multiple testing and spatial dependence using the False Discovery Rate (FDR) correction method. Sites with a Gi-Bin value of either $+3$ or -3 are statistically significant at the 99% confidence level; sites in the ± 2 bins are at the 95% confidence level; sites in the ± 1 bins reflect a 90% confidence level; and the clustering for cells with 0 for the Gi-Bin field are not statistically significant. These hotspot values were modelled in a linear framework to investigate factors influencing the incidence of snared animals detected as a proxy for potential risk of bush-meat poaching. Variables considered in the poaching model were Human Density (CIESEN, 2017); Human Appropriation of Net Primary productivity (HANPP), which is a measure of extraction of environmental resources by people (Imhoff et al., 2004); and Cattle Density (Gilbert et al., 2018) all extracted from a 20 km buffer surrounding each survey area; the ratio of perimeter to area of
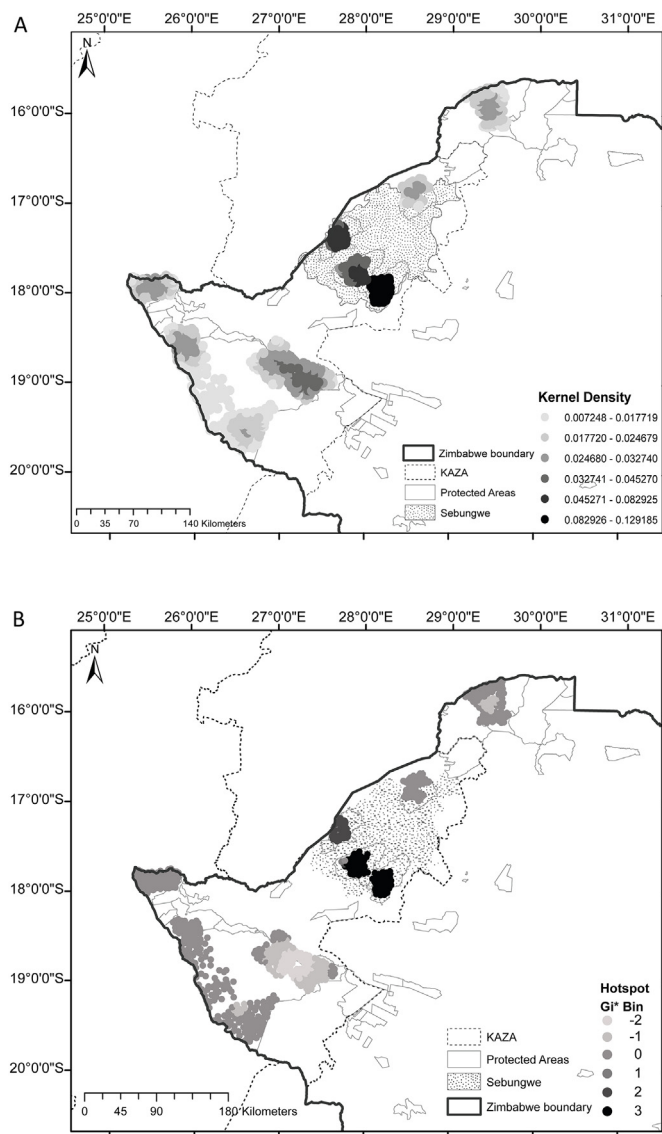
Fig. 3. Kernel density (A, low light grey-dark grey) depicts intense areas where snare records were found, whereas the Hotspot analysis (B) identifies the significant regions based on the clustering of incidents (black cold spot and grey hotspots) which are differentiated from the non-significant (no colour) at the 40 km distance band.

each survey site; total budget per km² ([Lindsey et al., 2018](#)); anthropogenic threat score (the composite of encroachment, livestock, bushmeat and commercial poaching, conflict, unsustainable trophy hunting quotas, meat hunting, mining, logging, charcoal extraction, disease), the total number of rangers per 100km² (from [Lindsey et al., 2017](#)); the weighted number of snared carnivores detected; an index of Hunting Pressure calculated as the sum of the effective hunting quotas of three carnivores and finally the percentage of each of these carnivore populations on quota (Table S3).

A model was developed using the site Gi-bin as a response variable. All covariates were standardized (mean-centred and divided by the s.d.) so that results were comparable within the model, and collinearity was checked before inclusion in the models (VIF $= 7$ and $|r| \geq 0.70$, ([Zuur et al., 2009](#)). Thereafter a global multivariate model with all possible combinations of the non-collinear variables was constructed and a stepwise algorithm was used to select the best model based on Akaike weights (wAIC). Boxplots of each variable used in the analysis in relation to the presence (significant clustering of snaring events) or absence (non-significant clustering or cold-spots) of a hotspot were plotted to

examine the effects of variables (Fig. S1).

3. Results

3.1. Prevalence of snared large carnivores

Overall, across all 17 survey sites, 92 (3.2%) of 2874 individually identified large carnivores showed evidence of having been recently caught in snares. There was noticeable spatial clustering of detections of snared animals, with three of the surveys (Chirisa, Chete SAs and Chizarira NP) having over 67% of the records. The majority of snared animals were spotted hyaenas (85 of 2037 identified individuals), with fewer snared lions detected (seven of 452 individuals). One male leopard (of a total of 386 individuals) had a scar on its neck that could not unequivocally be identified as a snare injury, therefore this record was not included in the analysis (Table S2).

Overall, large carnivores with evidence of having been snared were more likely to occur in hunting areas compared to national parks (hunting areas: 67 of 754 individuals; non-hunting areas: 26 of 2121 individuals; ($\chi^2 = 106.807$, d.f. $=1$, $p = .000$). Snared hyaenas were observed more often in hunting areas compared to national parks (63 of 534 individuals in hunting areas, 23 of 1503 individuals in national parks, ($\chi^2 = 102.722$, d.f. $=1$, p $= .000$). There were insufficient records of snared lions in hunted and non-hunted areas (fewer than five in each) to make a valid comparison. Although snared animals were most often recorded in hunting areas we acknowledge that we have no way of determining where the snares were originally set and snared animals could have been trapped in snares set in community land or other protected areas.

3.2. Predicting snare mortality based on estimates of survivorship of snared animals

Of a total of 171 lions (71 females and 100 males) collared in Hwange National Park from October 1999 to January 2019, and whose fates were subsequently monitored, 26 were caught in wire snares of which eight survived and 18 died. Of those snared, 10 were females of which only one survived, 16 were males of which five survived. However, the proportion of collared males and females caught in snares did not differ significantly ($\chi^2 = 0.118$, d.f. $= 1$, $p = .73$) nor did the proportion of snared males and females dying ($\chi^2 = 1.565$, d.f. $= 1$, $p = .21$). Based on the number that were snared and survived compared to those that died, the overall rate of a lion surviving a snare is 0.24. Therefore, if this rationale holds, then for every individual observed showing evidence of having been previously caught in a snare, roughly three individuals (using a mortality rate of 0.76) are likely to have died in-situ having been unable to escape. This suggests that for the seven lions observed with snare injuries across the 17 survey sites another 22 had probably died in snares (Table S2).

Similarly, applying the same logic to snaring survival rates of spotted hyaenas (0.25 and 0.62, [Hofer et al., 1993](#)), based on our observations of snared hyaenas, then between 52 and 255 hyaenas might have recently died undetected in snares across our surveyed sites (Table S2).

3.3. Modelling snaring hotspots

Distribution of snaring events is shown in [Fig. 3](#). Modelled maximum hotspot values for each survey were negatively correlated with the number of the five most common large predator species detected in each survey (Table S4, Spearman's rank correlation, $r_s = -0.574$, $p = .016$, $n = 17$).

Given collinearity problems, (VIF > 7), variables: Rangers/ km²; Percentage Leopard population on quota; Human Population, Weighted number of snared carnivores detected and the ratio of Periphery/Area were discarded. The initial global model included Area Size + Hunting

Table 1
Final model coefficients of hotspots of snaring events.

	Estimate	Std. error	t Value	Pr(> |t|)
(Intercept)	−4.55E-01	2.78E-01	−1.634	0.1333
Area size	9.489e-05	3.590e-05	2.643	0.02287
Hunting pressure	4.474e-01	1.993e-01	2.245	0.04629
HANPP	1.060e+00	2.372e-01	4.468	0.00095
Threat score	1.483e+00	2.034e-01	7.290	1.56e-05

Pressure + Cattle density + Budget + HANPP + Percentage of Lions on Quota + Percentage of Hyenas on Quota + Threat score. Non-significant variables were deleted using a stepwise algorithm and model improvement was inspected (wAIC) at each step. The best, final model included Area Size + Hunting Pressure + Budget + HANPP + Threat score (Table 1).

The most parsimonious model best describing hotspot occurrence included all significant variables. Given all factors were standardized, we infer that threat score is the most influential factor predicting snaring incidence. Area size, human appropriation of net primary productivity (HANPP) and Hunting Pressure were all found to be significant and of similar importance in predicting snaring hotspots. This final best performing model was evaluated against the original values (Pearson's product moment correlation 0.9169875, t = 8.6009, df = 14, p-value = 5.836e-07) and further validated by comparison with the averaged model resulting from the *dredge* function (MuMIn Package in R) of the global model, which revealed the same variables to be influential in predicting poaching hotspots (Tables S5–S7).

4. Discussion

One of the most significant threats to vertebrate biodiversity in protected areas across African forest and savannah biomes is illegal bush-meat poaching (Lindsey et al., 2017). The use of snaring incidents recorded during systematic camera trap surveys provides a robust and repeatable method for monitoring wire-snare bush-meat poaching and for evaluating levels of poaching between sites and across large spatial scales. Large carnivores, in particular, appear to be highly vulnerable to being snared as accidental bycatch (Becker et al., 2013; Hofer et al., 1993; Loveridge et al., 2016b; Van der Meer et al., 2014), likely due to being of similar size to target animals (large – medium sized herbivores), because they typically range widely and due to their tendency to be attracted to the carcasses of animals caught in other nearby snares (Knopff et al., 2010; Lindsey et al., 2013). As such, data on snaring rates of these species may provide a useful indicator to assess the prevalence of wire-snare poaching across savannah ecosystems.

In this study the majority of records of snared animals were of spotted hyaenas (92% of records, 4.1% of identified hyenas) with the remaining records being lions (1.5% of individual lions recorded). No records of smaller bodied leopards, wild-dog or cheetah were recorded. One possible reason for the high incidence of the larger bodied species in our records is that they may be more able to break out of snares to which smaller animals succumb. Similar variations in susceptibility and likelihood of survival could relate to the type of snare and material used. While this was impossible to quantify from camera trap images, in this part of Zimbabwe, snares tend to be high tensile steel or cable fencing wire or telecommunications cable (Lindsey et al., 2011; pers. obs.), from which small species have great difficulty in breaking free.

Concern about the impacts of bush-meat poaching on large carnivores often centres on prey depletion (Wolf and Ripple, 2016), however snaring may also have direct impacts on large carnivore populations. If our estimates of mortalities hold true then, for some sites, the number of the animals estimated to have recently died is close to or exceeds the number of extant individuals recorded during our surveys (Table S2), suggesting that snaring mortality may be extreme. Large carnivores tend to be relatively long lived and slow breeding with slow maturing,

altricial offspring (Crooks et al., 1998) and, as such, populations are sensitive to changes in survival rates of adult breeders (Persson et al., 2009; Van Vuuren et al., 2005). As snaring is largely unselective with potentially high mortality rates across all demographic groups including breeding age adults, and given the high mortalities we estimate, it is likely that hyaena and lion populations at the most affected sites in this study have experienced or are experiencing severe population declines. In fact, lion populations were virtually absent in the two worst affected sites (Chete and Chirisa SAs), with only a single sub-adult male detected in each site. Whilst African big cats are classified as either Vulnerable or Endangered by the IUCN and receive significant conservation attention (Macdonald et al., 2010), spotted hyaenas are considered as a species of Least Concern (Bohm and Höner, 2015). Our results suggest that, given their vulnerability to bush-meat snaring, more attention should be given to the conservation status of hyaena populations.

Our model predicting the spatial drivers of bush-meat hunting reveals the primary importance of the level of anthropogenic threat at each site, and human appropriation of environmental resources in the vicinity of surveyed protected areas. In Africa the human population is growing more rapidly than any other continent and is expected to double from 1 billion to 2.2 billion by 2050 (United Nations, 2015) resulting in increasing conversion of wild habitat to agricultural land, habitat fragmentation, resource extraction and human-wildlife conflict, resulting in declines in biodiversity and a trebling of extinction risk for large mammal species by 2060 (Tilman et al., 2017). These threats were also all associated with poor performance of protected areas in Africa (Lindsey et al., 2017). Indeed, composite anthropogenic threat scores calculated by Lindsey et al. (2017) for African protected areas appear to provide a good proxy measure for risk of bush-meat poaching in our survey sites. Based on these findings, it is unsurprising that in our study there was a strong association between human appropriation of net primary productivity and elevated levels of bush-meat poaching; a strong indicator of encroachment into wildlife habitat.

The size of protected areas and use of land for trophy hunting (using trophy quotas as a proxy for hunting pressure) were also important predictors of snaring hotspots. Small isolated protected areas are well known to be more prone to declines in biodiversity, particularly of predator species, (Brashares et al., 2001) and protected areas used for trophy hunting have been shown to be associated with higher levels of bush-meat poaching in a pan-African assessment of protected area effectiveness (Lindsey et al., 2017). The fact that trophy hunting areas were seemingly more prone to bush-meat snaring is surprising as it is generally accepted that hunting revenues and law-enforcement activities, undertaken by or supported by trophy hunters, are beneficial in reducing poaching in hunting areas (Jackson, 1996; Pasanisi, 1996). This does not appear to be the case in sites we surveyed, in that significantly more snared animals were found in trophy hunted sites compared to fully protected sites and overall trophy hunting activity (using number of large predators on hunting quotas) was shown to be an influential factor in predicting spatial intensity of snaring. There are several possible reasons for this. Firstly, despite generating revenues that are available for reinvestment into conservation, trophy hunting often realises relatively modest gross annual earnings of around $400/$km^2$ (Lindsey et al., 2018), with a fraction of that amount remaining for management. Yet annual costs of conserving habitat for lions (functioning as an umbrella species for savannah ecosystems) are in the region of $1000–2000 per km^2 (Lindsey et al., 2018). Given that hunting revenues are often expected to cover the costs of management, including law enforcement, it is likely that in many cases, except where management costs are subsidised, insufficient revenue is generated from trophy hunting for it to be financially viable and to simultaneously fund adequate investment in protecting hunting areas. Secondly, while people living around hunting areas are often cited as beneficiaries of conservation revenues, particularly from trophy hunting (Jones, 2009), these benefits may sometimes be overstated and local people can be

disempowered and marginalised by elites that dominate the hunting industry (Murombedzi, 2001) or revenues misappropriated through corruption (Leader-Williams et al., 2009; Lewis and Jackson, 2005). Disenfranchisement of local people is likely to increase incentives to engage in illegal activity such as poaching for commercial gain and to assert ownership rights (Dube, 2019). Finally, tenure leases for hunting areas are often short-term (3–5 years) which reduces incentives for concession holders to undertake long-term management and invest in protection activities (Brink et al., 2016; Lindsey et al., 2014).

The KAZA Trans-Frontier Conservation Area is a globally important stronghold for several endangered and vulnerable large carnivore species (KAZA, 2018) underlining the importance of this landscape for conservation and bringing into stark contrast the alarming results of this study. Across the surveyed area, covering almost the entirety of the protected areas in the Zimbabwean component of KAZA, predators with snares or snare injuries were detected in all but the most remote survey sites located in Hwange and Mana Pools National Parks. Analysis of snaring hotspots revealed that snaring incidents were most highly clustered in Chizarira NP and Chete and Chirisa SA in the Sebungwe Region. In these protected areas our surveys detected a high proportion of individually identified predators with evidence of having been caught in snares (between 26 and 44% of hyaenas across all three sites, 13% of lions in Chizarira). In addition, all four surveyed protected areas within the Sebungwe region (Matusadona and Chizarira NPs and Chete and Chirisa SAs) showed clear signs of impoverishment of the large predator guild. Cheetah were absent from three of these protected areas and functionally extirpated in Matusadona NP (only two males remaining, Van der Meer et al. in press). Lions occurred in low numbers in Matusadona and Chizarira NPs and were functionally extirpated in Chete and Chirisa SAs (only one sub-adult male detected in each). Wild dogs were not detected in any of these protected areas. Only spotted hyaenas and leopards were present in all four areas.

The vulnerability of protected areas in the Sebungwe region stems from several salient factors, all of which are predictors of high snaring levels in our current analysis: expanding human settlement, population growth, immigration of settlers, encroachment into wildlife habitat and increasing livestock production. Since eradication of the Trypanosomiasis vector the tsetse fly (*Glossina* spp) in the 1970s (Cumming and Lynam, 1997; Scudder, 1982), clearance of former wild habitat for settlement and farming occurred at rates of around 8% per annum in the 1980s and 1990s (Cumming and Lynam, 1997), with previously wild land adjacent to Chirisa SA and Chizarira NP and between Chizarira NP and Chete SA being most heavily settled.

Poor law enforcement and uncontrolled illegal hunting, both factors known to lead to declining mammalian biodiversity (Craigie et al., 2010; Hegerl et al., 2015), have been previously highlighted in the Sebungwe Region. Elephant populations have declined catastrophically since the late 1990s, almost certainly due to poaching, with concomitant increases in the number of observed incursions into protected areas (Chase et al., 2016; Dunham, 2008). Our study suggests that ecologically important apex predators may be faring equally badly.

The Sebungwe region is the second most important area of connected core habitat and the second highest ranked connectivity corridor for lion dispersal movements within KAZA (Cushman et al., 2018) and is likely to be similarly important for other wide-ranging savannah species. Threats such as bush-meat poaching severely undermine the importance of this area as a wildlife habitat corridor and could possibly result in irreversible fragmentation of the KAZA landscape and the permanent isolation of the protected areas of Hwange-Okavango system from those in the Zambezi Valley. As both these protected area complexes are critical strongholds for large predators and many other savannah species, isolation could have significant implications for future population dynamics and gene flow. The promise of integrated landscape conservation could potentially be undermined by poor law enforcement and declining biodiversity in the most vulnerable parts of KAZA. This study goes some way to quantifying this threat and highlights the parts of the landscape most in need of urgent protection.

CRediT authorship contribution statement

A.J. Loveridge: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition.**L.L. Sousa:**Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing.**J. Seymour-Smith:**Investigation, Data curation, Writing - review & editing.**J. Hunt:**Data curation, Writing - review & editing.**P. Coals:**Data curation, Writing - review & editing.**H. O'Donnell:**Data curation, Writing - review & editing.**P.A. Lindsey:**Data curation, Writing - review & editing.**R. Mandisodza-Chikerema:**Writing - review & editing.**D.W. Macdonald:**Writing - review & editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108504.

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