

Robust mapping of human-wildlife conflict: controlling for livestock distribution in carnivore depredation models

Timothy Kuiper^{1,2,3}, Andrew J. Loveridge^{1,3}, David W. Macdonald¹

¹*Wildlife Conservation Research Unit, Department of Zoology, The Recanati-Kaplan Centre, University of Oxford, Tubney House, Tubney, Oxon OX13 5QL.*

²*Interdisciplinary Centre for Conservation Science, Department of Zoology, University of Oxford, 11a Mansfield road, Oxford, OX1 3SZ*

³ *Authors contributed equally to this paper; *Corresponding author: timothykuiper@gmail.com*

Short title: Quantifying risk of livestock depredation

Robust mapping of human-wildlife conflict: controlling for livestock distribution in carnivore depredation models

Abstract

Shifting human-wildlife conflict towards coexistence requires a robust understanding of where conflict happens and why. Spatial models of livestock depredation by wild predators commonly identify depredation hotspots in areas where livestock are most abundant (e.g. nearer villages or pasture). This may reflect underlying livestock distribution, rather than imply these areas are inherently risky for livestock. This limits the predictive power of these models and their usefulness for conflict mitigation and wild carnivore conservation. Here we build spatial models of both cattle depredation (530 attacks mostly by lions and hyenas; 2009-2013), and cattle presence (14 GPS-collared herds; 2010-2012) near Hwange National Park, Zimbabwe. We use Bayes' theorem to combine the cattle depredation and presence models to quantify risk as the conditional probability of depredation given livestock presence. Our raw depredation models predicted higher depredation rates where cattle presence was more likely (near villages and in more open habitats). By contrast, our risk model predicted higher risk further from human activity and in more dense vegetation (where depredation rates were higher than expected given the low probability of cattle presence). Risk also increased sharply towards protected areas (core carnivore habitat). Our formulation of risk captures high risk areas as those where livestock are most accessible (i.e. vulnerable) to predators as opposed to simply where they are most available (as in much previous work). We make recommendations for livestock protection and wild carnivore conservation based on our quantification of risk, such as where to avoid herding livestock and which areas to prioritise for livestock protection. Our approach may be profitably applied to guide safer livestock grazing or herding in other contexts where depredation and livestock movement data are available. We hope that the concepts and methods that we develop here will help advance the future study and mitigation of human-wildlife conflict more generally.

Key words: Predation risk, human-wildlife conflict, coexistence, livestock depredation, spatial predictive modelling, mapping, *Panthera leo*, human-wildlife interactions, spatial depredation risk model.

53 Introduction

54 Large terrestrial carnivores regulate ecological processes as apex predators (Ripple et al. 2014),
55 generate economic value through ecotourism or hunting (Lindsey et al. 2005; Treves 2009), and
56 capture the public imagination as charismatic conservation flagships (Macdonald et al. 2015).
57 Nevertheless, these same species are amongst the most vulnerable to extinction, owing largely to
58 habitat loss and conflict with humans over livestock (Ripple et al. 2014). Their large size, carnivorous
59 diet and wide-ranging behaviour make these species particularly prone to conflict (Pooley et al.
60 2017). There is a growing literature attempting to understand the ecological and sociological aspects
61 of human-wildlife conflict and human-carnivore interactions (Rust & Marker 2014; Van Eeden et al.
62 2017; Treves & Santiago-Ávila 2020). Such research is essential to the development of effective
63 solutions for both people and predators. Many recent studies in this field focus on understanding
64 where in the landscape predators attack livestock and why (spatial depredation risk models). The aim
65 is to predict hotspots of livestock depredation by relating depredation sites to
66 environmental/landscape attributes, using correlative statistical models (Abade et al. 2014; Miller et
67 al. 2015a; Naha et al. 2020; McInturff et al. 2021). The conservation relevance of predation risk
68 modelling is clear: if one can predict where depredation is likely to occur and why, then mitigation
69 strategies can be designed to minimize lethal encounters between predators and livestock (Miller &
70 Schmitz 2019). This in turn will result in a reduction in retaliatory killings of wild carnivores (Merson
71 et al. 2019).

72

73 A limitation of previous work on the spatial risk of livestock depredation is the lack of methods to
74 account for livestock distribution. Models may therefore simply suggest that depredation is most
75 likely to happen where livestock are present (Treves et al. 2011). Beattie et al. (2020), for example,
76 found lion depredation of livestock to be higher in areas of higher vegetation greenness, closer to
77 water, and closer to livestock enclosures (all of which reflect livestock distribution). Yet these areas
78 may experience high depredation simply because of livestock abundance not because they are
79 inherently risky. While there a significant body of literature quantifying the risk of predation faced by
80 prey (see Gaynor et al. 2019 for a recent review), relatively few studies attempt to account for prey
81 distribution. We have not found any studies on livestock depredation that explicitly account for the
82 confounding effects of livestock distribution, but pioneering work in North America on the spatial
83 patterns of predator-prey interactions have demonstrated the value of accounting for prey

distribution. In a study of wolf predation on elk in Yellowstone National Park, for example, Kauffman et al. (2007) included elk distribution (based on modelled GPS data) as a factor in their models of the distribution of kill sites as a function of both wolf and elk distribution (based on GPS data). This improved model fit significantly, and allowed the researchers to identify the true effect of landscape variables on the risk of elk depredation (i.e. effects remaining after elk distribution was accounted for), thus identifying clear prey refugia and hunting grounds (as opposed to simply hotspots of wolf or elk abundance).

Models predicting where livestock depredation occurs on the basis of past depredation sites will to a large extent reflect where carnivores and livestock are most likely to encounter each other, such as nearer villages (higher probability of livestock presence) and closer to protected areas (PAs) or forests (higher probability of carnivore presence). Such models are useful in so far as they predict areas where future attacks are most likely to occur (Karanth et al. 2012; Abade et al. 2014). The explanatory power of such models, however, may be limited because they do not capture the probability of depredation *given* livestock presence in a particular area (which we define here as inherent risk of depredation). For example, increasing levels of depredation closer to villages or in grazing pasture (as observed for wolf depredation in Wisconsin; Treves et al. 2011), may simply reflect that livestock predominantly use these areas and does not suggest that it is inherently risky for livestock to roam into them. While recorded depredation levels may be lower in areas further from villages or away from grazing pastures, these areas may nevertheless be riskier for livestock when one considers that livestock are less likely to be present in these areas (i.e. rates of depredation may actually be high when accounting for the low probability of livestock presence). Indeed, areas further from villages may in fact be more risky for livestock as predators tend to avoid areas close to human activity due to risks to their own survival (Miller et al. 2015a).

The way risk of future depredation is conceived and formulated has clear implications for reducing livestock losses and conserving carnivores. The usefulness of our concept of inherent risk lies in its value for guiding livestock herding patterns by identifying areas that are more or less risky to herd livestock into. Models that use raw depredation data do not distinguish between high and low risk areas in the same way. This does not mean that such models are not useful. Even though they are likely to predict future hotspots of depredation in areas or villages where livestock are most abundant, such areas are still good targets for livestock protection interventions because absolute

levels of livestock loss may be high (even though relative risk may be low). These areas/villages of highest absolute livestock losses may also be a good focus for carnivore conservation interventions, because retaliation by livestock owners is often proportional to loss (Ikanda & Packer 2008).

In this study we account for this confounding effect of variations in the probability of livestock presence by weighting the predictions of models on the distribution of depredation incidents by model predictions of the probability of livestock presence. We first build a traditional spatial depredation model using a five-year data set of 530 incidents in which cattle were attacked by large carnivores adjacent to Hwange National Park (Hwange NP), Zimbabwe. Next, we use data from 14 GPS-collared cows, representing 14 separate herds, across our study area to create a spatial model of cattle presence. Finally, we combine the cattle depredation and presence models to introduce a model of spatial depredation risk that quantifies the conditional probability of depredation given livestock presence. By accounting for livestock presence, our risk model more directly represents variations in the risk of livestock encountering predators (and hence the true risk of depredation), compared to previous studies (e.g. those reviewed by Miller, 2015). In the discussion, we explore how such a concept of risk might guide livestock husbandry policy to reduce losses to predators, in turn leading to reduced retaliatory killing of wild carnivores. More generally, our approach and findings are relevant to the broader science and management of human-wildlife conflict and coexistence going forwards, through better prediction of sites of negative interactions (Treves & Santiago-Ávila 2020).

Materials and Methods

Study area

Our study encompassed two rural community lands adjacent to Hwange NP: Tsholotsho and Mabale (Fig. 1). Both are characterized by subsistence agriculture and livestock husbandry. Rainfall is low (annual average of 600mm; inter-annual CV of 25%) with most falling between November and March. In Tsholotsho, we recorded a density of 7.03 rural homesteads per km², while in Mabale the density was 23.30 homesteads per km² (Fig. 1). Cattle in our study area are kept in protective enclosures at night, from which they are herded each morning to find suitable grazing and water. Grazing pasture is often far from villages, and cattle are not always accompanied by herders (Kuiper et al. 2015).

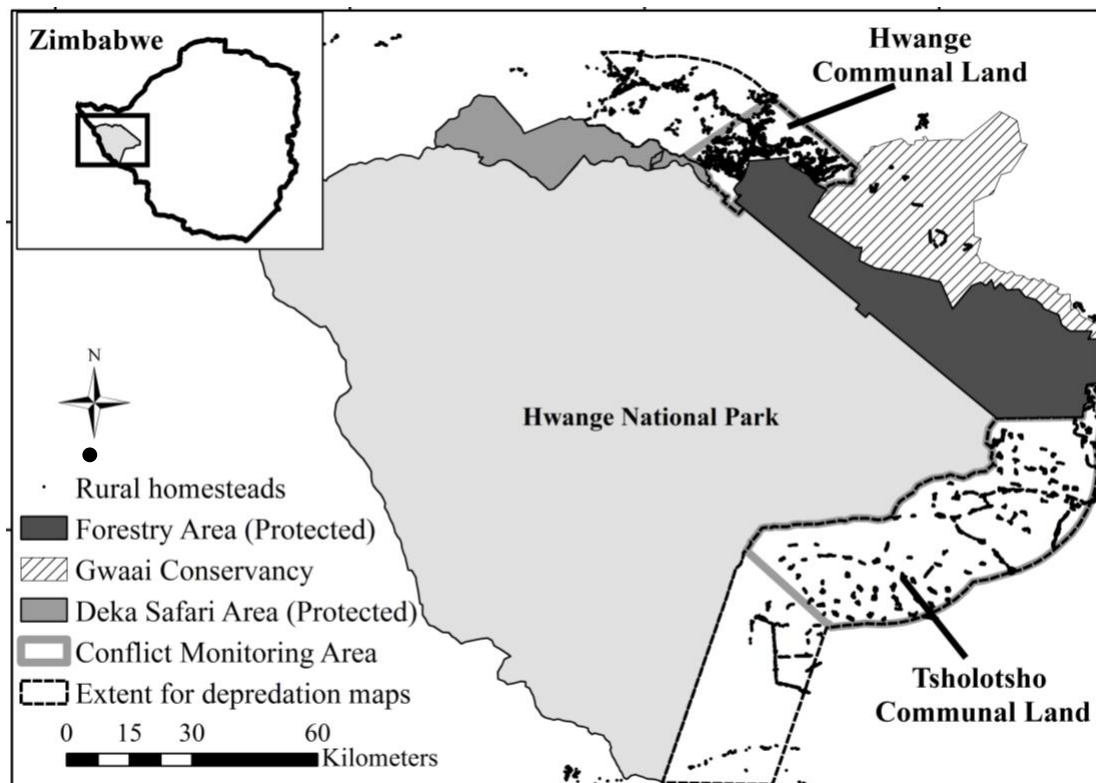


Figure 1. The study area, showing the location of the Tsholotsho and Mabale Communal Lands alongside Hwange National Park, Zimbabwe. The conflict monitoring area (25km buffer of Hwange NP), over which depredation incidents were recorded, is shown. Black dots represent rural homesteads.

Depredation and cattle movement data

Five years (Jan 2009 to Dec 2013) of comprehensive monitoring of livestock (cattle, donkeys, and others) depredation by large carnivores (lion, spotted hyena, leopard and others) was conducted in Tsholotsho and Mabale (Fig. 1). Here we focus on cattle depredation (we have accurate movement data for cattle but not other livestock species). We define a depredation incident as an event in which a cow was killed or injured by any large carnivore species. Records included, amongst others, information on the predator and livestock species involved (where possible), and the GPS location. Full details of depredation monitoring and data are provided in Loveridge *et al.* (2017). We used data from 14 adult cows fitted with GPS collars (African Wildlife Tracking, Pretoria, South Africa) to model cattle space use in our study area. Of the 56 villages across Tsholotsho regularly surveyed for human-carnivore conflict data, 14 were randomly selected and one cow collared in each. Each cow was part of a herd averaging 26 individuals in size, and collars were fitted for 15 to 20 months (2010-2012), recording fixes hourly (full details in Kuiper *et al.* 2015).

Risk modelling approach

We produced separate models to quantify spatial patterns in (a) the relative probability of cattle depredation (based on attack locations), and (b) the relative probability of cattle presence (based on GPS-collar data) (Fig. 2). We compared the predictions of these models to assess the degree to which hotspots of depredation are influenced by underlying cattle distribution. By keeping the models separate, rather than including cattle distribution as a predictor or process in the depredation model, we are better able to independently understand the factors influencing cattle distribution and hence the mechanisms behind its effects on depredation. Finally, we use Bayes' theorem to weight the predictions of cattle depredation by the predictions of cattle distribution to produce a spatial map of the risk of depredation, defined as the conditional probability given livestock presence (Fig. 2).

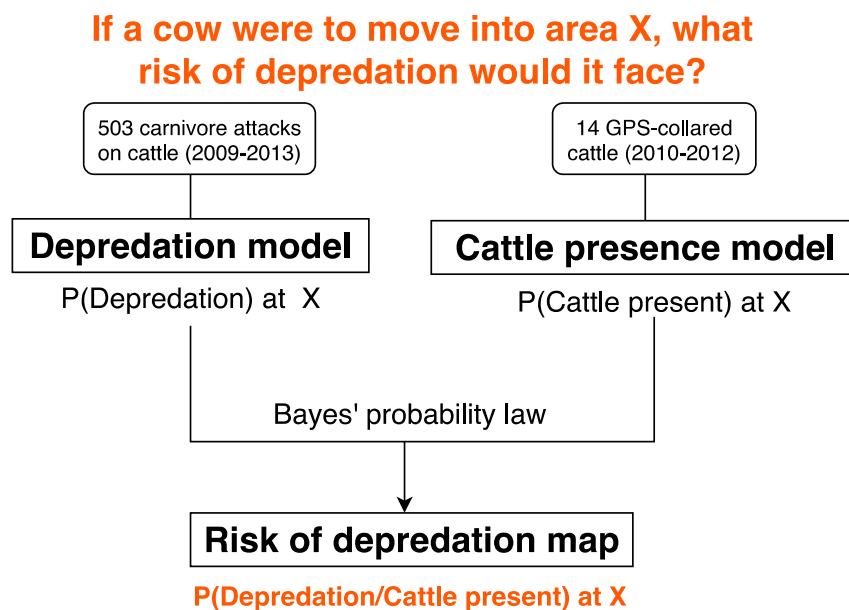


Figure 2. A schematic showing our risk modelling approach to quantify risk more intuitively as the probability of attack given livestock movement into an area. We combine depredation and cattle distribution models via Bayes' probability theorem to map risk spatially as the conditional probability of depredation given cattle presence.

Spatial patterns of cattle depredation

We used a resource selection function, based on a logistic regression, to model the relative probability of cattle depredation across our study area as a function of landscape characteristics

(Manly et al. 2002). The binary response variable was '1' for depredation sites ($n = 530$) and '0' for an equal number of 'available' sites (Miller 2015). Availability sites were randomly generated within the monitoring area, with the condition that they could not fall within a 500m radius of depredation sites (to avoid overlap with depredation sites; we considered 500m an appropriate scale at which to define a site as depredated). We used the GIS ArcMap 10.2 (ESRI 2013) to extract: (1) the percentage woody cover, (2) human density, and the distance to the closest (3) homestead, (4) PA boundary, and (5) water source (pumped waterholes as well as seasonal pans) for use as predictor variables. Previous work in our study area suggests woody cover may provide concealment for ambush predators (Loveridge et al. 2017a). Human density and distance to homestead were included because they are related to livestock availability and may also represent risk of anthropogenic mortality for carnivores (Loveridge et al. 2017b). Carnivores are largely resident within the PAs at our site, hence the inclusion of distance to PA boundary. Finally, water distribution affect livestock distribution and herding patterns in our study area. Woody cover was extracted using the MOD44B vegetation continuous fields MODIS imagery (Hansen et al. 2002). We used the number of individual homestead huts (mapped from satellite imagery) in a 2km buffer of each location as a proxy for human density. We found no evidence for multicollinearity among predictor variables, with all predictors having variance inflation factor scores below 3 (Dormann et al. 2012).

Our sample did not contain depredation and absence sites in proportion to their true presence in the landscape, because not all possible absence sites were included in the sample. Thus our sampling design does not provide true probabilities (Keating & Cherry 2004) and we instead use the term *relative probability* of depredation (Pearce & Boyce, 2006).

Model selection was performed using Akaike Information Criterion (Burnham & Anderson 2002), using a dredge of all combinations of the predictors (32 models). We did not include any interaction terms as none were considered sufficiently plausible. Clearly dominant ($w_i > 0.90$) models were used, otherwise we used model averaging to determine model coefficients. We converted model coefficients to odds ratios (ORs) to represent effect sizes. Statistical analyses were performed in R 3.0.2 (R Development Core Team 2013). Following Morris et al. (2016), the coefficients of the dominant depredation model were used in the exponential RSF equation as input in the Raster Calculator tool in ArcMap 10.2.0 (ESRI 2013) to map the relative probability of cattle depredation (PCD) across our study area. Due to large effect sizes, the predicted RSF scores were strongly right skewed and the resulting map was not visually meaningful. To allow for better interpretation, we

divided the exponent of the RSF equation by 10 and transformed the RSF scores to range between 0 (area of very low probability of depredation) and 1 (area of very high probability of depredation) using a linear stretch (Johnson, Seip & Boyce 2004). This normalised the RSF scores while still preserving a relative scale (as in Loveridge et al. 2017b). Finally, the model was validated using tests for explanatory power, predictive accuracy (k -fold cross-validation) and fit (r^2) (details in Online Supporting Information).

Spatial patterns of cattle presence

We used a Generalized Linear Mixed Model (GLMM) with a binomial error structure and logit link function to model the relative probability of cattle presence (PCP) in our study area from cattle GPS data (Gillies et al. 2006). We randomly sampled 10% of all GPS locations for inclusion in the RSF model as ‘used’ locations. An equal number of ‘available’ locations were randomly generated within the cattle home-ranges (Chetkiewicz & Boyce 2009). Home ranges were determined using 100% Minimum Convex Polygons (MCPs) (Gillies et al. 2006). Cow identity was entered as a random effect to deal with non-independence of GPS locations from each cow, and to account for individual-level differences in habitat selection (Gillies et al. 2006). The same predictors used in the cattle depredation model were used as fixed effects in the cattle presence GLMM, except for distance to the closest PA boundary. The home villages of the collared cattle were located at varying distances from the PA boundaries and, since a cow’s movements are constrained by the position of its home village, inclusion of distance to PA boundary would be tenuous. The R function *glmer* in the package *lme4* was used to develop the GLMMs (Bates et al. 2013). We used the same model selection, mapping and validation procedures used for the cattle depredation model (see Online Supporting Information). We found no evidence for multicollinearity among predictor variables, with all predictors having variance inflation factor scores below 3 (Dormann et al. 2012).

Quantifying spatial risk

We quantified the spatial risk of cattle depredation using a proxy for the conditional probability of cattle depredation at a location given cattle presence at that location (as discussed above our data does not yield true probabilities). This was to answer the question: what risk of depredation would a cow face *given* it were to move into a certain area? (Fig. 2). We relied on Bayes’ theorem:

$$P(A|B) = P(B|A) \times \frac{P(A)}{P(B)}$$

Defining event A as cattle depredation and event B as cattle presence, we have:

$$P(\text{depredation}|\text{cattle present}) = P(\text{cattle present}|\text{depredation}) \times \frac{P(\text{depredation})}{P(\text{cattle present})}$$

Cow presence is certain at depredation sites, so we have $P(\text{cattle present}|\text{dep}) = 1$ and:

$$P(\text{depredation}|\text{cattle present}) = \frac{P(\text{depredation})}{P(\text{cattle present})}$$

Then, using the relative probability of cattle depredation (PCD) and the relative probability of cattle presence (PCP) as estimates for $P(\text{depredation})$ and $P(\text{cattle present})$, respectively, we calculated R_X , the risk of depredation at location X:

$$R_X = \frac{PCD_X}{PCO_X}$$

Variation in risk across space

Using the R_X equation above, we generated a map of risk of depredation across the study area by dividing the PCD raster map by the PCP raster map using the Raster Calculator tool in ArcMap 10.2.0 (ESRI 2013). Thus, in two areas with the same pixel value for the relative probability of depredation but different values for the relative probability of cattle presence, the area with the lower value for cattle presence has the higher risk value. Our concept of risk is similar to that of Loveridge *et al.* (2017b) who weighted models on lion mortality risk by data on lion occurrence, and to the risk of wild prey depredation in models where prey distribution is accounted for (e.g. Kauffman et al. 2007). Risk values were rescaled to vary between 0 and 1 using a linear stretch and then categorized into eight categories using classification by quantiles to aid interpretation. To gain a qualitative understanding of how risk changed with each predictor (distance to homestead, woody cover, etc.), 1000 points were randomly generated within the area over which the risk map was generated and then predictor values as well as the risk pixel value were extracted to these points. Relationships between each predictor and risk were then assessed using scatter plots. We stress that risk scores are on a relative ordinal scale, and do not represent absolute values. The absolute value for change in risk between categories is also not constant. This is because the cattle depredation and presence maps involved linear stretches. Thus, patterns in the generated risk map, and the relationship

between each predictor and risk, should be regarded as giving a strong but relative indication of patterns of risk in space.

Results

Spatial patterns of cattle presence and depredation

A total of 686 incidents of cattle depredation by large carnivores were recorded between 2009 and 2013, of which 530 had accurate location information. Most attacks were by lion (51%) and hyena (45%) and involved at least one cow being killed (more details in Loveridge *et al.* 2017a). All predictors were retained in the dominant cattle depredation model (Table 1; see Table S2 for model coefficients). The relative probability of cattle depredation decreased with increasing distance from the closest homestead, PA boundary, and water source, and decreased with increasing human density and woody cover (Figs 3 and 4). The relative odds of depredation reduced by 38% (odds ratio [OR]: 0.62) with each 1km increase in distance to homestead and by 18% (OR: 0.82) for each 1km increase in the distance to the PA boundaries (Fig. 3).

Table 1. Model selection statistics for the cattle depredation (logistic regression) and cattle presence (GLMM) models. DH: distance to the closest homestead (km), DP: distance to a PA (km) boundary, DW: distance to the closest water source (km), HD: human density (no. of huts within a 2km buffer), and W: percentage woody cover. Models are ranked according to their Akaike weights (w_i). The five highest-ranking models are shown.

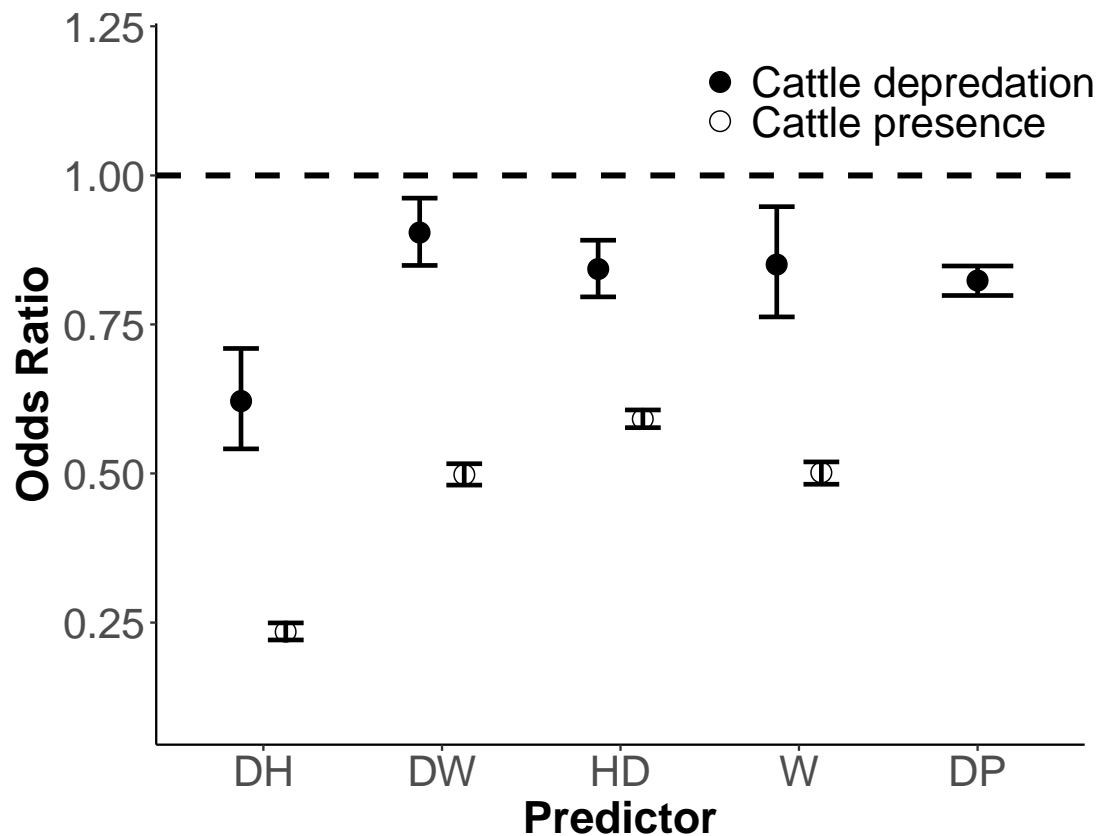
Predictors	K	AIC	Δ AIC	w_i
Cattle depredation model				
DH+DP+DW+HD+W	6	1125.25	0.00	0.95
DH+DP+DW+HD	5	1131.86	6.61	0.04
DH+DP+HD+W	5	1133.55	8.30	0.02
DH+DP+HD	4	1141.71	16.46	0.00
DH+DP+DW+W	5	1159.85	34.60	0.00
Cattle presence model				

DH+DW+HD+W	6	30025.88	0	1
DH+DW+HD	5	31386.35	1360.473	0
DH+DW+W	5	31601.57	1575.695	0
DH+HD+W	5	31728.39	1702.516	0
DW+HD+W	5	32462.79	2436.912	0

292

293 The dominant cattle presence model retained all four predictors (Table 1; see Table S2 for model
 294 coefficients). Cattle presence showed a very similar relationship with each predictor as cattle
 295 depredation. The locations where cattle were most likely to be present (closer to homesteads and
 296 water and in areas of lower woody cover and lower human density) were also the areas where
 297 depredation was more likely (Figs 3 and 4). However, each predictor had a substantially stronger
 298 effect on the relative probability of cattle presence than the relative probability of cattle depredation
 299 (lower odd ratios in Fig. 3 indicate stronger effect sizes, as do steeper curves in Fig. 4). Cattle presence
 300 hotspots were predicted around homesteads (Fig. 5A), while areas close to homesteads, particularly
 301 those near the PA boundaries, were hotspots of cattle depredation (Fig. 5B). The cattle depredation
 302 and presence models both demonstrated high predictive accuracy and explained a reasonable
 303 proportion of the spatial variation in cattle depredation/presence (Table S1, Online Supporting
 304 Information).

305



306

307 Figure 3. Odds ratios (ORs), with 95% confidence intervals, for the dominant cattle depredation and
 308 presence models. OR < 1 show probability of depredation/presence decreasing with the predictor.
 309 DH: distance to the closest homestead (km), DW: distance to the closest water source (km), HD:
 310 human density (no. of huts within 2km buffer), W: percentage woody cover, and DP: distance to the
 311 closest PA. Increments of 50 huts for human density and 5% for percentage woody cover were used
 312 in ORs for more meaningful interpretation. Distance to PA was not considered in the cattle presence
 313 model (see Methods)

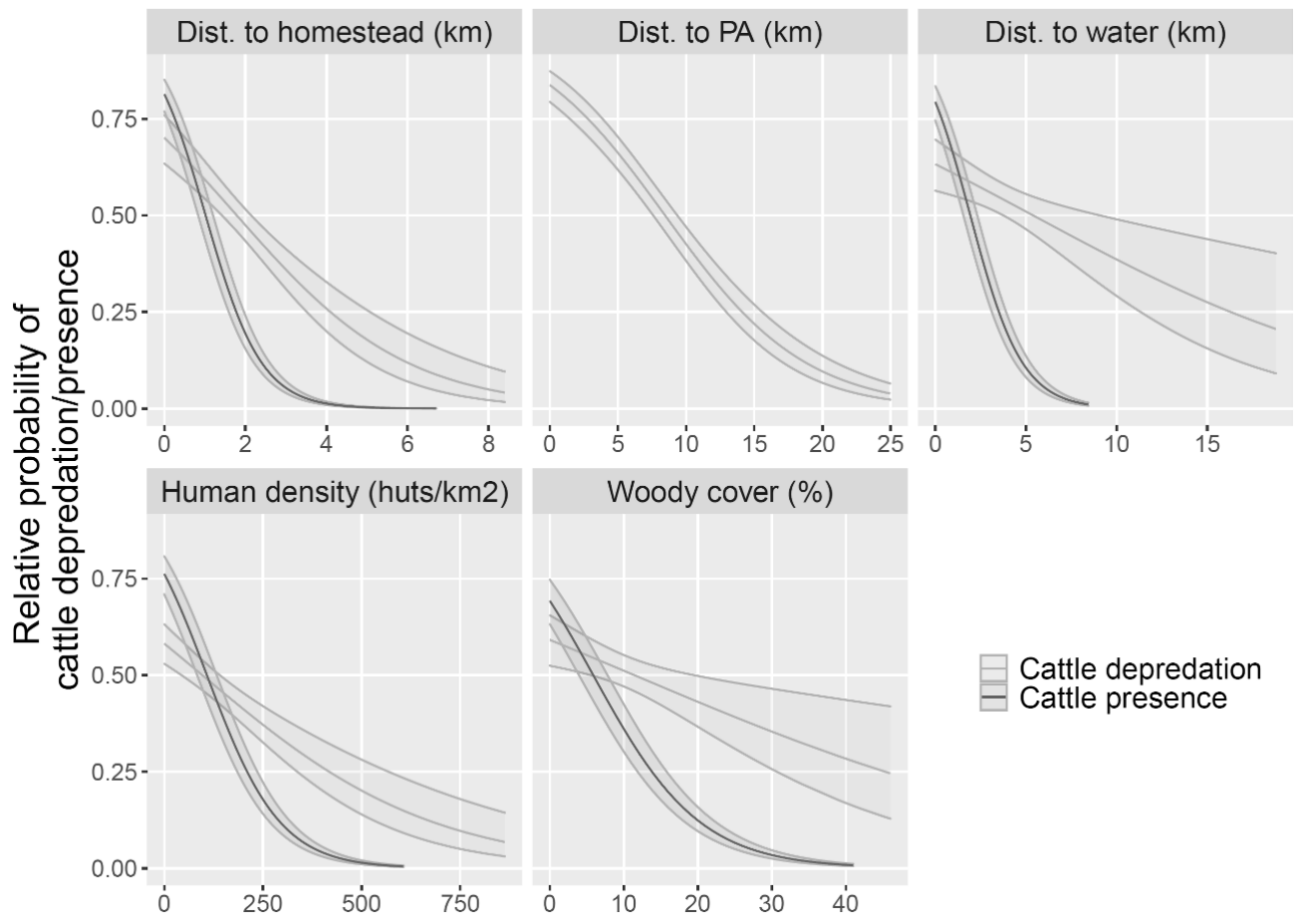
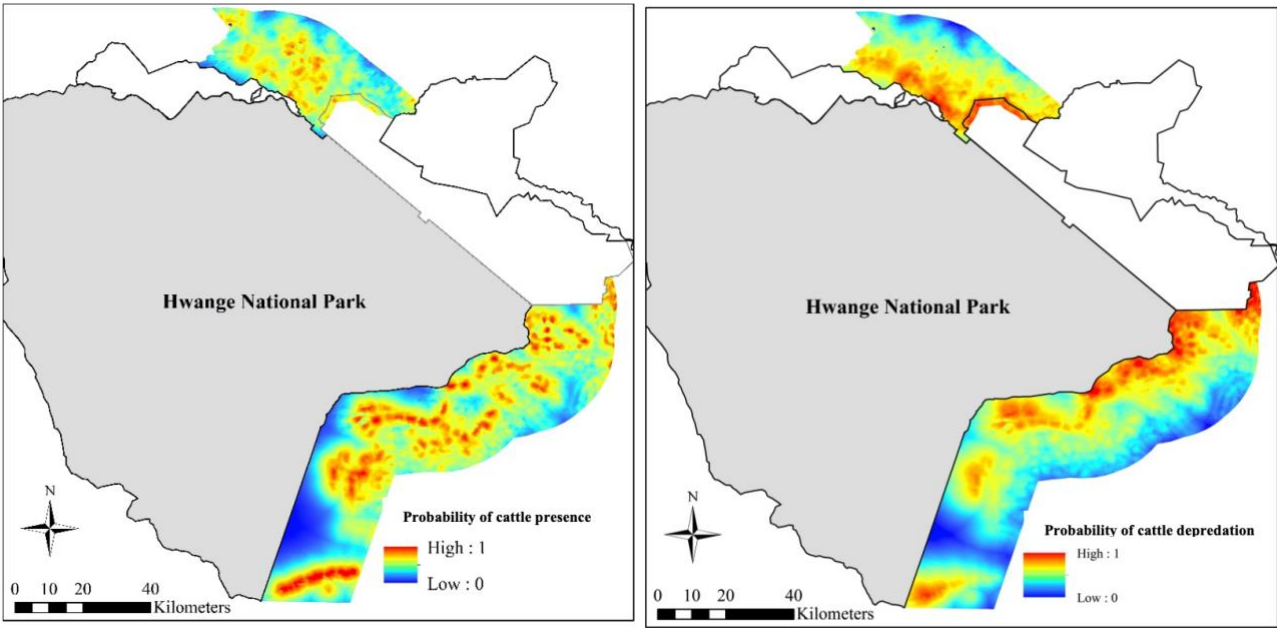
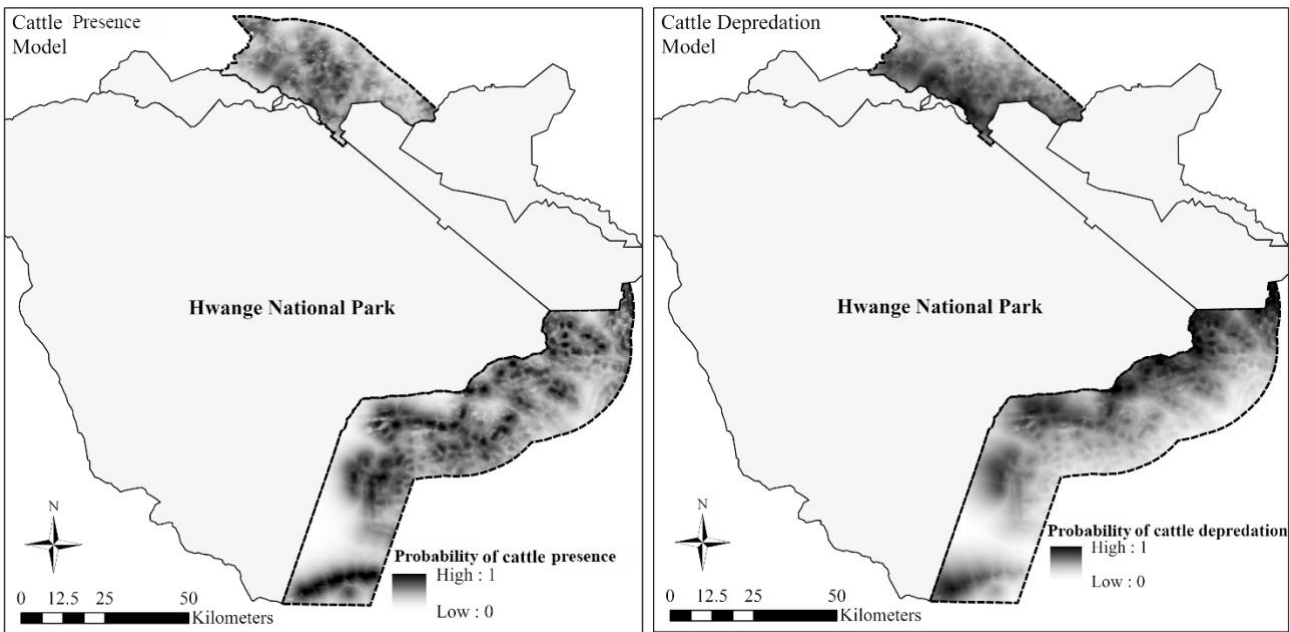


Figure 4. The effect of landscape variables on the probability of cattle depredation (light lines) and cattle presence (dark lines). The relative probability values are derived from the dominant models in each case and lines represent marginal regression effects with 95% confidence intervals (created using the R package *ggeffects*). Distance to PA was not considered in the cattle presence model (see Methods).



320

321 Figure 5. Predicted spatial patterns in the relative probability of cattle depredation by large
322 carnivores and the relative probability of cattle presence alongside Hwange NP, Zimbabwe. Pixel
323 values represent the resource selection function scores derived from the coefficients of the cattle
324 depredation model (logistic regression) and the cattle presence model (Generalized Linear Mixed
325 Model), respectively.



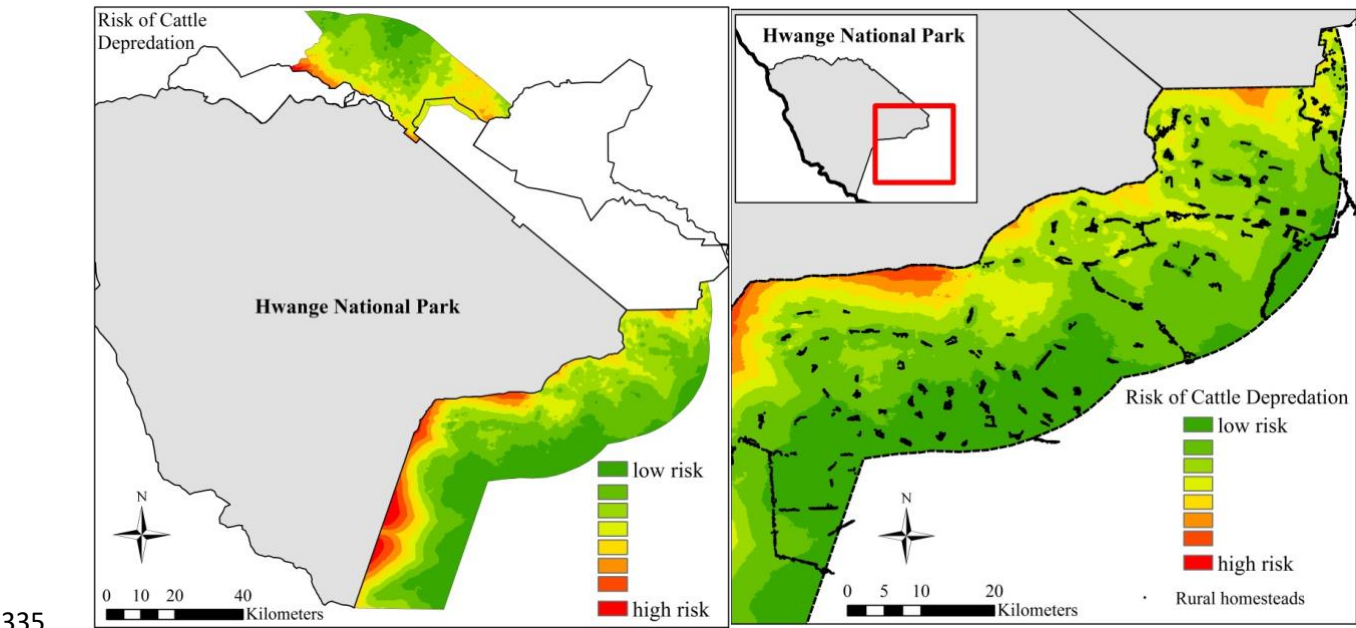
326

327 Figure 5. Black and white version (for the colour blind)

328

329 Depredation risk map

330 Although the relative probability of cattle depredation was highest close to homesteads, cattle were
331 least at risk of depredation by large carnivores in these areas, with risk increasing rapidly >2-3km
332 from homesteads (Figs 6 and 7). Risk was highest close to Hwange NP, with risk decreasing sharply
333 further from PAs (Figs 6 and 7). Risk increased with decreasing human density and increasing woody
334 cover, although these effects were small (Fig. 7).



336 Figure 6. (A) Spatial patterns in the risk faced by cattle of depredation by large carnivores within a
337 25km buffer of Hwange NP, Zimbabwe. The right panel is a zoomed view of Tsholotsho, showing the
338 position of rural homesteads. The risk map was generated by dividing the pixel values for the cattle
339 depredation raster by the pixel values for the cattle presence raster (Fig. 5). (B) Zoomed view of (A)
340 covering the Tsholotsho Communal Land and showing the position of rural homesteads.

341

342

343

344

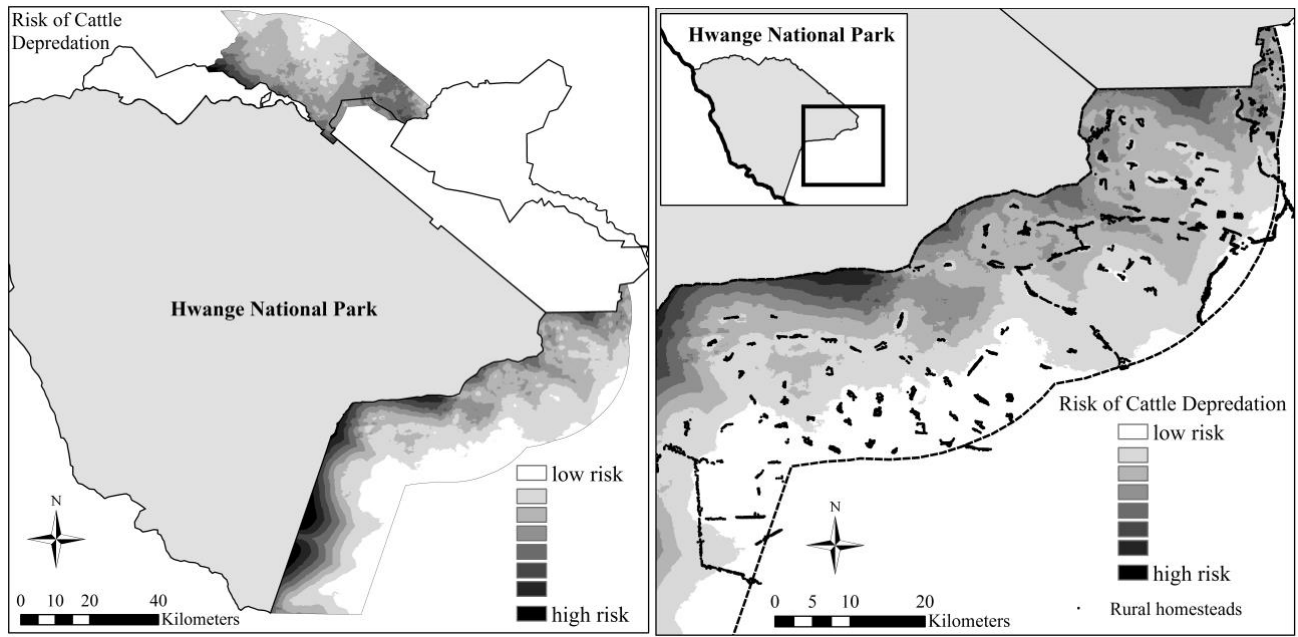


Figure 6. Black and white version (for the colour blind).

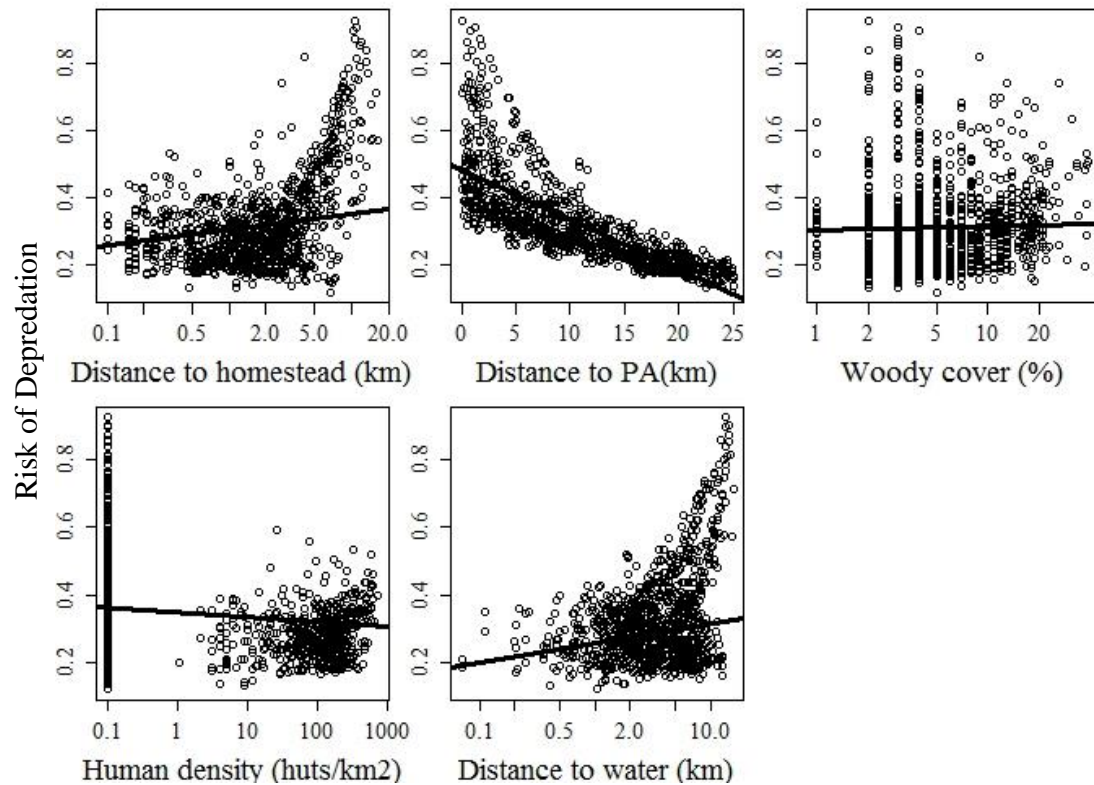


Figure 7. The relationship between the risk of cattle depredation (probability of depredation given cattle presence) and five landscape variables. Data were generated by extracting risk and landscape variable values at 1000 points randomly generated across the study area. Lines for simple linear models are shown to help indicate trends. Given risk values are relative, and changes in risk are not constant, plots should be regarded as giving a qualitative and relative measure of these relationships. All axes, apart from distance to PA, are log-scaled to better indicate risk thresholds. .

Discussion

In this study we present a unique definition of depredation risk that accounts for variations in the probability of livestock presence. Previous spatial depredation risk models do not account for these variations, meaning that some of the identified hotspots of risk may simply reflect areas where livestock are most likely to be present. Our model is similar in concept to those developed to account for wild prey distribution when modelling spatial patterns of predator-prey dynamics (such as wolf-elk kills sites; Kauffman et al. 2007). Our formulation of risk is able to more precisely distinguish between the availability (density) and accessibility (vulnerability) of livestock to predators. In other

words, our model captures high risk areas as those where livestock are most accessible (i.e. vulnerable) to predators as opposed to simply capturing where livestock are most available. For example, our depredation models predicted an increased probability of depredation closer to homesteads (where livestock are more available), whereas our risk models showed increasing risk further from homesteads. This aligns with the above discussion on carnivore behaviour which predicts a reduced probability of predator presence in areas of higher human activity due to the risk of anthropogenic mortality (Oriol-Cotterill et al. 2015). It is more accurate to conclude that livestock are more at risk of depredation further from homesteads, which is opposite to the conclusion based only on depredation data. Similarly, the sharp decline in depredation probability in more wooded areas is also misleading. Our risk model again suggests the opposite trend, indicating a slight increase in the risk of depredation in more wooded areas. Kuiper et al. (2015) found that in our study system the months of highest cattle loss to lions coincided with the months when cattle were herded into more wooded areas. Whilst cattle are more available in open areas, predators may prefer to attack them in more wooded areas that offer more concealment for ambushing and for avoiding humans.

Depredation hotspots and livestock distribution

The congruence between cattle depredation and presence in our models suggests that patterns of depredation were influenced by livestock distribution. Many of the spatial depredation risk studies reviewed by Miller (2015) documented, unsurprisingly, increased probability of depredation (incomplete definition of risk) in areas of higher livestock density. In a study in the Western Ghats, Karanth et al. (2013) found higher livestock losses for households with more livestock individuals owned. In a study in northern Tanzania, Beattie et al. (2020) documented higher levels of dry season livestock depredation by lions in areas closer to water and with higher vegetation greenness (livestock require pasture and water), and in areas near livestock enclosures in the wet season. Baruch-Mordo et al. (2008) found that clusters of bear-human conflict overlapped with Colorado counties with high sheep densities. In our models, predicted depredation decreased further from homesteads, likely reflecting the sharp reduction in cattle presence. Cattle in our study area spend most of their time within 500m of their home enclosure (Kuiper et al. 2015). The higher relative probability of cattle depredation in more open areas may also be explained by higher cattle presence. Grazing grass is more available in open versus wooded areas, and cattle in our study area have been shown to prefer open areas year-round (Kuiper et al. 2015). Treves et al. (2011) similarly found that

higher pasture coverage was the strongest predictor of wolf depredation. As acknowledged by the authors, this may simply reflect greater livestock availability in pasture areas.

Wild prey species optimize their movements to meet their nutritional needs while avoiding predation risk (the ecology of fear; Brown, Laundré & Gurung 1999). An interesting consideration is whether livestock (and their herders) are able to optimize resource access and avoid predators with the same effectiveness as do wild prey. There exists a trade-off between accessing suitable resources for livestock (grazing and water) and avoiding areas where encounters with predators are more likely. This trade-off becomes acute when grazing areas overlap with areas of high predation risk. Abade et al. (2014a), for example, highlight that areas of high depredation risk overlapped with suitable grazing land. Similarly, seasonal peaks in cattle depredation in our study area coincide with cattle movements closer to PAs, where grazing opportunities are better (Kuiper et al. 2015).

The spatial ecology of carnivores

Areas closer to core carnivore habitat will be riskier for livestock (Miller & Schmitz 2019). Our cattle depredation model predicted a steep decline in depredation further from PAs (prime carnivore habitat; Loveridge *et al.* 2010). In the Western Ghats, Karanth et al. (2013) found greater losses of livestock to predators for homesteads closer to reserves and those that practiced grazing within protected reserves. In their Ruaha study area in Tanzania, Abade et al. (2014a) point out that areas identified as having a high probability of depredation (i.e. areas closer to rivers) coincided with areas preferred by large carnivores.

The risk that carnivores face themselves when entering human-dominated landscapes may also explain the above patterns. Carnivores face the risk of retaliatory killing by humans, which is common in our study area (Loveridge et al. 2017b). In human-dominated landscapes, large carnivores may alter their spatiotemporal movement behaviours to minimise encounters with humans (Valeix et al. 2012; Oriol-Cotterill et al. 2015). Such behaviour may be explained by the theory of the ecology of fear, more commonly used to understand prey species response to carnivores (Laundré et al. 2010). Thus, predation patterns are certainly not entirely explained by livestock distribution, and one must differentiate between livestock availability in the landscape, and their accessibility to predators. While livestock may be most available closer to human activity, their accessibility to predators in these areas may be reduced by virtue of the high risk that human activity poses to predators. Other species may also face similar trade offs between accessing food and encountering humans. In

Botswana, Songhurst & Coulson (2014) found that crop fields closer to established elephant pathways were significantly more vulnerable to elephant crop-raiding. Elephants made various behavioural adjustments to avoid human-associated risk (avoidance of pathways near human settlements, and movement in larger groups) (Songhurst et al. 2016). In cases where livestock are not guarded by people, predators may however opportunistically take advantage of areas of higher livestock density (choose according to availability rather than accessibility).

This trade-off between availability and accessibility may explain why, while the predicted probability of cattle presence was close to zero beyond 3km from homesteads, the probability of depredation was comparatively higher in these areas (Fig. 4). This may shed light on why some studies report reduced depredation closer to human settlement (Ogada et al. 2003; Davie et al. 2014) while our model and those of Behdarvand et al. (2014) predict increased depredation. Depredation in relation to vegetation cover also bears out this accessibility/availability distinction. In an Indian tiger reserve, the risk of livestock depredation by tigers was found to be higher in more densely forested areas (Miller et al. 2015b), while jaguars in the Brazil were more likely to attack livestock in more densely vegetated areas (Balbuena-Serrano et al. 2021). These results are likely explained by the ambush hunting style of the tiger and puma (livestock become more accessible as prey to these predators in areas of denser cover). An additional effect may be the reduced exposure to humans of predators themselves. In Mongolia, Davie et al. (2014) found that livestock depredation by wolves was elevated in areas with tall surrounding vegetation and suggest this minimizes the detection of wolves by people. We found however elevated depredation in more open areas, even though some predators in our system (lions and leopards) rely on ambush hunting. This may be explained by the significantly reduced availability of livestock in wooded areas (the odds of cattle presence halved with every 5% increase in cover), which are less suitable for grazing. But are more open areas and those closer to homesteads in fact riskier for livestock?

Alternative risk modelling approaches

Our method of directly weighting depredation predictions by predictions of cattle presence is simple, and we acknowledge that more sophisticated statistical approaches may have been useful. The spatial layer of the relative probability of cattle depredation could have been used as a predictor in our depredation models, such that any effects of the other predictors would have represented

residual variation not explained by livestock distribution. Also, raw cattle distribution data may have been incorporated into our depredation models directly, using a hierarchical modelling structure (as in Beale et al. 2014; Critchlow et al. 2015). However, our formulation of the conditional probability via Bayes' theorem allowed us to define risk directly and intuitively, producing a simple map of relative risk. Also, by presenting cattle depredation and presence models separately, we were better able to demonstrate how predictions of the former were strongly influenced by the latter. Our calculation of risk across space provides only a relative scale of risk, allowing only qualitative comparisons of risk between one area and the next. Ultimately, however, our aim was to make clear the difference between raw patterns in depredation, and patterns of 'true' depredation risk, showing that livestock distribution is an important confounding factor. We believe the simplicity of our analysis, and relative differences in risk across space, adequately achieve this aim.

Implications for conflict mitigation

Predictive maps of risky areas have been used to help livestock owners prioritize areas to implement livestock protection and carnivore deterrent strategies (Miller 2015). The usefulness of these strategies will depend on how well risk is captured. Mitigation measures that suggest that certain areas be avoided may not be successful if these areas are not themselves inherently risky but are simply more likely to be used by livestock. In so far as the elevated depredation in these areas is explained by the higher probability of livestock presence, herding livestock elsewhere may simply result in risk shifting to these new areas. A more profitable focus of mitigation strategies may instead be the avoidance of areas where the probability of encountering predators is highest, i.e. areas of inherently higher risk. Based on their spatial models of the probability of depredation, Treves et al. (2011) recommend that livestock owners "act to mitigate the risk posed by high concentrations of grassland, pasture, or hayfield far from forest and near wolf packs". We agree that avoiding pasture areas nearer wolf territory is a helpful recommendation, but grassland/pasture areas themselves may not be inherently risky.

This is not to say that the prescriptions of models that do not account for livestock distribution are not useful. Such models provide a reliable means for predicting areas where future attacks on livestock are most likely to occur. Even if these models predict future attacks in areas of high livestock abundance, these areas are still legitimate targets for interventions to reduce livestock losses and

the retaliatory killing of predators. By contrast, the concept of risk we developed here is geared more towards guiding livestock herders by identifying areas that are relatively safer to roam into. This may also prove useful for the future development of communal herding areas, or the expansion of small-scale rural development (higher risk areas should be avoided where possible).

Our risk model suggests that the most risky areas for livestock to move into are areas distant from human activity, closer to PAs (i.e. prime predator habitat) and with greater woody vegetation cover (more suitable for ambush hunters like lions). The most obvious practical application of these insights is to ensure that these areas are avoided by herders. However, this may be unrealistic in cases where the best grazing occurs in risky areas. For example, extensive cultivation of crops around villages in our study area means that cattle need to be herded further from their home enclosures in the wet season to avoid damaging crops and to access better grazing towards the PA boundaries (Kuiper et al. 2015). Where risky areas cannot be completely avoided, the next obvious strategy is to focus efforts to protect livestock and deter carnivores on risky areas (Miller & Schmitz 2019). In many scenarios, the social and financial capacity to protect livestock may be limited and focussing on high risk areas can ensure the more efficient use of limited resources. For example, villages closer to PA boundaries may be prioritized for improvements in predator-proof livestock enclosures. Another simple strategy is to ensure the presence and heightened vigilance of herders (or guard dogs) accompanying livestock when grazing in higher risk areas (Abade et al. 2014; van Eeden et al. 2018). The Trans-Kalahari Predator Programme, of which this research is a part, is developing mobile livestock enclosures that move with and protect communal herds of livestock while they are grazing, and these will be particularly useful in risky areas. Mobile bomas may be particularly useful if spatial depredation risk shifts over time.

Concluding remarks

The effectiveness of conservation strategies depends on the quality of evidence underpinning them. Here we present a method for quantifying the risk of livestock depredation by large carnivores that accounts for the confounding effects of livestock distribution, in an effort to provide robust evidence for livestock owners, rural development planners, and conservationists seeking to reduce human-wildlife conflict. The concept of risk advocated here is conceptually and methodologically different from previous definitions of risk in the literature, and therefore has distinct implications for conflict mitigation. Furthermore, our approach is easily transferrable to other livestock herding and grazing

contexts for which depredation and livestock movement data are available. We recommend that future studies of human-wildlife conflict and depredation risk collect data on movements of livestock and other at-risk resources. We hope that the concepts and methods of depredation risk that we develop here will help advance the future study of human-wildlife conflict more generally, and the commensurate design of coexistence strategies. Finally, we encourage future work to investigate how spatial depredation risk varies over time (space-time dependence).

Data accessibility

All data used for analyses in this manuscript will be archived on the Dryad digital depository.

Literature Cited

- Abade L, Macdonald DW, Dickman AJ. 2014. Assessing the relative importance of landscape and husbandry factors in determining large carnivore depredation risk in Tanzania's Ruaha landscape. *Biological Conservation* **180**:241–248. Elsevier Ltd. Available from <http://www.sciencedirect.com/science/article/pii/S0006320714003863>.
- Balbuena-Serrano, Zarco-González MM, Monroy-Vilchis O, G. Morato R, C. De Paula R. 2021. Hotspots of livestock depredation by pumas and jaguars in Brazil: a biome-scale analysis. *Animal Conservation* **24**:181–193.
- Baruch-Mordo S, Breck SW, Wilson KR, Theobald DM. 2008. Spatiotemporal Distribution of Black Bear–Human Conflicts in Colorado, USA. *Journal of Wildlife Management* **72**:1853–1862. Available from <http://www.bioone.org/doi/abs/10.2193/2007-442>.
- Bates D, Maechler M, Bolker B. 2013. lme4: Linear mixed-effects models using Eigen and Eigen. R package version 0.999999-0. 2012. URL: <http://CRAN.R-project.org/package=lme4>.
- Beale CM, Brewer MJ, Lennon JJ. 2014. A new statistical framework for the quantification of covariate associations with species distributions. *Methods in Ecology and Evolution* **5**:421–432.
- Beattie K, Olson ER, Kissui B, Kirschbaum A, Kiffner C. 2020. Predicting livestock depredation risk by African lions (*Panthera leo*) in a multi-use area of northern Tanzania. *European Journal of Wildlife Research* **66**. European Journal of Wildlife Research.
- Behdarvand N, Kaboli M, Ahmadi M, Nourani E, Salman Mahini A, Asadi Aghbolaghi M. 2014. Spatial risk model and mitigation implications for wolf–human conflict in a highly modified agroecosystem in western Iran. *Biological Conservation* **177**:156–164. Elsevier Ltd. Available from <http://linkinghub.elsevier.com/retrieve/pii/S0006320714002511>.
- Brown JS, Laundré JW, Gurung M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of mammalogy*:385–399. JSTOR.
- Burnham K., Anderson D. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic

- 569 ApproachNo Title. Springer-Verlag, New York.
- 570 Chetkiewicz C-LB, Boyce MS. 2009. Use of resource selection functions to identify conservation corridors. *Journal of*
571 *Applied Ecology* **46**:1036–1047. Available from <http://doi.wiley.com/10.1111/j.1365-2664.2009.01686.x>
572 (accessed March 20, 2014).
- 573 Critchlow R, Plumptre AJ, Driciru M, Rwetsiba A, Stokes EJ, Tumwesigye C, Wanyama F, Beale CM. 2015. Spatiotemporal
574 trends of illegal activities from ranger-collected data in a Ugandan national park. *Conservation Biology* **29**:1458–
575 1470.
- 576 Davie HS, Murdoch JD, Lhagvasuren A, Reading RP. 2014. Measuring and mapping the influence of landscape factors on
577 livestock predation by wolves in Mongolia. *Journal of Arid Environments* **103**:85–91. Elsevier Ltd. Available from
578 <http://linkinghub.elsevier.com/retrieve/pii/S0140196314000135>.
- 579 Dormann CF et al. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their
580 performance. *Ecography* **36**:27–46.
- 581 Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk M a., Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL. 2006.
582 Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* **75**:887–
583 898. Available from <http://doi.wiley.com/10.1111/j.1365-2656.2006.01106.x> (accessed March 20, 2014).
- 584 Hansen M., DeFries R., Townshend JR., Sohlberg R, Dimiceli C, Carroll M. 2002. Towards an operational MODIS
585 continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. *Remote Sensing of*
586 *Environment* **83**:303–319. Available from <http://linkinghub.elsevier.com/retrieve/pii/S0034425702000792>.
- 587 Ikanda D, Packer C. 2008. Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania.
588 *Endangered Species Research*.
- 589 Johnson CJ, Seip DR, Boyce MS. 2004. A quantitative approach to conservation planning: using resource selection
590 functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*
591 **41**:238–251. Available from <http://doi.wiley.com/10.1111/j.0021-8901.2004.00899.x>.
- 592 Karanth KK, Gopalaswamy AM, DeFries R, Ballal N. 2012. Assessing patterns of human-wildlife conflicts and
593 compensation around a Central Indian protected area. *PloS one* **7**:e50433. Available from
594 <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3515612&tool=pmcentrez&rendertype=abstract>
595 (accessed May 11, 2014).
- 596 Karanth KK, Gopalaswamy AM, Prasad PK, Dasgupta S. 2013. Patterns of human–wildlife conflicts and compensation:
597 Insights from Western Ghats protected areas. *Biological Conservation* **166**:175–185. Elsevier Ltd. Available from
598 <http://linkinghub.elsevier.com/retrieve/pii/S0006320713002176> (accessed May 7, 2014).
- 599 Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS. 2007. Landscape heterogeneity shapes
600 predation in a newly restored predator-prey system. *Ecology Letters* **10**:690–700.
- 601 Keating K, Cherry S. 2004. Use and interpretation of logistic regression in habitat selection studies. *Journal of Wildlife*

- 602 Management **68**:774–789.
- 603 Kuiper TR, Loveridge AJ, Parker DM, Johnson PJ, Hunt JE, Stapelkamp B, Sibanda L, Macdonald DW. 2015. Seasonal
604 herding practices influence predation on domestic stock by African lions along a protected area boundary.
605 Biological Conservation **191**:546–554. Elsevier B.V. Available from
606 <http://linkinghub.elsevier.com/retrieve/pii/S0006320715300628>.
- 607 Laundré JW, Hernández L, Ripple WJ. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology
608 Journal **3**:1–7. Bentham Science Publishers B. V., P. O. Box 1673 Hilversum 1200 BR Netherlands.
- 609 Lindsey PA, Alexander RR, Du Toit JT, Mills MGL. 2005. The potential contribution of ecotourism to African wild dog
610 *Lycaon pictus* conservation in South Africa. Biological Conservation **123**:339–348.
- 611 Loveridge AJ, Hemson G, Davidson Z, Macdonald DW. 2010. African lions on the edge: reserve boundaries as ‘attractive
612 sinks.’ Pages 283–304 Biology and Conservation of Wild Felids. Oxford University Press, Oxford.
- 613 Loveridge AJ, Kuiper TR, Parry R, Stapelkamp B, Sibanda L, Macdonald DW. 2017a. Bells, bomas and beef-steak:
614 complex patterns of human-predator conflict at the protected area- agro-pastoral interface. PeerJ **5**:e2898.
- 615 Loveridge AJ, Valeix M, Elliot NB, Macdonald DW. 2017b. The landscape of anthropogenic mortality: how African lions
616 respond to spatial variation in risk. Journal of Applied Ecology **54**:815–825.
- 617 Macdonald DW, Loveridge AJ. 2010. Biology and conservation of wild felids. Oxford University Press Oxford.
- 618 Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW. 2015. Conservation inequality and the
619 charismatic cat: *Felis felis*. Global Ecology and Conservation **3**:851–866. Elsevier.
- 620 Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical
621 analysis and design for field studies. Page Nordrecht, The Netherlands: Kluwer. Kluwer, Dordrecht, The
622 Netherlands.
- 623 McInturff A, Miller JRB, Gaynor KM, Brashares JS. 2021. Patterns of coyote predation on sheep in California: A socio-
624 ecological approach to mapping risk of livestock–predator conflict. Conservation Science and Practice **3**:1–15.
- 625 Merson SD, Dollar LJ, Johnson PJ, Macdonald DW. 2019. Retaliatory killing and human perceptions of Madagascar’s
626 largest carnivore and livestock predator, the fosa (*Cryptoprocta ferox*). PLoS ONE **14**:1–18.
- 627 Miller JRB. 2015. Mapping attack hotspots to mitigate human-carnivore conflict: approaches and applications of spatial
628 predation risk modeling. Biodiversity and Conservation. Springer Netherlands.
- 629 Miller JRB, Jhala Y V., Jena J. 2015a. Livestock losses and hotspots of attack from tigers and leopards in Kanha Tiger
630 Reserve, Central India. Regional Environmental Change. Springer Berlin Heidelberg. Available from
631 <http://link.springer.com/10.1007/s10113-015-0871-5>.
- 632 Miller JRB, Jhala Y V., Jena J, Schmitz OJ. 2015b. Landscape-scale accessibility of livestock to tigers: implications of
633 spatial grain for modeling predation risk to mitigate human-carnivore conflict. Ecology and Evolution **5**:1354–
634 1367. Available from

- 635 <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4377277&tool=pmcentrez&rendertype=abstract>.
- 636 Miller JRB, Schmitz OJ. 2019. Landscape of fear and human-predator coexistence: Applying spatial predator-prey
637 interaction theory to understand and reduce carnivore-livestock conflict. *Biological Conservation* **236**:464–473.
638 Elsevier. Available from <https://doi.org/10.1016/j.biocon.2019.06.009>.
- 639 Morris LR, Proffitt KM, Blackburn JK. 2016. Mapping resource selection functions in wildlife studies: Concerns and
640 recommendations. *Applied Geography* **76**:173–183.
- 641 Naha D, Dash SK, Chettri A, Chaudhary P, Sonker G, Heurich M, Rawat GS, Sathyakumar S. 2020. Landscape predictors
642 of human–leopard conflicts within multi-use areas of the Himalayan region. *Scientific Reports* **10**:1–12. Nature
643 Publishing Group UK. Available from <https://doi.org/10.1038/s41598-020-67980-w>.
- 644 Ogada MO, Woodroffe R, Ouge NO, Frank LG. 2003. Limiting depredation by African carnivores: the role of livestock
645 husbandry. *Conservation Biology* **17**:1521–1530. Wiley Online Library.
- 646 Oriol-Cotterill A, Macdonald DW, Valeix M, Ekwanga S, Frank LG. 2015. Spatiotemporal patterns of lion space use in a
647 human-dominated landscape. *Animal Behaviour* **101**:27–39. Elsevier Ltd. Available from
648 <http://www.sciencedirect.com/science/article/pii/S0003347214004394>.
- 649 Pearce JL, Boyce MS. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*
650 **43**:405–412. Available from <http://doi.wiley.com/10.1111/j.1365-2664.2005.01112.x> (accessed March 22, 2014).
- 651 Pooley S et al. 2017. An interdisciplinary review of current and future approaches to improving human-predator
652 relations. *Conservation Biology*:1–31.
- 653 Ripple WJ et al. 2014. Status and ecological effects of the world’s largest carnivores. *Science* **343**:151–164. Available
654 from <http://www.ncbi.nlm.nih.gov/pubmed/24408439>.
- 655 Rust NA, Marker LL. 2014. Cost of carnivore coexistence on communal and resettled land in Namibia. *Environmental*
656 *Conservation* **41**:45–53.
- 657 Songhurst A, Coulson T. 2014. Exploring the effects of spatial autocorrelation when identifying key drivers of wildlife
658 crop-raiding. *Ecology and Evolution* **4**:582–593.
- 659 Songhurst A, McCulloch G, Coulson T. 2016. Finding pathways to human–elephant coexistence: a risky business. *Oryx*
660 **50**:713–720. Available from http://www.journals.cambridge.org/abstract_S0030605315000344.
- 661 Treves A. 2009. Hunting for large carnivore conservation. *Journal of Applied Ecology* **46**:1350–1356.
- 662 Treves A, Martin K a., Wydeven AP, Wiedenhoeft JE. 2011. Forecasting Environmental Hazards and the Application of
663 Risk Maps to Predator Attacks on Livestock. *BioScience* **61**:451–458.
- 664 Treves A, Santiago-Ávila FJ. 2020. Myths and assumptions about human-wildlife conflict and coexistence. *Conservation*
665 *Biology* **34**:811–818.
- 666 Valeix M, Hemson G, Loveridge AJ, Mills G, Macdonald DW. 2012. Behavioural adjustments of a large carnivore to

667 access secondary prey in a human-dominated landscape. *Journal of Applied Ecology* **49**:73–81.

668 van Eeden LM et al. 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biology* **16**:1–8.

669 Van Eeden LM, Crowther MS, Dickman CR, Macdonald DW, Ripple WJ, Ritchie EG, Newsome TM. 2017. Managing
670 conflict between large carnivores and livestock. *Conservation Biology*:1–21. Available from
671 <http://doi.wiley.com/10.1111/cobi.12959>.

672