

# Spatial correlates of livestock depredation by Amur tigers in Hunchun, China: Relevance of prey density and implications for protected area management



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## ABSTRACT

Livestock depredation by highly endangered Amur tigers is a major source of human-tiger conflict in Northeast China. We model livestock depredation risk to understand factors shaping the spatial distribution of depredation conflicts using Hunchun, China as a case study. Ungulate occupancy survey data, presence of ungulate snares and other landscape covariates (such as elevation, slope and tree cover) were first used to model ungulate prey densities using generalised least squares. Predicted densities were then incorporated together with landscape covariates as predictors for actual livestock depredation incidents in a zero-inflated negative binomial model for depredation risk. Lower overall prey densities were associated with proximity to snares, and other anthropogenic-related covariates like distances to villages and roads were also important predictors of prey densities. Depredation conflicts were associated with closer proximity to snares and rivers, greater distances from roads, greater tree cover, and deciduous forest habitats. High-risk areas were found to be concentrated in community-management zones in Hunchun National Nature Reserve (HNR). The results suggest that compensation payments for depredations within HNR provide an unwanted incentive for local people to continue to use the protected area (especially in community co-managed zones) as grazing lands, leading to increased conflict. Eliminating cattle and snaring from HNR and other tiger recovery zones within Northeast China may be essential to reduce conflicts and minimise detrimental impacts on tiger populations.

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## 1. Introduction

Three of nine subspecies of tigers became extinct in the 20th century, and wild tiger populations have dwindled from about 100,000 in the last century to less than 3500 currently (Walston et al., 2010). Poaching and habitat destruction are the leading causes of tiger population declines across Asia, but conflicts with humans are also responsible for losses (Morell, 2007). Tigers kill dozens of people each year across Asia (Karanth and Gopal, 2005), thus fear of tiger attack is a strong motivation for precautionary killings (Goodrich et al., 2011). Attacks on humans and livestock depredation are the two most common types of human-tiger

conflicts (Goodrich, 2010; Goodrich et al., 2011; Gurung et al., 2008; Johnson et al., 2006; Nyhus and Tilson, 2004), and strategies to guide mitigation actions have been developed in some places (Barlow et al., 2010).

Models have also been increasingly utilised to identify parameters associated with tiger conflict situations, especially to complement limited field data, in hopes that better understanding can reduce levels of conflict. These include models that simulate tiger interactions with prey and humans (Ahearn et al., 2001; Imron et al., 2011), predict tiger densities from prey abundance (Karanth et al., 2004; Miquelle et al., 1999), and identify landscape correlates of livestock depredation (Li et al., 2009; Liu et al., 2006). However, there exists a gap in current tiger studies (Hebblewhite et al., 2012; Li et al., 2010; Zhang and Zhang, 2011; Zhou, 2008) to examine the impacts of human actions and compensation policies on wild prey and livestock dynamics, and consequently on the occurrence of conflicts such as livestock depredation.

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There were an estimated 4000 tigers in China in 1950s when the Government labelled tigers as pests, resulting in a rapid decline. It is estimated that no more than 50 tigers remain in China (Global Tiger Initiative Secretariat, 2012), mostly scattered along its southern and northern borders. The vast majority of Amur tigers remain in the Russian Far East, but individuals regularly cross over into China, providing a unique opportunity for increasing tiger population in Northeast China. Analyses suggest suitable habitat still exists in Northeast China (Hebblewhite et al., 2012) and a National Tiger Recovery Programme provides a framework for recovery in some of these habitats (Wikramanayake et al., 2011), but understanding and mitigating human-tiger conflicts will be vital to the success of such efforts.

The Hunchun–Wanqing region of Jilin Province is considered the highest priority Tiger Conservation Area in China, with the largest connected network of habitat patches that is contiguous with tiger source populations in Russia (Hebblewhite et al., 2012). Livestock depredation in Hunchun, Jilin has been well documented since 2002 when the Hunchun National Nature Reserve (HNR) was officially established (Li et al., 2009; Liu et al., 2006), with an increasing trend over the years (Pettigrew et al., 2012). A winter survey from 2003 to 2005 found seven tigers possibly living in or visiting HNR (Li et al., 2008), but only signs of three tigers were found in the 2009–2010 survey (Chen et al., 2011). Compared to an average tiger density of 0.8/100 km<sup>2</sup> in the protected area of the Sikhote-Alin mountain range in neighbouring Primorsky Krai, Russia (Miquelle et al., 2009), tiger numbers in HNR could be below its possible carrying capacity of eight assuming the same density per km<sup>2</sup>, although long term tiger monitoring in HNR is required before establishing if the tiger population in HNR is in need of recovery. As a Category IV protected area under the International Union for Conservation of Nature Protected Area Classification, HNR is not strictly protected from human uses, thus management of wildlife conflicts such as livestock depredation is even more paramount. Villagers living within HNR have the right to graze livestock in all but the core area of the reserve, and receive full compensation from the government for cattle killed by tigers wherever else depredation occurs. Most cattle in HNR are stall-fed in winter, reducing depredation rates (Li et al., 2009), but during summer livestock are free ranging, unlike in neighbouring small villages in Russia where livestock are herded back into barns at night. Additionally, wild ungulate densities are reduced due to competition with livestock for forage and snaring and poisoning by local villagers looking to supplement their food source (Liu et al., 2007; Zhang and Zhang, 2011). Since availability of ungulate prey is crucial to the persistence of any tiger population (Karanth et al., 2004; Li et al., 2010; Tian et al., 2011), depressed prey densities may be associated with high livestock depredation rates (Loveridge et al., 2010; Miquelle et al., 2005).

We conducted an analysis of livestock depredation by tigers in the Hunchun region from 2002 to 2011 to identify spatial correlates of livestock depredation that can assist in designing preventive mitigation measures. We built an ungulate prey density model, followed by a spatial model to predict livestock depredation risk by Amur tigers that incorporated landscape covariates as well as prey densities and distance to ungulate snares. We then derived a depredation risk map to generate insights into the effect of human actions (ungulate snaring and livestock husbandry practices) on tiger prey density and livestock depredation losses to aid in designing appropriate conflict mitigation measures.

## 2. Materials and methods

### 2.1. Study area

Hunchun municipality with an area of 4938 km<sup>2</sup> (green and light brown areas in Fig. 1) is part of Jilin province in Northeast Chi-

na (130°17'08"–131°14'44"E, 42°42'40"–43°28'00"N), of which HNR covers 1087 km<sup>2</sup> (green area in Fig. 1). HNR borders Russia to the east and North Korea to the south west and includes four management zones (core area, experimental area, buffer zone and community co-management area) (Li et al., 2009). 29 villages of about 14,953 people lived within the protected area of HNR even before it was established (Li et al., 2009); currently there are around 98 villages and 4 towns inside.

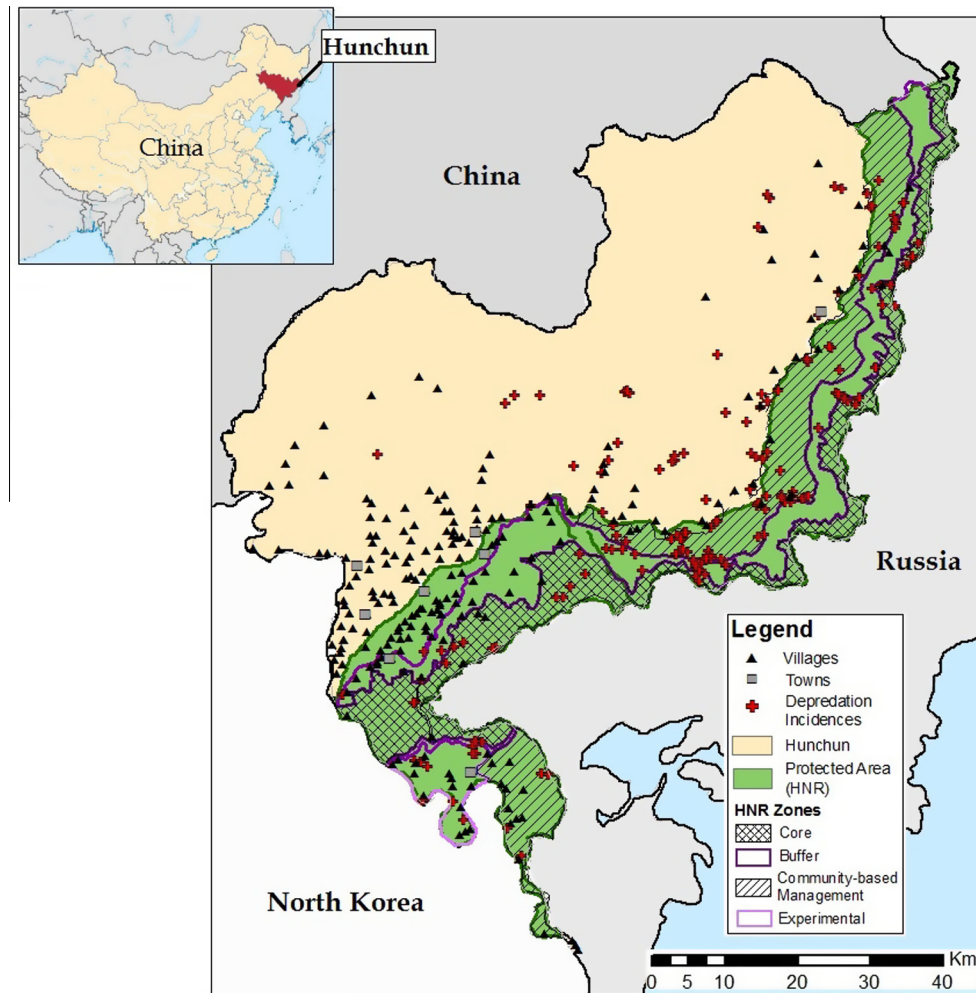
The rural economy depends mainly on crop cultivation, gathering of non-timber forest products and livestock husbandry, with the latter representing about 17.3% of household income for villagers living within HNR (Li et al., 2009). A recent multi-part survey of 113 randomly selected households from villages in and around HNR found that 57.5% of these households raised on average 6.6 cattle per working villager (Chin, 2012). Given these estimates and current census data, there appears to be 44,000 cattle that graze at least part of the year in HNR. Ungulate species occurring in HNR that are also potential tiger prey include red deer (*Cervus elaphus*), Siberian roe deer (*Capreolus pygargus*), sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) (Li et al., 2009; Tian et al., 2011). Meanwhile, other predators in Hunchun include the Amur leopard (*Panthera pardus orientalis*), the Asiatic black bear (*Ursus thibetanus*) and the sable (*Martes zibellina*) (Han et al., 2012). However, these predators are unlikely to contribute significantly to livestock depredation, due to low numbers of the former (WWF, 2012) and different dietary requirements of the latter two (Hashimoto et al., 2003; Hwang et al., 2002; Miyoshi and Higashi, 2005).

### 2.2. Data collection

We analysed 184 records of livestock depredation for which spatial coordinates were available. Data used from 2002 to 2009 were verified and geo-referenced by field staff from the Wildlife Conservation Society (WCS) China Programme, while data from 2010 to 2011 were provided by the Wildlife Depredation Compensation Office of the Forestry Bureau of Jilin Province, collected collaboratively by staff of the WCS China Program and Hunchun Municipal Forestry Bureau. WCS China and Jilin Academy of Forestry conducted an ungulate occupancy winter survey from 15th December 2010 to 15th January 2011 based on track counts. These data were analysed to map the estimated abundance for each prey species based on the Royle/Nichols Model of abundance-induced heterogeneity ( $\lambda$ ) across each of the 132 surveyed sub-grids covering 3.25 km<sup>2</sup> each (Fig. A1 in Appendix). GPS locations of all villages and towns in Hunchun, HNR boundaries, a digital elevation model for the Jilin area, as well as 233 recorded sites of ungulate snares (some of which had snared animals) encountered by HNR patrol teams from 2009 to 2012 were utilised in the analyses. Road networks and river layers (scale of 1:1,000,000) were obtained from the Geographic Information System database of Virtual Information Center for Amur River Region of the World Wide Fund for Nature (WWF, 2008). Maps of habitat types were provided by HNR. Lastly, tree and shrub cover data were obtained from remotely-sensed vegetation continuous fields raster maps derived from the MODIS satellite, accessed online via the Global Land Cover Facility, Earth Science Data Interface (GLCF, 2004). These data layers were then projected together in ArcMap 10.1 (ERSI, 2012), based on the Pulkovo 1942 Gauss Kruger Zone 22 Coordinate System.

### 2.3. Data analysis: prey density model

As prey survey data are missing for most parts of Hunchun County, a generalised least squares (GLS) model was first used to extrapolate site-specific prey abundance estimates ( $\lambda$ ) of red deer,



**Fig. 1.** Hunchun National Nature Reserve (HNR) in Hunchun, Jilin, China. Jilin province is shown in figure insert on top left, shaded in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sika deer, roe deer and wild boar as a function of 12 landscape covariates (elevation, aspect, slope, tree cover, shrub cover habitat types, distance to towns and villages, distance to rivers, distance to roads, distance to the Russian border, distance to ungulate snares and location within or outside the protected HNR area) based on HNR's 2010/2011 ungulate occupancy winter survey. Habitat types were classified into ten distinct categories, including wetlands, agricultural areas, coniferous forests and deciduous forests (full description found in [Table A1 in Appendix](#)). Aspect was extracted with slope and elevation from the digital elevation model in ArcMap, with flat land classified as '-1' and the various facings of slopes classified from 1° to 360° ([Table A2 in Appendix](#)). Euclidean distances to villages, rivers, roads, the Russian border and records of ungulate snares were also included. As the ungulate occupancy survey had been done in deep snow conditions, remote areas, steep slopes, and areas with less than 10% vegetation cover were not surveyed ([Management Bureau of Hunchun Amur Tiger National Nature Reserve et al., 2011](#)). Hence, model predictions for these areas would be non-representative and could not be used. Instead, manual inputs were used for these areas based on a priori knowledge from past studies in Russia, which had shown that red deer, roe deer, sika deer and wild boars tend to avoid higher altitude spruce-fir forests above 700 m elevation in Central Sikhote-Alin ([Miquelle et al., 1999](#); [Stephens et al., 2006](#)). Slopes greater than 12° were considered steep and accumulated deep snow that was difficult for ungulates to pass ([Stephens et al., 2005](#)), and also

generally avoided by tigers ([Miquelle et al., 1999](#)). Grid units with extracted covariates that matched either of these criteria or had less than 10% tree cover were considered absent of ungulates.

The mean of each landscape covariate was extracted from each of the 132 surveyed sub-grids using zonal statistics in ArcMap. A combined analysis of all species was then done in the R environment version 2.15.2 ([R Core Team, 2012](#)). The combined analysis was done by concatenating the data for each species, adding an extra covariate 'Species' that accounts for species identity and setting the dependent variable as the  $\lambda$  value for each species. This allowed for the evaluation of the overall effect of the explanatory variables on the dependant variable across all data points while considering the presence of four different species ([Zuur et al., 2009](#)). Meanwhile, separate analyses for each species were also conducted and the predicted densities were subsequently used to build another depredation risk model for comparison with the risk model built using prey density data from the combined prey model, which yielded quantitatively very similar results ([See Appendix B1 for the results and discussion of using separate species models](#)).

Collinear variables based on inspection of variance inflation factors (VIF) with the cut-off set at >4 were inspected and removed. Cleveland dot plots of covariates and diagnostic plots of standardized residuals versus fitted values and residuals versus each explanatory covariate of the linear model showed a violation of homoscedasticity assumptions. Thus, GLS with the option of including variance structures was used to fit the maximal model,

including two-way interactions of explanatory variables. All two-way interactions could not be included due to limited degrees of freedom, thus the random forests statistical technique was used to determine variable importance. Interactions between variables of low importance were not considered. To account for potential problems of pseudoreplication due to the concatenated 528 data points being treated as independent samples in R when they are in fact four sets of spatially-identical samples with 132 points for each species sampled, a new variable 'grid' was included as a random effect in a linear mixed effects model and this was compared to the GLS model to see if the random effect was significant using a likelihood ratio test.

As adding the random effect did not improve the model, GLS using restricted maximum likelihood estimation was used instead of the linear mixed effects model. Variance structures were then added for the covariates that demonstrated heteroscedasticity, with comparisons of different structure types made based on the Akaike information criterion (AIC) values to determine the optimal variance structure. This was followed by backward selection for the optimal fixed component of the model using likelihood ratio tests, where each explanatory variable that was not significant at the 5% level was dropped in turn. Spatial autocorrelation was checked by plotting an experimental variogram of the standardised residuals from this GLS model, and spatial correlation structures were also added for further comparison of AIC values between these models.

Finally, graphical validation of residuals against fitted values showed no heteroscedasticity problems in the variance (Fig. A2 in Appendix), and ten repeats of 10-fold cross validation of the model were performed to find the average prediction error of the model.

#### 2.4. Data analysis: depredation risk model

Counts of livestock depredation were used as a proxy for depredation risk. The number of depredation counts in each of the 1 km<sup>2</sup> grid units was extracted in ArcMap. As there were only 184 counts in total over 5012 grid units, most units (97.3%) had depredation counts of zero. Comparison of the distribution of cases with the expected frequencies of equivalent Poisson and negative binomial distributions showed an excess of zero counts (Fig. A3 in Appendix) that could consist of 'false zeros', in instances where depredation incidents were not included in the analysis due to missing spatial coordinates and also, when depredation incidents were not reported or recorded. In such situations, a zero-inflated model is commonly used (Mullahy, 1986), which can avoid biasing the estimated parameters and standard errors (Zuur et al., 2009). The zero-inflated model is a mixed model comprising of two sub-models: a Poisson or negative binomial GLM that models the count process (count model) conditional on a binomial model that models the probability of the count observation being a 'false zero' (zero-inflation model).

However, having many zeros in the data does not necessarily mean that a zero-inflated model would be a better fit (Cameron and Trivedi, 2010), thus statistical tests were used to compare four models: the Poisson generalised linear model (GLM), the negative binomial GLM, the zero-inflated Poisson (ZIP) model, and the negative binomial zero-inflated (ZINB) model. Before fitting the models, variables with multicollinearity problems were removed based on inspection of VIFs. The Vuong Statistic for non-nested models was then used to compare the Poisson GLM with the ZIP model and the negative binomial GLM with the ZINB model, while a likelihood ratio test was used to compare between the negative binomial and Poisson GLMs and the ZIP and ZINB (Yesilova et al., 2010).

The ZINB model was significantly better based on these tests, hence it was chosen to model depredation risk. All continuous covariate inputs were standardised to allow easier interpretation

of model coefficients (Gelman and Su, 2013). All main covariates (similar to those in the prey density model and with the inclusion of predicted prey densities) were included for both count model and zero-inflation model parts of the initial maximal ZINB model, but interactions were not included as they resulted in either a singular Hessian matrix error or a GLM fitting error in R. 'Distance to the Russian border' was expected to be an important covariate since depredation incidents may be influenced by livestock husbandry management in neighbouring countries, where in this case free-ranging livestock in Hunchun could be more readily accessible to tigers than barn-kept livestock from neighbouring villages in Russia. However, this covariate was highly collinear with the other explanatory variables and was dropped during inspection of VIFs.

Because records of ungulate snares (2009–2012) were non-completely overlapping with data of depredation incidents (2002–2011) and due to the dynamic nature of the snare data, an uncertainty analysis was also carried out by fitting another depredation risk model without using distance to snares as an explanatory variable, which yielded qualitatively similar results (See Appendix B2 for a discussion of the ungulate snare data and comparison of results).

Each of the explanatory variables was then dropped in turn and likelihood ratio tests were used to compare each nested model until no further terms could be dropped at the 5% significance level. A diagnostic plot of Pearson residuals against fitted values and a variogram to check for spatial correlation were done for this final model. A receiver operating characteristic (ROC) curve was also plotted to evaluate the discriminatory power of the model in distinguishing sites with high probabilities of depredation from sites with low probability of depredation. Ten repeats of 10-fold cross validation of the model were performed to find the average prediction error of the model as well.

### 3. Results

#### 3.1. Prey density model

Sika deer and roe deer densities, distances to snares, roads and villages, slope inclination, and habitat types of open woodland, coniferous and deciduous forests were significant predictors of prey density (Table 1). Taking red deer densities as the baseline reference, the model predicted roe deer and sika deer to be significant positive predictors of prey densities. There were significant positive interactions of some species with particular landscape covariates, where roe deer and wild boar densities were predicted to be higher further away from snares, and on steeper slopes. There were also significant interactions between certain landscape covariates that affected prey density. Prey densities were predicted to be higher at sites further away from villages when inside HNR and on steeper slopes, nearer to roads on more gentle slopes, and in greater tree cover on steeper slopes. Taking into account both main and interaction effects of each covariate, prey densities were predicted to be higher closer to snares for red deer but further away from snares for sika deer, roe deer and wild boar, further away from roads when on steeper slopes, nearer to villages when outside HNR and on more gentle slopes, on more gentle slopes for red deer and sika deer, and in open woodland, coniferous and deciduous forests.

Variance structures for species, tree cover, slope, elevation, distance to villages and distance to snares were added to deal with heteroscedasticity before backward selection for the optimal fixed effect terms. The addition resulted in a lower AIC value of 1066 from an initial of 1229, indicating a better fit.

The semi-variogram of standardised residuals obtained from the final prey model (Fig. A4 in Appendix) did not indicate obvious

**Table 1**

Covariate coefficients in the final prey density model with corresponding standard errors and *p*-values, and two-way interaction terms separated by ':' symbol. Bold texts indicate significance at the 5% level.

Prey model covariates	Coefficients	Standard error	<i>p</i> -Value
<b>(Intercept)</b>	<b>0.33</b>	<b>0.15</b>	<b>0.029</b>
<b>Species roe deer</b>	<b>0.80</b>	<b>0.19</b>	<b>&lt;0.001</b>
<b>Species sika deer</b>	<b>0.46</b>	<b>0.08</b>	<b>&lt;0.001</b>
Species wild boar	−0.12	0.13	0.35
<b>Distance to snares</b>	<b>−1.99</b>	<b>0.84</b>	<b>0.018</b>
<b>Distance to roads</b>	<b>4.67</b>	<b>2.29</b>	<b>0.042</b>
<b>Distance to villages</b>	<b>−7.91</b>	<b>3.39</b>	<b>0.020</b>
Tree cover	−0.00	0.00	0.536
Protected area (PA)	−0.13	0.08	0.096
<b>Slope</b>	<b>−0.05</b>	<b>0.02</b>	<b>0.036</b>
Elevation	−0.00	0.00	0.053
Agricultural land	0.05	0.07	0.460
<b>Open woodland</b>	<b>0.16</b>	<b>0.08</b>	<b>0.037</b>
Small-leaved forest on logged and burnt area	0.05	0.06	0.428
River valley	0.20	0.13	0.134
<b>Coniferous forest</b>	<b>0.30</b>	<b>0.15</b>	<b>0.046</b>
<b>Deciduous forest</b>	<b>0.28</b>	<b>0.08</b>	<b>&lt;0.001</b>
Broad-leaved Korean-pine forest	−0.00	0.08	0.923
<b>Species roe deer: distance to snares</b>	<b>8.46</b>	<b>2.57</b>	<b>0.001</b>
Species sika deer: distance to snares	1.20	1.15	0.299
<b>Species wild boar: distance to snares</b>	<b>5.31</b>	<b>1.74</b>	<b>0.003</b>
<b>Species roe deer: slope</b>	<b>0.08</b>	<b>0.03</b>	<b>0.012</b>
Species sika deer: slope	−0.01	0.01	0.488
<b>Species wild boar: slope</b>	<b>0.05</b>	<b>0.02</b>	<b>0.016</b>
<b>Distance to roads: slope</b>	<b>−0.87</b>	<b>0.38</b>	<b>0.023</b>
<b>Distance to villages: PA</b>	<b>6.68</b>	<b>2.08</b>	<b>0.001</b>
<b>Distance to villages: slope</b>	<b>1.63</b>	<b>0.50</b>	<b>0.001</b>
<b>Tree cover: slope</b>	<b>0.00</b>	<b>0.00</b>	<b>0.022</b>

spatial correlation in the data. Indeed, adding various spatial correlation structures to the final model also did not improve the fit of the model.

From the predicted prey density distribution of each species, red deer had the lowest abundance estimates ranging from 0 to 1.6 per km<sup>2</sup> grid unit, followed by sika deer with estimates from 0 to 1.9, wild boar from 0 to 2.9 and finally roe deer with a much higher abundance estimate overall of 0 to 5.5 (Fig. 2). High red deer densities were more likely to be at the northeast end of HNR and along the northern border with Russia, while there were generally much lower red deer densities outside of HNR especially in the northern and western mountainous parts of Hunchun. A similar distribution pattern was also observed for sika deer, with high sika deer densities mostly correlated with high red deer densities, except that there were more high density patches, some of which are outside of HNR in the central part of Hunchun. In contrast, both roe deer and wild boar densities were predicted to be highest in the northern and western mountainous part of Hunchun outside of HNR. However, roe deer and wild boar densities inside of HNR were still predicted to be much higher than red deer and sika deer densities generally, even where patches of high red deer or sika deer densities occurred (Fig. 2).

The average prediction error from ten repeats of 10-fold cross validation was 0.05, which showed good performance of the model (Molinario et al., 2005).

### 3.2. Depredation risk model

After simplifying the ZINB model applied to the depredation risk data, most of the remaining covariates were significant at the 5% level (Table 2). Log (theta) in the ZINB model is a dispersion parameter that suggests over-dispersion when it is significantly different from zero as compared to a Poisson distribution, which

was the case here and reinforced that the ZINB model was a better choice over the ZIP model. From the count model part of the ZINB model, it could be seen that there were significantly higher depredation risk nearer to snares and rivers, further away from roads, in areas with greater tree cover and in deciduous forests compared to other habitats (Table 2).

From the zero-inflation model part of the ZINB model, it could be seen that the nearer to snares and the further away from villages, the higher the chances of a zero depredation risk representing unmapped or unreported depredation incidents (false zeros). The model also showed that there were higher chances of false zeros occurring outside of HNR, while there were lower odds of false zeroes in open woodland and young regenerated forest habitats compared to other habitats (Table 2).

A horizontal smoothing spline added to the plot of residuals versus fitted values, indicated no evidence of heteroscedasticity (Fig. A5 in Appendix). However, the semi-variogram of standardised residuals obtained from the final depredation risk model (Fig. A6 in Appendix) indicated that there might be slight spatial autocorrelation in the data, especially within the first 15 km.

The ROC curve for the depredation risk model had an area under the curve of 0.80 and showed that for a specificity of 50%, the model had a sensitivity of 93%, while accepting a sensitivity of 80% would give about 75% specificity (Fig. A7 in Appendix). Thus, concentrating conflict mitigation efforts in 50% (or 25%) of the area would still ensure that conflict encounter will be accurate 93% (or 80%) of the time. The average prediction error from ten repeats of 10-fold cross validation was 0.01, which also shows good performance of the model (Molinario et al., 2005).

The predicted livestock depredation probability map of Hunchun (Fig. 3) showed that most areas with a high risk of depredation (ranging from 0.2 to 0.6) were located inside the community managed zone in HNR.

## 4. Discussion

The key finding from the depredation risk model indicated that the probability of livestock depredation by Amur tigers increased in areas closer to ungulate snares. While snare presence does not equate to successful poaching, it can be an indicator of poaching intensity (Becker et al., 2013; Kahler and Gore, 2012). Thus, proximity to snares may be an indicator of greater poaching pressure, which could depress wild prey density and lead to greater livestock depredation by tigers (Dinerstein, 1979; Gurung et al., 2006). Our prey density model supported this by showing that there was an overall lower density of ungulate preys closer to snare sites. This was expected as poaching by humans is a crucial determinant of the diversity and abundance of ungulate populations and has been known to depress species densities (Fa and Brown, 2009). While a switch in prey selectivity from depleted wild prey to livestock does not hold true for all large carnivores (Meriggi et al., 2011; Odden et al., 2008; Sidorovich et al., 2003), tigers had been shown to preferentially prey on the largest ungulate they can safely kill to optimise energy gains (Biswas and Sankar, 2002; Sunquist and Sunquist, 1989), as with other carnivores like snow leopards (Bagchi and Mishra, 2006) and African wild dogs (Gusset et al., 2009). Thus, livestock like cattle, which are of comparable biomass to the primary preys of the Amur tigers such as red deer and wild boar (Miquelle et al., 1996), may be more likely preferred by the tigers when large ungulates are scarce.

In contrast in India, Reddy et al. (2004) showed with scat analysis that even in a tiger reserve where wild prey densities were low and livestock densities were high (60% of total ungulate density), the total contribution of livestock in the diet of tigers remained low. This difference could be due to many possible factors, such

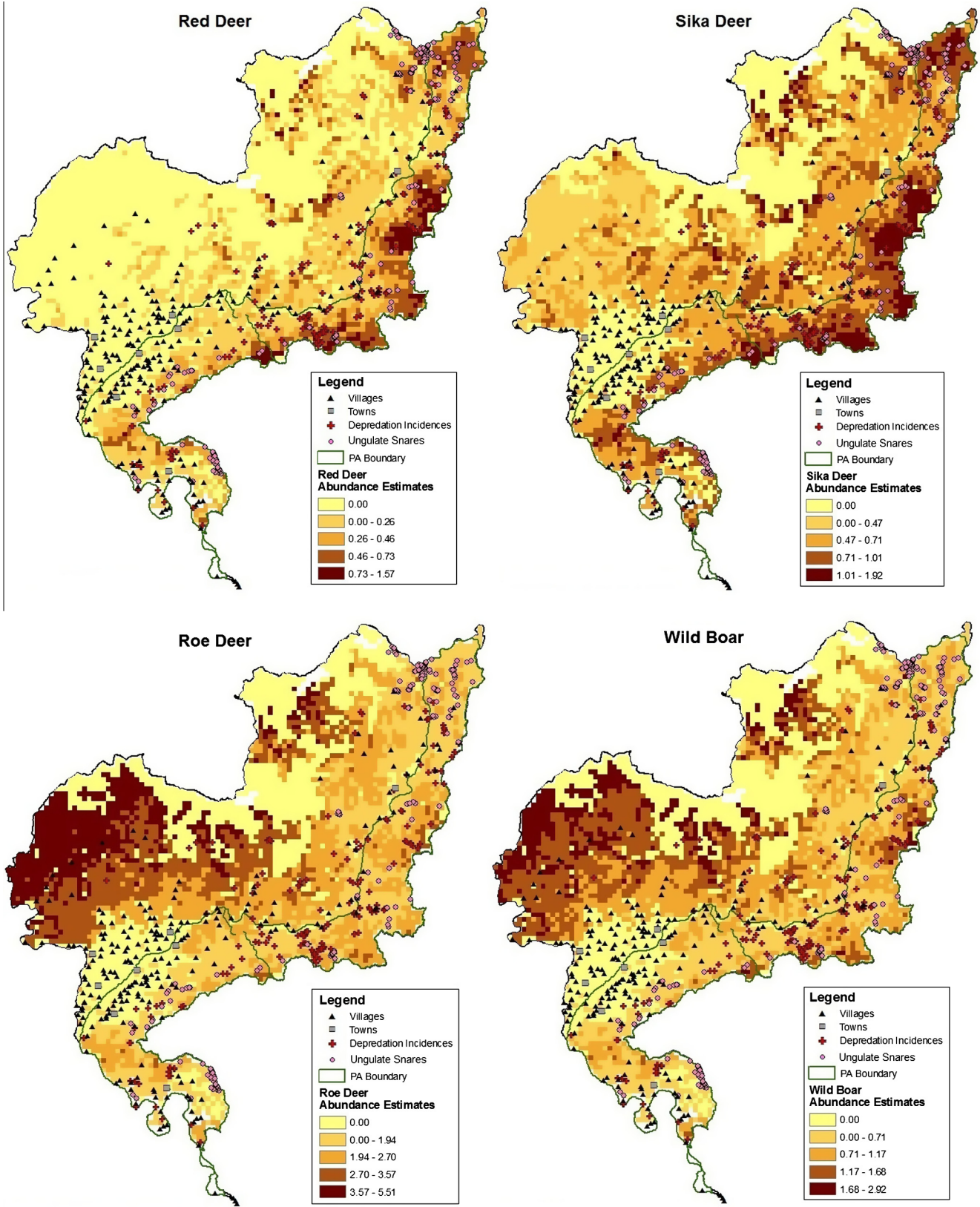


Fig. 2. Predicted prey density map showing abundance estimates per km<sup>2</sup> grid unit in Hunchun for each prey species.

as local climate, where mountainous northern systems have greater spatial and temporal fluctuations in ungulate prey densities (Luccarini et al., 1997), and local ungulate prey types, but perhaps

most importantly the local husbandry techniques of villagers. For instance, Bagchi et al. (2003) found that in Ranthambore National Park, India, livestock still accounted for a high proportion

**Table 2**

Standardised covariate coefficients in the final depredation risk model with corresponding standard errors and *p*-values. Bold texts indicate significance at the 5% level.

	Coefficients	Standard error	<i>p</i> -Value
<i>Count model covariates</i>			
(Intercept)	<b>-3.69</b>	<b>0.26</b>	<b>&lt;0.001</b>
Aspect	<b>-0.47</b>	<b>0.18</b>	<b>0.008</b>
Distance to snares	<b>-4.71</b>	<b>0.56</b>	<b>&lt;0.001</b>
Distance to rivers	<b>-0.70</b>	<b>0.19</b>	<b>&lt;0.001</b>
Distance to roads	<b>0.87</b>	<b>0.39</b>	<b>0.026</b>
Tree cover	<b>0.70</b>	<b>0.20</b>	<b>&lt;0.001</b>
Coniferous forest	-15.15	997.35	0.988
Deciduous forest	<b>1.00</b>	<b>0.33</b>	<b>0.002</b>
Log (theta)	<b>-0.98</b>	<b>0.33</b>	<b>0.003</b>
<i>Zero-inflation model covariates</i>			
(Intercept)	0.52	0.67	0.434
Distance to snares	<b>-5.75</b>	<b>1.68</b>	<b>&lt;0.001</b>
Distance to villages	<b>2.67</b>	<b>0.78</b>	<b>&lt;0.001</b>
Protected area	<b>-2.33</b>	<b>0.53</b>	<b>&lt;0.001</b>
Agricultural land	-17.16	2727.62	0.995
Open woodland	-2.21	1.14	0.052
Small-leaved forest on logged and burnt area	-1.11	0.57	0.051

(10–12%) of the tigers' diet despite the park's high wild prey densities, due apparently to extensive open livestock grazing in the park, reinforcing that tigers do readily prey on livestock when they are available.

Although higher red deer densities were predicted closer to snares contrary to the other prey species, this contributed little to overall prey density due to the comparatively very low densities of red deer. One reason for higher red deer densities nearer to snares could be due to the greater interspecific competition between greater abundances of sika deer, roe deer and wild boar with red deer further away from snares (Abernethy, 1994; Gebert and Verheyden-Tixier, 2001; Latham et al., 1996). Such competition for resources (See Appendix B1 for details) could outweigh the effect of snaring on reducing red deer numbers, especially since the snares are indiscriminate and were likely to catch more abundant prey.

Another reason could be that most of the red deer population in Hunchun might have come from source populations in Russia (Chen et al., 2011), resulting in potentially higher densities in HNR near the Russian border even though there are more snaring incidents there. As such, neighbouring countries like Russia could play an important role in providing connected sources of ungulates that help to maintain populations which are hunted in the sinks of surrounding communities (Naranjo and Bodmer, 2007; Novaro et al., 2000).

Thus, elimination of snares for poaching ungulate prey could be imperative to ensure that natural prey populations do not deteriorate, and together with proper livestock husbandry techniques, can help reduce depredation conflicts and minimise detrimental impacts on tiger populations in the Hunchun region.

The livestock depredation model indicated that landscape covariates remained crucial correlates of depredation risk as well. There were increased chances of livestock depredation at sites nearer to rivers, further away from roads and had greater tree cover, consistent with the findings by Li et al. (2009) in a study of environmental factors affecting livestock depredation in Hunchun. In addition, our model found other significant covariates of depredation. Depredation risk increased in deciduous forests compared to other habitat types, which were not included in the analysis by Li et al. (2009). Interestingly, most depredation incidents occurred in forests at the edges of agricultural land within or adjacent to the boundary of HNR (Fig. A8 in Appendix); this is likely due to the fact

that villagers usually graze their livestock within a few kilometres of their settlement (Chin, 2012). This is also supported by findings from the zero-inflated part of the depredation risk model, where the probability of unmapped or unreported depredation incidents increase with greater distance away from villages or in areas outside of HNR. Applying a ZINB model in this case is useful in identifying and accounting for explanatory variables that may contribute to unrecorded depredation data.

The prey density model predicted prey densities to be higher further away from towns and villages in HNR, and further away from roads on gentle slopes. It is expected that ungulate densities increase with greater distance away from human-dominated landscapes (Marchal et al., 2012). However, prey densities were predicted to be higher nearer villages outside of HNR. This could be because there were no snare patrols and records in the relatively isolated villages of the northwest area outside of HNR (See Appendix B2), or that landscape covariates there were more favourable with less encroachment and usage of surrounding forest resources by these local communities. Thus, it may be important to collect more information about ungulate prey dynamics in this area, which could contain vital source populations of roe deer and wild boar. Predicted prey densities may have been unrealistically high in that area (up to 5.5 roe deer per km<sup>2</sup>) possibly due to missing model parameters such as the amount of food resources and climatic conditions that could limit ungulate carrying capacities (Stephens et al., 2006). In general, the prey density model showed that anthropogenic activities greatly affect prey populations.

Our modelling approach presented several limitations. The 2010/2011 Hunchun ungulate winter occupancy survey used in our prey density model covered only about 426 km<sup>2</sup> in Northeast Hunchun (including sites both inside and outside of HNR, Fig. A1 in Appendix), in a possibly more pristine area of the reserve according to the survey report (Management Bureau of Hunchun Amur Tiger National Nature Reserve et al., 2011), thus it might not be accurate to extrapolate the results to the whole of Hunchun, especially in western and northwest areas of Hunchun where ungulate surveys have not been carried out previously and predicted densities could not be verified (See Appendix B3 for a discussion on alternative ungulate surveys). Similarly, a greater number of depredation incidence records could have allowed for a more robust analysis. Also, we noted that the mapping of snare presence was dependent on detection and reports by HNR anti-poaching patrols, which did not equally cover all areas and hence were likely biased to some extent (Knapp et al., 2010). However, the snare records were compiled over a period of four years (2009–2012) and over an extensive area (See Appendix B2), thus they could be a good representation of the snaring occurrences despite possible temporal variability, due to non-complete overlap with the timeframe (2002–2011) for which livestock depredation data were collected. The fact that most snares were found in forested areas along the edges of agricultural land and open woodland (Fig. A9 in Appendix) (i.e., closer to human settlements) where it is easier to set and monitor snares is probably representative of the situation on the ground as well. Another data limitation would be extracting the mean for a circular variable like aspect, which may have been problematic for a small number of grid cells where the bearing changes abruptly.

Furthermore, as most depredation incidents occurred in the summer and not in the winter when livestock are mostly in stalls, the winter survey of wild ungulate distribution may not be indicative of ungulate densities and distribution in the summer. While the optimal time for track count surveys is in winter when snow provides an excellent medium for detecting tracks, summer ungulate track count surveys could still help determine if distribution changes significantly. However, recent analyses of red deer

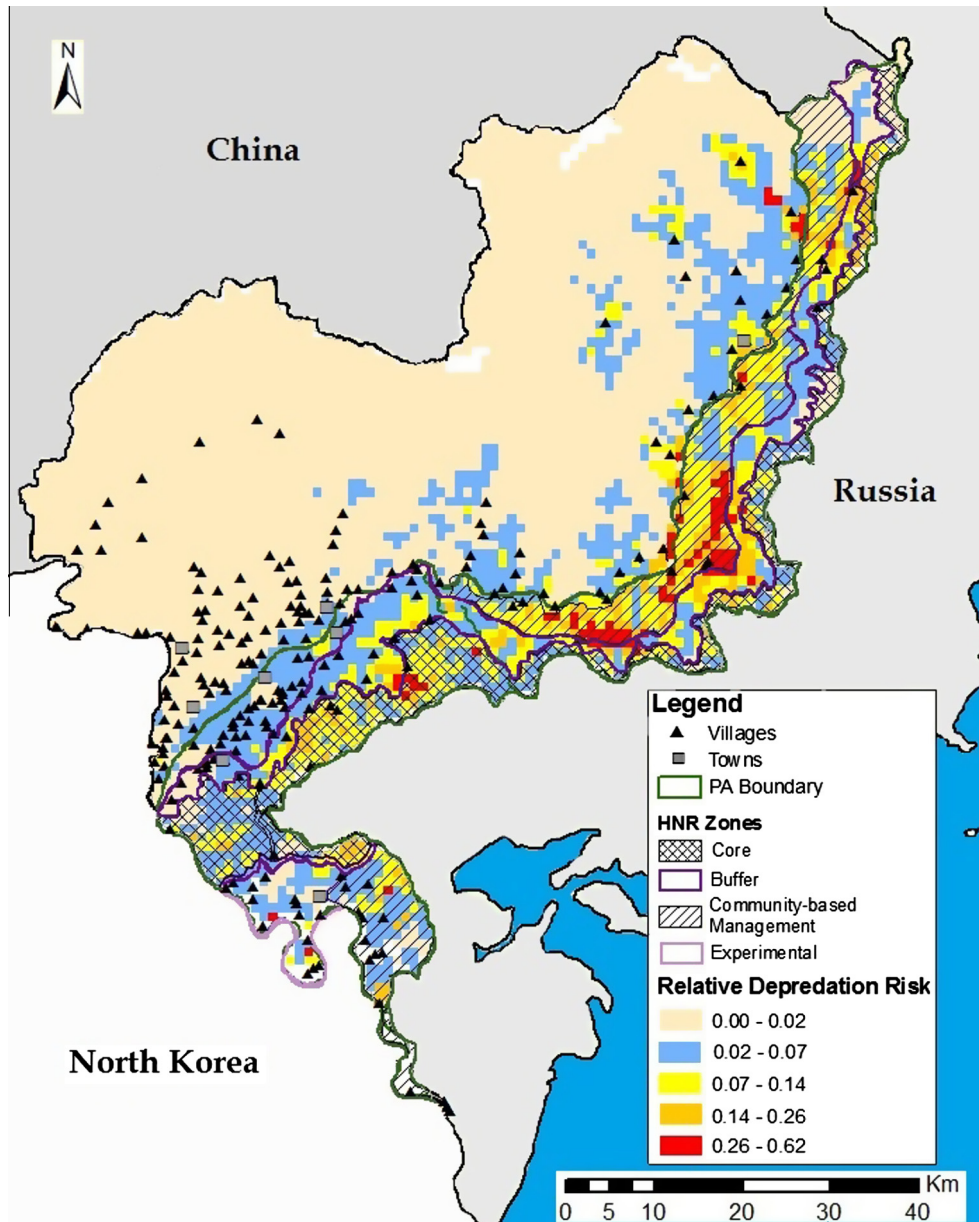


Fig. 3. Predicted livestock depredation risk map of Hunchun generated from final zero-inflated negative binomial depredation risk model. White areas indicate alpine and wetland habitats where no predictions were made.

movements in the Russian Far East, at least, suggest that migration is fairly uncommon (Hojnowski et al., 2012).

Lastly, the distribution of free-grazing domestic livestock has not been documented, but could be an important covariate in examining the effect of competitive grazing on wild ungulate prey populations, and in determining risk of depredation.

#### 4.1. Management policy implications

Overall, the concentration of high depredation risk areas in the community co-managed zone of HNR could indicate that current strategies require re-evaluation. Community-co-management zones serve to improve conservation goals within protected areas, by including the participation of local stakeholders in implementing initiatives that account for their socioeconomic sacrifices from living in and adhering to the regulations of protected areas (Pechacek et al., 2013; Wells and McShane, 2004). The aim here

is not only to conserve Amur tigers, but to build up the capacity for long term human welfare as well, such as in minimising losses from wildlife conflicts (Ogra and Badola, 2008; Sifuna, 2010).

Because preferred tiger prey are large ungulates like red deer and wild boar (Hayward et al., 2012; Miquelle et al., 1999; Ramakrishnan et al., 1999), efforts to strengthen law enforcement to minimise wild ungulate snaring are imperative for the recovery of wild ungulate populations that could support the recovery of Amur tigers and reduce the level of livestock depredation.

Stricter zoning enforcement to prevent livestock grazing in the core areas would probably decrease depredation incidents (Goodrich, 2010; Nyhus et al., 2010) but may not do so significantly, as the extensive home ranges of Amur tigers (Smirnov and Miquelle, 1999) would mean that zoning would only be effective at very large spatial scales (Linnell et al., 2005). Given the number of villages located within HNR and the narrow elongated shape of HNR, even livestock in buffer and community co-management



zones of HNR and outside HNR will continue to face high depredation risk that will only increase if Amur tigers begin to recover. Thus it is recommended that not only should livestock be eliminated from core zones of HNR completely, more effective livestock husbandry practices will have to be implemented especially in community co-managed zones. These include returning of livestock to protected enclosures during the night, and placing legal restrictions on livestock numbers and habitat encroachment by cattle farms (Goodrich, 2010), all of which can be aided by using the depredation risk map. With better knowledge of where high risk zones existed, villagers might be more willing to invest in location-specific measures tailored to the unique needs of each village.

Finally, the entire compensation scheme for livestock depredation should be reviewed. Currently livestock losses from tiger depredation are compensated at the full market value regardless of location or livestock management practices, thus eliminating any incentives for locals to improve husbandry practices to prevent losses (Pettigrew et al., 2012). In fact, pastoralists may even reduce efforts to protect livestock and rear more than can be managed in cases where receiving compensation is easier than caring for and selling livestock (Bulte and Rondeau, 2005). Compensation in Jilin for wildlife damages amounted to US\$270 thousand in 2007, and quickly reached US\$1.1 million in 2008 and US\$1 million in 2009 (Cai et al., 2011), placing a heavy financial burden on the government. These costs are only likely to spread and escalate if there is any increase in tiger occurrence in the region. A new compensation scheme designed with stricter eligibility criteria and also long-term insurance pay-outs may provide the financial incentive for villagers to invest in preventive measures (Pettigrew et al., 2012).

In summary, increasing wild prey numbers, improving livestock husbandry techniques, and eliminating monetary incentives that reward farmers for illegal and poor management practices are priorities both for tiger population recovery in Northeast China and to motivate responsible stewardship of HNR among the locals as well.

#### 4.2. Conclusion

Both the prey density model and livestock depredation risk map showed that anthropogenic factors are significant correlates of human-tiger conflict in addition to environmental factors. In particular, proximity to human snaring activities likely depresses wild ungulate prey numbers and also increases depredation of livestock by Amur tigers. However, environmental conditions like distance to rivers, tree cover and habitat types remain vital in determining depredation risk. Depredation risk maps can help motivate and focus preventive and mitigation efforts in depredation conflicts, but fundamental changes are needed in livestock management and compensation programs to ultimately sustain ecologically functioning protected areas especially in community co-managed zones, for the conservation of endangered wildlife in mixed-use landscapes where humans and wildlife co-exist.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.10.011>.

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