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Spatial distribution drivers of Amur leopard density in northeast China

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ABSTRACT

The Amur leopard (*Panthera pardus orientalis*) is highly elusive, rare species, critically threatened with extinction worldwide. In this study, we conducted camera-trap surveys of an Amur leopard population in Jilin Province, northeast China. We estimated population abundance and density distribution, and explored the effects of prey population densities and biomass of prey, habitat and anthropogenic factors on the spatial distribution of Amur leopard density. Our results suggested that Amur leopard density was 0.62 individuals/100 km^2 and 16.58 individuals might live within the study area. The spatial distribution of Amur leopard density exhibited different responses to the population densities of different prey species. We found that two ecological thresholds existed in maximum responses of Amur leopard distribution to elevation and prey biomass. Vegetation and anthropogenic factors also showed significant effects on leopard population distribution. In general, there was a combination of habitat factors including, not only prey assembly and biomass, but also vegetation, anthropogenic and geographical factors driving the spatial distribution of Amur leopard population. These insights informed us that comprehensive adaptive landscape and prey conservation strategies should be conducted for saving this critically endangered predator.

1. Introduction

The Amur leopard (*Panthera pardus orientalis*) is an elusive subspecies of leopard, which currently occurs in northeast China and the Russian Far East. It is the most rare felid subspecies in the world and has been listed as critically endangered on the IUCN red list since 1996 (Jackson and Nowell, 2008). The Amur leopard is also a first class protected subspecies in China (Wang, 1998). There were an estimated 50 individuals in Russia according to the winter tracking survey of 2013 (http://www.tx2.org.cn/picvideo/ShowArticle.asp?ArticleID=831) and 41 individuals estimated in Russia by camera trap surveys from 2003 to 2011 (Aramilev et al., 2012). Yang et al. (1998) estimated less than 10 Amur leopards in China; however, this estimate for the size of the Amur leopard population is derived from a snow track survey, conducted in China primarily for Amur tigers (*Panthera tigris altaica*). During recent years, while searching for snow tracks of Amur leopards, a large part of the Amur leopard range in China was also surveyed. There were 8–11 Amur leopards found during one survey on the southern slopes of Laoye Mountain in Jilin, China, taken during the winter 2011 to spring 2012 (Wu et al., 2013). An additional 5–7 leopards have been identified on the southern slopes of Laoyeling Mountain in Heilongjiang, China, during a winter survey in 2013 (http://www.tx2.org.cn/News/ShowArticle.asp?ArticleID=894). However, the snow track method may not estimate the number of individual leopards accurately.

All wildlife requires food and space for life activities (Morris, 2003). Habitat loss is a leading cause of population decline and extinction of endangered or threatened species (Halley and Iwasa, 2011). Food shortage is also a limiting factor of top predator populations, particularly large carnivores (Ullas Karanth and Chellam, 2009). Therefore, abundance, and the spatial distribution of prey population, may influence habitat selection and spatial distribution of predators (Aryal et al., 2014). Animals select habitat under the concomitant influences of habitat quality, resource availability, interspecific competition and interspecific interaction (Fretwell and Calver, 1969; Rosenzweig, 1981; Morris, 1988). Abundance and the associated spatial distribution of prey or food resources also play a crucial role in determining when and where predators forage (Santora et al., 2011; Karanth et al., 2004). Consequently, carnivore density or abundance may be correlated with preferred prey densities and may, in turn, affect the relative abundance of prey (Trites, 2002; Karanth et al., 2004; Hayward et al., 2007). Studies concerning the effects of prey abundance and spatial distribution on the use of space by carnivores provide insights into more effective ways to ensure the conservation of large carnivores (Karanth et al., 2004). Leopards usually live in remote areas, which are difficult to access, but they also occasionally visit the outskirts of urban areas adjacent to their ranges (Khorozyan and Abramov, 2007). Amur leopards prefer Korean pine forests at low elevations, well away from main roads, and avoid deciduous forests, meadows, shrubs and agricultural fields

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(Hebblewhite et al., 2011). Little is known regarding the effects of both prey species and population abundance on the spatial distribution of the Amur leopard population in northeast China, in the regions bordering the Russian Far East.

Reliable spatial distribution estimates of population density are crucial to population conservation and habitat management of elusive endangered species (Sollmann et al., 2013; Li and Wang, 2013; Zimmermann et al., 2013; Zhang et al., 2014). Camera trapping is an effective, non-invasive technique for wildlife surveys and is currently a popular tool for estimating population sizes of elusive, rare species (Karanth, 1995). Individual identification technology based on distinctive fur patterns makes identification of individual large mammals possible and accurate with camera trap photograph data (Hiby et al., 2009). To our knowledge, no studies have estimated the population size of Amur leopards using statistical estimators based on camera trap data in China. Therefore, we used the camera trap method to survey Amur leopards starting in the spring of 2012 in the southern Laoye Mountain in Jilin. Subsequently, the first evidence of a wild Amur leopard with two kittens was obtained in October 2013 by camera traps (Jiang and Qi, 2014).

In this study, we first estimated the density and spatial distribution of Amur leopard populations using spatially explicit capture–recapture (SECR) models with camera trap data (Royle et al., 2009). Then we assessed relationships between leopard density distribution and prey abundance, total prey biomass, or other habitat factors. We hypothesized that: (1) the population abundance and spatial distribution of prey species influence the spatial distribution of the Amur leopard population; (2) anthropogenic disturbances would decrease the spatial distribution of Amur leopard density; and (3) vegetation and elevation are the main habitat factors determining the spatial distribution of Amur leopard density.

2. Methods

2.1. Study area

The study area is located in the southern slopes of the Laoye Mountain of Jilin Province, northeast China, and borders Russia (E 130.609°–131.309°, N 43.231°–43.559°; Fig. 1). The study area is an important part of Amur leopard habitat in China. It is a mountainous area, with elevations ranging from 200 m–1200 m. The climate is temperate continental monsoonal with annual average temperature of 1.5 °C. Total annual precipitation is 450–600 mm, and occurs mainly from May to September. The dominant vegetation at low elevations is secondary deciduous forest and mixed coniferous–deciduous forest is distributed at high elevations (usually 600–1200 m). Roe deer (*Capreolus pygargus*) and wild boar (*Sus scrofa*) are the dominant prey of Amur leopards. Other prey, such as red deer (*Cervus elaphus*) and sika deer (*Cervus nippon*), are found at low densities.

2.2. Field surveys

For this Amur leopard survey, we divided the study area into 84 units, with approximately 10 km^2 for each one. Camera traps were placed on leopard trails or at locations where mammal traces were found within each unit (Fig. 1). Two infrared cameras (LTL-5210A and LTL-6210, Shenzhen Weikexin Science & Technology Development Co., Ltd, Shenzhen, China) were set facing each another at each trap station to increase capture probabilities and capture the fur patterns on both sides of the leopard (Silver et al., 2004). Cameras were attached to trees 45–50 cm above the ground at a distance of 3.5–4 m from animal trails in order to take quality pictures of Amur leopards (Nichols and Karanth, 2002). Previous studies have found that female Amur leopard

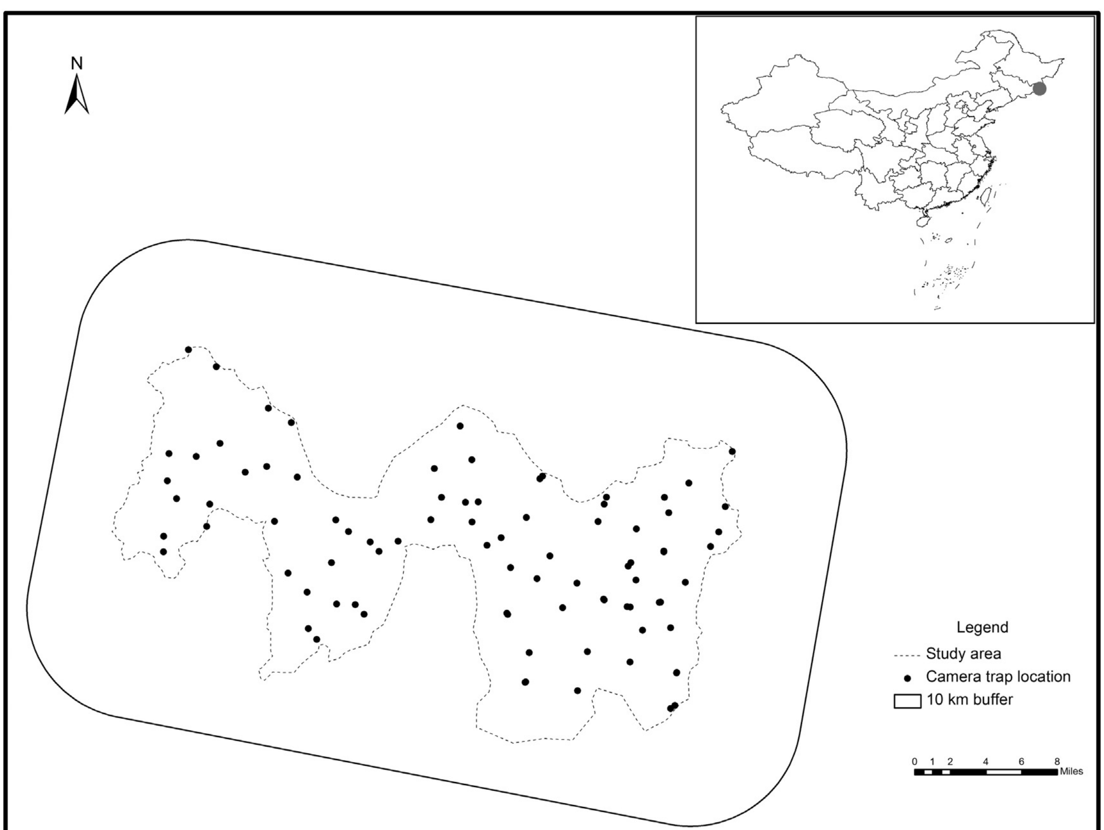

Fig. 1. Illustration of camera traps locations and survey area with a 10 km buffer zone. The study area is located in Jilin province, northeast China. The camera trap stations (black points) were in operation from April 2013 to July 2014.

Table 1
Habitat variables tested for association with Amur leopard (*Panthera pardus orientalis*) density and its prey density distribution. Note: Data were processed in ArcGIS 9.0 in grid format (0.5 km × 0.5 km pixel) based on re-sampled or interpolated measurements. Data were extracted from the Environmental and Ecological Science Data Center for West China (EESDCWC), National Natural Science Foundation of China (NSFC) (website: http://westdc.westgis.ac.cn) and Information Center of Amur-Heilong River Basin (ICAHRB) (http://amur-heilong.net/) databases.

	Description of the habitat factor	Data type	Unit
Vegetation			
Forest	Forest area ratio including all types of forest types of each pixel. The vegetation vector map of China (1:1 million) in 2000 year was converted into grid with 0.5 km resolution	Continuous	[Ratio]
Mixed broad leaf-conifer forest	Mixed broad leaf-conifer forest area ratio of each pixel. Source is the same to forest with 0.5 km resolution.	Continuous	[Ratio]
Firs spruces forest	Firs–spruces forest area ratio of each pixel. Source is the same to forest with 0.5 km resolution.	Continuous	[Ratio]
Broad leaf Korean pine forest	Mixed broad leaf-Korean pine forest area ratio of each pixel. Source is the same to forest with 0.5 km resolution.		[Ratio]
Anthropogeneic factors			
Distance to road	Distance from the central point of each pixel to the nearest road.	Continuous	[km]
Topography and river			
Elevation	Elevation grid with 0.5 km resolution.	Continuous	[m]
Distance to river	Distance from the central point of each pixel to the nearest river.	Continuous	[km]

home ranges are between 45 and 65 km^2 (Augustine et al., 1996). To ensure that at least 4–6 camera trap units worked in each home range, the average distance between camera trap stations was 3.7 km (min = 1.4 km, max = 4.1 km), also to ensure the capture independence of between neighboring trap stations (Fig. 1). As there were 2 non-timber product gathering areas located in the study area, about 8 study units were influenced greatly by stolen cameras, a total of 76 pairs of camera traps were set for approximately 15 months (476 days) from 2013 to 2014. Camera trap data were retrieved from the cameras every two months. Cameras recorded capture dates and times of the Amur leopards.

From February to March 2014, 10 plots were conducted to estimate ungulate densities, following the methods of Zhang et al. (2013) and Liu et al. (2015). Each plot with the area of approximately 10 km^2 (i.e., 5 km × 2 km) consisted of five parallel 5-km transect lines separated by 500 m. Two perpendicular transect lines were placed at the two ends of the five parallel transect lines to create four sections in each plot. Five survey teams conducted prey surveys simultaneously on each plot within 24 h after snowfall. All participants were able to distinguish the snow tracks of various ungulate species and estimate group sizes based on the number of ungulate snow tracks. We recorded the geographic coordinates, species, group size and direction of movement of the individuals or groups.

2.3. Data analysis

We used Extract Compare software to identify the photos of individual Amur leopards, with the location and time of initial capture being taken into account (Hiby et al., 2009). Then, leopard density was estimated using information on capture histories in combination with the spatial locations of captures under a unified Bayesian modeling framework (Gopalaswamy et al., 2012). The SECR model was a logistic regression model for binary observations of individual captured at a particular camera trap during sampling occasions (Gopalaswamy et al., 2012). It not only included individual heterogeneity in capture probabilities, but also offered estimates of spatial variation in animal densities (Royle et al., 2009). We used this model implemented in SPACECAP, a user-friendly R software package, to estimate the densities of the Amur leopard population (i.e., number of leopards per 100 km^2) using all the collected camera trap data (Gopalaswamy et al., 2012).

Although the camera trap method is regarded as a non-invasive monitoring method for elusive animals, Wegge et al. (2004) found that tigers exhibited behavioral responses to camera traps, leaving the trail just before camera flashed and returning to the trail after the flashes. The potential of individual heterogeneity in capture probabilities should be considered in model analyses (Wang and Macdonald, 2009). In this study, we used the "trap response present" option to build the SECR models.

We added a 10 km buffer zone surrounding our camera trap area to ensure that no individual animals outside the buffered area had a probability of being photo captured, given that female Amur leopard have home ranges of 45–65 km^2 (Augustine et al., 1996). With the buffer, the area extended north into Russia; however, we used data to predict prey density and biomass from the area located in China only.

We only used animal tracks within <24 h after snowfall to calculate the number of individuals of each prey species in each sample plot (Zhang et al., 2013). The number of individuals in each sample plot was calculated using the following equation:

$$w = \sum_{i=1}^{n} \sum_{j=1}^{m} j \times \left(x_{ij}\text{-}y_{ij}\right)$$

where w is the total number of animals; j is group size ($j = 1, 2, 3,....m$) based on the specific number of snow tracks of individual animals of each group; i is the ith section of a sample plot, $i = 1,2,3,4$; x_{ij} is the number of groups having j individuals entering the sector i; and y_{ij} is the number of groups having j individuals leaving the section i. Ungulate density was calculated by dividing w by the area of each actual surveyed sample plot.

Prey number in each plot was converted to biomass using published adult female body weights for northeastern China (roe deer: 30 kg; wild boar: 120 kg; referring to Zhou et al., 2011). We then linked ungulate density and ungulate biomass with habitat and anthropogenic variables separately with linear regression models to predict both the density and the biomass for the study area (Table 1). Data on plot areas, habitat and anthropogenic variables were extracted by ArcGIS 9.3 (ESRI, 2004).

Table 2
Posterior summaries of the parameters of SECR model for the Amur leopard camera trapping data based on the 10 observed individuals. Note: N is the number of Amur leopard activity centers in the population exposed to sampling and D is the density per 100 km^2, ψ is the data augmentation parameters, and σ is the parameter in the bivariate normal pdf, β is regression coefficient that measures the behavioral response, and $p0$ is detection probability, the estimates of "$p1$" and "$p2$" are also reported. $p1$ is the encounter probability for individuals that have not previously been encountered, and $p2$ is the encounter probability for individuals subsequent to their initial encounter.

Parameter	Mean	SD	5%	95%
ψ	5.76	1.16	3.38	7.85
σ	0.00	0.00	0.00	0.01
β	1.62	0.50	0.48	2.43
$p0$	0.34	0.10	0.16	0.54
N	16.58	3.99	10	24
D	0.62	0.15	0.37	0.90
$p1$	0.00	0.00	0.00	0.01
$p2$	0.77	0.15	0.42	0.93

Table 3
Population densities (individuals/km^2) of 5 ungulate species were calculated through sample plot survey.

Plot no.	Area (km^2)	Roe deer	Red deer	Wild boar	Sika deer	Musk deer
1	7.14	0.42	0.00	0.00	0.00	0.00
2	12.01	0.17	0.00	0.00	0.00	0.00
3	11.29	1.68	0.00	0.27	0.09	0.00
4	11.53	0.78	0.17	0.09	0.26	0.00
5	5.90	2.37	0.00	0.34	1.02	0.00
6	5.93	1.86	0.00	2.53	0.00	0.34
7	7.76	3.35	0.00	0.26	0.00	0.00
8	6.39	0.16	0.00	0.94	0.00	0.00
9	5.17	0.00	0.00	0.19	0.00	0.00
10	6.17	1.46	0.00	0.65	0.16	0.00
Average $\pm$ SD	7.93 $\pm$ 0.26	1.22 $\pm$ 0.11	0.02 $\pm$ 0.01	0.53 $\pm$ 0.08	0.15 $\pm$ 0.03	0.03 $\pm$ 0.01

Lastly, we linked leopard densities with the total biomass of both roe deer and wild boar by generalized additive models (GAMs) (Table 1) (Guisan et al., 2002). We also used GAMs to determine relationships between roe deer density, wild boar density and leopard density. We used Spatial Analysis in Macroecology (SAM) software to check the spatial auto-correlation in the residuals of GAMs, and then ran the order of "kriging" in Arcmap to realize the spatial interpolation to ensure that the spatial auto-correlation was mitigated (Stein, 1999; Childs, 2004).

3. Results

3.1. Estimates of Amur leopard abundance, ungulate density and biomass

During about 15 months (totally 476 days) from 2013 to 2014, a total of 76 camera trap stations were set up at a density of one camera trap station per unit (i.e., 10 km^2). We obtained a total of 76 photographic "captures" of Amur leopards in an area of 1214.53 km^2. Ten individuals were unambiguously identified using the Extract Compare software from 68 of the photographic captures, whereas the remaining eight photographic captures were unidentifiable.

During February and March 2014, red deer and musk deer were found in only one of the 10 plots. The average densities of roe deer and wild boar were 1.22 $\pm$ 0.11 individuals/km^2 and 0.53 $\pm$ 0.08 individuals/km^2, respectively (Table 3). The biomass of prey (i.e., roe deer and wild boar) was calculated at 99.88 kg per km^2.

3.2. Amur leopard population size and density assessment

The parameters of SECR models for the Amur leopard camera trap data based on 10 observed individuals were summarized in Table 2. The Amur leopard density was 0.62 (0.37–0.90) individuals/100 km^2 in this area. The total number of leopard individuals was 16.58 (10–24) individuals. The spatially explicit leopard density distribution map was created as a raster image with a resolution of 0.25 km^2 per grid cell or pixel (Fig. 2).

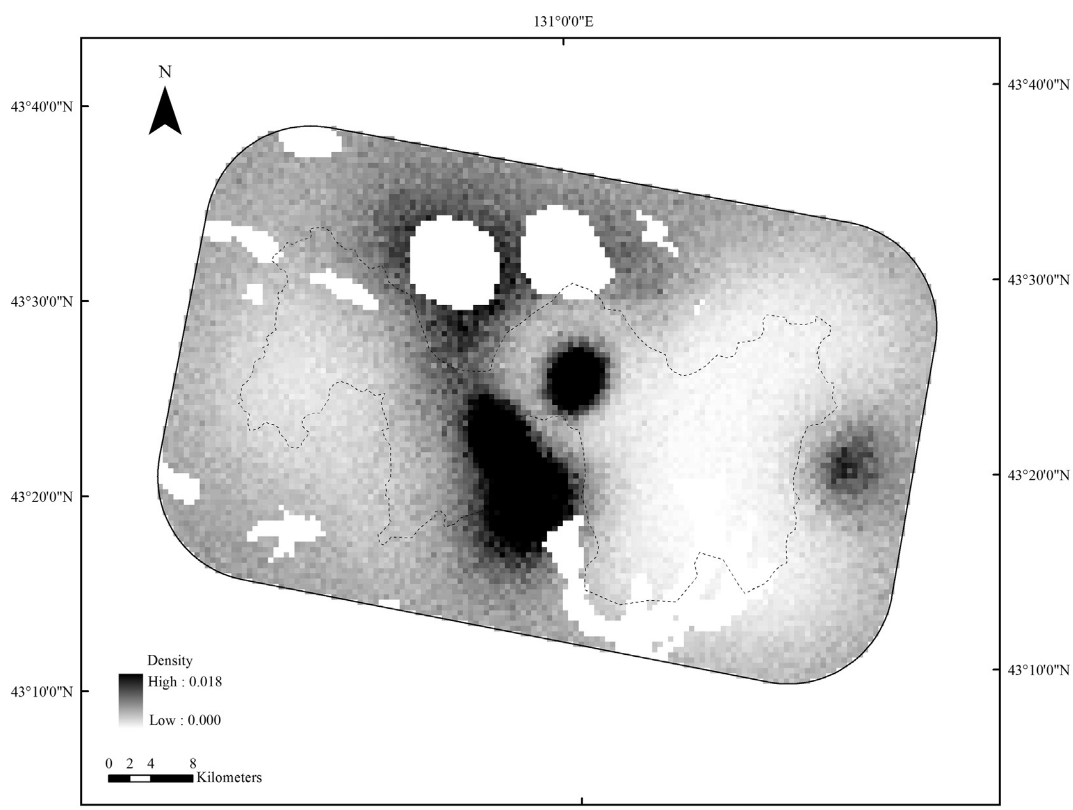

Fig. 2. The spatial distribution of the Amur leopard density was predicated by SECR model. The color gradient of each pixel represents the density gradient of Amur leopard population at each pixel. Only pixels judged to be suitable habitat are included and the size of each pixel is 0.25 km^2.

3.3. Relationships between ungulate density or biomass and habitat factors

Results of linear regression models showed that the density of wild boar population and biomass of prey population increased with increasing proportions of mixed broad leaf conifer forests and with decreasing distance to the nearest river, respectively. Roe deer densities only showed a negative relationship with distances to the nearest river (Supplementary data 1). Density of roe deer and wild boar was 0–2.55 individuals/km^2 and 0–2.28 individuals/km^2, respectively. The biomass of prey population was 0–351.83 kg/km^2 (Supplementary data 2–4).

3.4. Response of Amur leopard density to prey and habitat factors

Results of GAMs showed that leopard density increased with increased roe deer density, increased with a greater distance to the nearest road, increased with the proportion of mixed broad leaf Korean pine forests, but decreased with increased wild boar density and with an increased proportion of spruce–fir forest. However, responses of leopard density to elevation and prey biomass peaked at the elevation of 600–650 m and at the biomass of 100–150 kg per 0.25 km^2 (Figs. 3–4).

4. Discussion

Individual recognition of the studied population is a precondition for the capture recapture method using camera traps (Foster and Harmsen, 2012). In this study, eight of the photographic captures were unidentifiable due to either high darkness of the leopard pictures or the high speed of the leopard when passing in front of the camera trap. Noss et al. (2003) assumed that when an individual captured by the camera trap cannot be identified, it could be attributed to one of the previously unidentified individuals from the same area. However, in this study, we excluded unidentifiable photographic captures (Mazzolli, 2010) because leopards are not strictly solitary animals. The sample size of uniquely identified individuals in this study fell within the sample size range of previous studies of spatially explicit density estimations for large cats, which ranged from 2–31 individuals with a mean of 10.2 individuals (Foster and Harmsen, 2012). The Amur leopard population abundance estimate of this study provides wildlife biologists and managers with the first-hand information on the current spatial distribution status of Amur leopard density in northeast China.

Hebblewhite et al. (2011) suggested that habitat quality of Amur leopards might be related to the relative abundance of primary prey. Although leopards prey on a wide variety of species, medium-sized ungulates constitute the large part of their diets (Hayward et al., 2006). Our survey suggests that the main ungulate species in our study area were roe deer and wild boar. Results of linear models showed that the roe deer population was more abundant near rivers, similar to the findings of Telleria and Virgós (1997) and Abaigar et al. (1994), whereas wild boar were abundant in habitats with more mixed broad leaf conifer forests, consistent with the findings of Telleria and Virgós (1997). Mixed broad leaf conifer forest may produce abundant food, such as hard and soft masts, and, with thin snow cover there, these forests are suitable to wild boar.

Results of GAMs showed that an abundance of roe deer likely increases Amur leopard density. However, there was an optimal abundance of wild boar for Amur leopards, with Amur leopard population increasing at low wild boar population abundance but decreasing at high wild boar population abundance. Pikunov and Korkishko (1990)

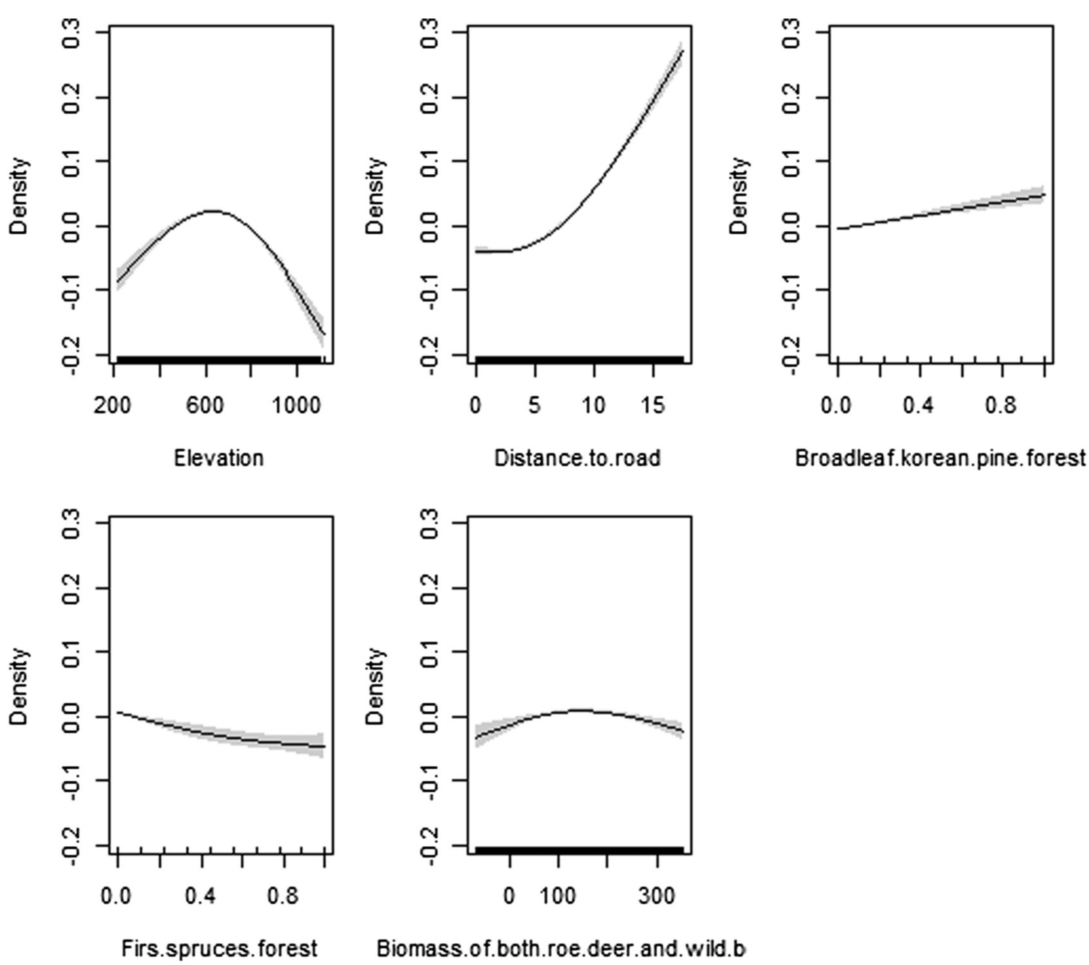

Fig. 3. Relationships between Amur leopard density (individuals/0.25 km^2) and variables by generalized additive model (GAM).

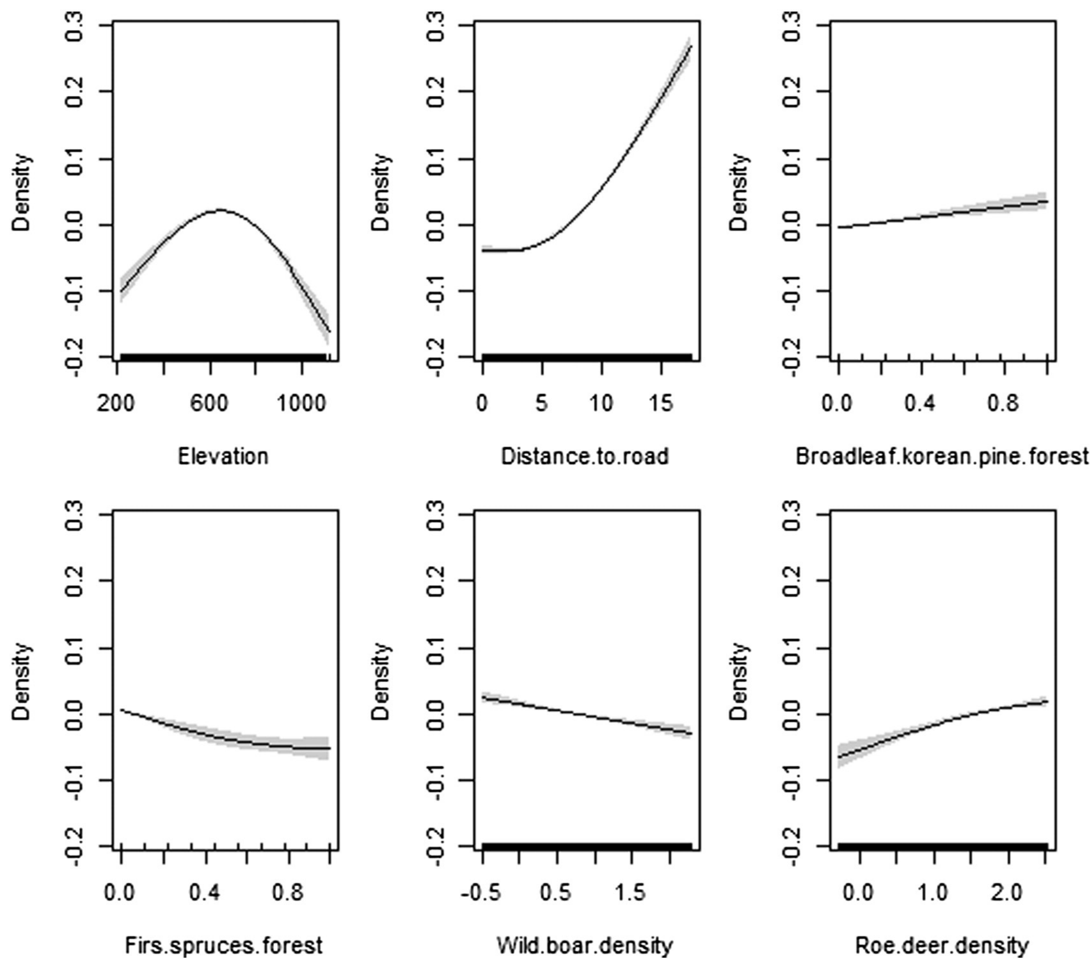

Fig. 4. Relationships between Amur leopard density (individuals/0.25 km^2) and variables by the generalized additive model (GAM), the biomass of roe deer and wild boar population (kg/0.25 km^2) were changed into the densities of roe deer and wild boar (individuals/0.25 km^2).

found that roe deer was the most common prey of Amur leopards. Wild boar is a prey of Amur leopards, particularly young boar, but is less common than small- or medium-sized deer in the diet of Amur leopards (Pikunov and Korkishko, 1990). Wegge et al. (2009) suggested that the leopard avoids large prey species that they can't kill, and that adult wild boars are probably dangerous prey for leopards. In India, for example, it appears that leopards are more likely to prey on subadults and young boars only. Leopards are opportunistic stalking predators, which can efficiently hunt prey of a mean body size of 23 kg (Hayward et al., 2006). Hayward et al. (2006) found that leopards preferred small prey in dense vegetation and avoided large prey in open habitat. Consequently, Amur leopards benefit from abundant small- and medium-sized ungulates, such as roe deer and young wild boar, with increasing population abundance or density. Increasing wild boar population with more large-sized adults may reduce Amur leopard population abundance either directly with less food available or indirectly through competition with roe deer.

Amur leopard density exhibited a non-linear response to increases in the biomass of prey (Fig. 3). Large carnivores, including Amur leopards, require sufficient amount of herbivores as food for survival and reproduction. For instance, Aryal et al. (2014) concluded that 19 snow leopards (*Panthera uncia*) lived in the upper Mustang region of Nepal need to consume approximately 38,925 kg biomass of blue sheep (*Pseudois nayaur*) for survival. Pereira (2010) found that as prey abundance declined, two individuals of Geoffroy's cat (*Leopardus geoffroyi*) dispersed from that study area and seven females died of starvation. Therefore, initial increases in ungulate biomass may increase Amur leopard densities. On the other hand, habitat may be deteriorated or even destroyed once ungulate population size is beyond the environmental carrying capacity (Côté et al., 2004). In our study area, the wild boar, particularly adult boars that seem to, be avoided by Amur leopards, is the main biomass component of the ungulate assembly. Thus, management practices to control wild boar population and increase roe deer population should be implemented to recover the Amur leopard population.

Our results are consistent with the findings of Hebblewhite et al. (2011) that Amur leopards select habitat dominated by mixed conifer forests at intermediate elevation distant from roads. However, Amur leopards avoid the spruce–fir forest found at an average elevation of 1100–2100 m in the Changbai mountains (Chen and Bradshaw, 1999), also beyond optimum elevation (For example, 400–800 m in the Changbai mountains; Jiang et al., 2014) for the survival of Amur tigers. Because Amur tigers are also distributed in the same range as Amur leopards, it is likely that Amur tigers compete for food or habitat with Amur leopards. We found Amur tigers captured by four camera traps during our study. Marker and Dickman (2005) argued that leopard density may not be unduly depressed by the presence of other large carnivores, but, for the Amur leopard in China, this still needs further study.

In general, there was a combination of habitat factors including, not only prey assembly and biomass, but also vegetation, anthropogenic and geographical factors driving the spatial distribution of the Amur leopard population. These insights informed us that comprehensive adaptive landscape conservation strategies should be adopted for saving this critically endangered predator. And our study highlighted the role that the prey assembly structure and spatial distribution plays in the distribution of leopard density by displaying the spatial distribution of leopard and its prey, as well as the prey biomass considering the other factors. The prey is the key for the recover of large predator, for the Amur leopard conservation, as a highly elusive subspecies, the prey management need more meticulous. Only reasonable community structure and moderate population density of leopard prey is in, the recovery of Amur leopard is going well. For Amur leopard conservation, we may adopt modify the habitat structure benefiting the roe deer by selection harvest, and at the same time control the local wild boar density by hunting to keep a reasonable density. Thus, the combination of camera trap technology and spatially explicit capture–recapture model is just perfect on the big cat study and GAM reveals the nonlinear relationship between leopard density and each habitat factor. This comprehensive method, especially spatial predication of predator and prey population density, may be applied in revealing interactions of other large predators and their prey or landscape variables, and provide key habitat or prey conservation strategies for these big carnivores at landscape.

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