



Habitat selection and their interspecific interactions for mammal assemblage in the Greater Khingan Mountains, northeastern China

Authors: Guo, Kai, Liu, Hui, Bao, Heng, Hu, Jingui, Wang, Shoubo, et al.

Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00261>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Habitat selection and their interspecific interactions for mammal assemblage in the Greater Khingan Mountains, northeastern China

Kai Guo, Hui Liu, Heng Bao, Jingui Hu, Shoubo Wang, Weihua Zhang, Yuzhuo Zhao and Guangshun Jiang

K. Guo, H. Liu, H. Bao, Y. Zhao and G. Jiang (jgshun@126.com), Feline Research Center of Chinese State Forestry Administration, College of Wildlife Resources, Northeast Forestry University, CN-150040 Harbin, Heilongjiang, China. – J. Hu, S. Wang and W. Zhang, Inner Mongolia Hanma National Nature Reserve, Genhe, Inner Mongolia, China

Patterns of habitat use profoundly influence interactions among wildlife species and ecological communities, the sustainability of species and the stability of populations. The Eurasian lynx *Lynx lynx*, sable *Martes zibellina*, moose *Alces alces*, roe deer *Capreolus pygargus* and mountain hare *Lepus timidus* are sympatric carnivore and herbivore species in Hanma Nature Reserve in the Greater Khingan Mountains, northeastern China. We conducted snow track sample plot surveys of these mammals during the winter of 2012–2013 and analyzed habitat selection characteristics and interspecific interactions. We screened the preferred habitat variables of each species and predicted their potential occurrence probability by generalized linear mixed model (GLMM) and further, selected the best model of each species that incorporated other species' potential occurrence probability in GLMM. Our results showed that when we only considered habitat factors in the model: 1) river valley was the most favored habitat factor in winter that lynx, moose and mountain hare showed strong selection on; 2) lynx preferred areas with steep slope and coniferous forest; 3) sable only avoided the forest edge; 4) roe deer avoided sparse shrub forest but preferred coniferous forest. When we incorporated other species' presence probability in GLMM: 1) the presence probability of moose and roe deer had no significant relationship with other species; 2) lynx preferred areas with higher mountain hare potential occurrence probability; 3) sable preferred areas with higher mountain hare but less lynx occurrence probability; 4) mountain hare preferred to inhabit areas with sympatric roe deer and lynx. These results will provide guidance for species specific habitat conservation and restoration, and wildlife population management based on interspecific interactions.

Animals make habitat selection based on the tradeoff between the costs and benefits perceived by the animals (Lima and Dill 1990, Lima and Bednekoff 1999). Wildlife habitat selection is driven by habitat-related factors, such as forage quality and availability, shelter, predation pressure and mating system (Creel et al. 2005, Godvik et al. 2009). The most common tradeoff occur on many large sized herbivores is that closed habitats provide shelter against harsh weather and/or predators, while exposed habitats provide better forage (Godvik et al. 2009). What's more, prey density is another important factor affecting habitat selection for carnivores. Differences in the body sizes of sympatric herbivores may mean they prefer forage of different heights and quality (Kuiters et al. 2005) and for predators, body sizes were important factors deciding their prey species, and their different roles in regulating ecosystems at the top of food net (Beschta and Ripple 2009, Ritchie et al. 2012).

Much work has been done on wildlife habitat selection, correlations between mammals and climate, resource availability, habitat diversity, environment factors, sympatric

species, predators and human interference (Batcheler 1960, Menéndez et al. 2007, Bjørneraas et al. 2011, 2012, Nicholson et al. 2014). Researches showed that harsh winter pushed animals to choose places with low snow cover and more abundant forage (Dussault et al. 2005, Street et al. 2015), such as river basins (Nicholson et al. 1997). When wildlife use habitat, it is critical that they adjust their behaviors to adapt to the environment to ensure viability. The coexistence mechanisms of multiple sympatric species, how animals adjust to intraspecific and interspecific competition, and how environment resources are utilized to avoid strong competition are well studied (Kuiters et al. 2005, Jiang et al. 2010), but geographic gaps remain. The Eurasian lynx *Lynx lynx*, sable *Martes zibellina*, moose *Alces alces*, roe deer *Capreolus pygargus* and mountain hare *Lepus timidus* are sympatric predator and herbivore species in Hanma Nature Reserve in the Greater Khingan Mountains, northeastern China. Until recently, few researches have been carried out in this area, we tried to find factors affecting habitat selection of these species and explore possible explanations for these effects.

Environmental factors can directly regulate species richness by providing caves, nests and shelter for animals (Wright 1983). Water-energy aspects of the environment can constrain species richness via a trophic cascade: water-energy availability determines plant richness, which determines herbivore richness and in turn carnivore richness (Huston 1994, Mittelbach et al. 2001). Vegetation has direct effects on herbivore richness and abundance, so herbivore species diversity is often closely correlated with plant diversity (Siemann et al. 1998), and grazing can alter vegetation configuration and patch heterogeneity (Adler et al. 2001). Exploring driving factors for habitat selection of sympatric predators and herbivores, reactions of herbivores on habitat utilization under predation pressure, and vegetation–herbivore–predator relationships can help to deepen our understanding of herbivore and predator coexistence mechanism. Hanma Nature Reserve in the Greater Khingan Mountains, northeastern China is such an optimum area to stress this problem, where lynx *L. lynx*, sable *M. zibellina*, moose *A. alces*, roe deer *C. pygargus* and mountain hare *L. timidus* coexist. In this research, snow track sampling method and generalized linear mixed model (GLMM) were used to examine the characteristics of habitat selection of both herbivores and carnivores and possible interspecific interactions in this area to test the hypotheses that 1) different environment factors determine habitat selection and distribution of carnivores and herbivores 2) predators prefer areas where herbivores occur more frequently.

Material and methods

Study area

Hanma National Nature Reserve (51°20′02″–51°49′48″N, 122°23′34″–122°52′46″E) is located in the Greater Khingan Mountains, Inner Mongolia, northeastern China (Fig. 1). The reserve covers an area of 1073 km² with a subfrigid climate: a cold dry season from October to June and a warm wet season from July to September. The annual mean temperature is −5.3°C; the highest temperature in summer is 35.4°C and the lowest temperature in winter is −49.6°C. Average rainfall of 450 mm is concentrated between July and September (70% of yearly precipitation) and the snow depth is usually around 30 cm in harsh winter. At higher elevations, the dominant tree species is Siberian dwarf pine *Pinus pumila*, while lower place are characterized by Dahurian larch *Larix gmelinii*, and deciduous trees are white birch *Betula platyphylla*, willow *Salix* spp., hazel *Corylus avellane* and Siberian alder *Alnus hirsuta* var. *sibirica*, while shrub berry, reed grass and moor grass dominate the forest floor of the thickets. We divided vegetation into four types: coniferous, deciduous, sparse shrub and swamp patches. Coniferous forest is the main habitat type and accounts for 82% of total vegetation cover. Hanma Nature Reserve is far away from towns and villages and landscape keeps quite natural because no logging has ever been carried out before, hence, there are no road-net and few human activities exist in this area.

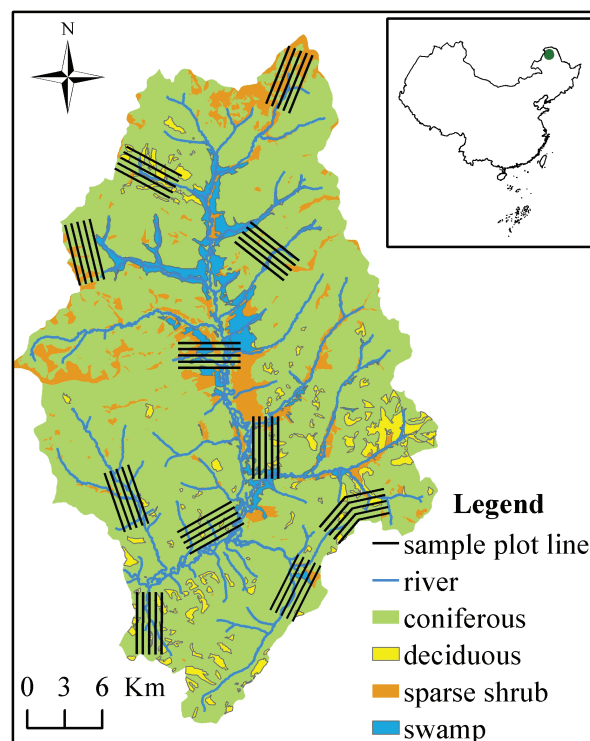


Figure 1. Sample plot distribution in Hanma Nature Reserve.

Data collection

To collect species presence data, we carried out sample plot surveys (Qi et al. 2015) during the winter of 2012–2013. Vegetation type depended stratified sampling methods were used to design transect lines, and 55 transects with a total length of 275 km were set up. We used ArcGIS 9.3 to design the line transect distribution: five transect lines composed of one sample plot, and each transect was 5 km in length and the interval between two transects was 500 m. Each transect line was surveyed by two experienced local workers and they recorded animal tracks in the snow left in 24 h and corresponding location coordinates. When field work was completed, we used ArcGIS 9.3 to acquire 25 points on each transect line with an interval of 200 m, and extracted slope, aspect, elevation, distance to the edge of the nearest coniferous patch (hereafter conifer), distance to the center of the nearest swamp patch (hereafter swamp), distance to the center of the nearest sparse shrub patch (hereafter shrub), distance to the center of the nearest deciduous patch (hereafter deciduous), distance to the nearest river (hereafter river), and distance to the nearest patch edge (Table 1) as environmental indicators for species habitat selection modeling processing. In addition, we attributed the presence information of mammal species (i.e. tracks) to the nearest points.

Data analysis

We normalized all the habitat variables in order to avoid the condition that some variables were too skewed, and for the species presence data, we used binomial distribution

Table 1. Habitat variables extracted to test relationships among presence data for five mammals in northeastern China.

Habitat factor			Description of the habitat factor	Data type	Unit
Vegetation	river		distance to the nearest river. the river includes the primary river and their branches	continuous	(m)
	forest		forest area including all main types of forest types in the reserve	continuous	
	conifer		distance to the nearest coniferous patch edge	continuous	(m)
	swamp		distance to the center of nearest swamp patch	continuous	(m)
	shrub		distance to the center of nearest sparse shrub patch	continuous	(m)
	decid		distance to the center of nearest deciduous patch	continuous	(m)
Topography	elevation		elevation grid with 1 km resolution	continuous	(m)
	slope		slope grid with 1 km resolution derived from the digital elevation model above	continuous	(°)
	aspect		aspect grid with 1 km resolution derived from the digital elevation model above	continuous	(°)

Note: Data was processed in ArcGIS 9.3 in grid format. Data extracted from the stock map was provided by Hanma Nature Reserve.

(presence = 1 and absence = 0). Pearson's correlation matrix was used to identify whether problematic collinearities exist among covariates (Loyn et al. 2001), which suggested that the deciduous variable had problematic collinearities with swamp ($r = 0.57$), so we deleted it to avoid autocorrelation problem in our analysis.

For each species, we used logistic regression to build a linear combination of terrain and vegetation variables, through stepwise regression method; we selected the most parsimonious model that best explained their occurrence and distribution. We used Akaike's information criterion difference adjusted for small sample sizes (AICc) and Akaike model weights (ω_i) to get the most parsimonious model (i.e. fewest variables to explain the most variation). After we knew each species' optimal model, we used the model to predict their potential presence probability (P_i) considering only the terrain and vegetation variables.

When examining the interactions among the five species, we defined each species a second model: for carnivores, to incorporate prey species' potential presence probability (P_i) as a variable to its first habitat selection model, and for herbivores, to incorporate potential presence probability (P_i) of predator and other herbivore competitors. And once again, we used Akaike's information criterion (AICc) and Akaike model weights (ω_i) to evaluate and identify models and get the most parsimonious model for each species, so that, we got the second most parsimonious model to predict their secondary presence probability (P_i). Generalized linear mixed model analysis was carried out in R ver. 3.2.2 using the 'lme4' package (<www.r-project.org>) and the 11 sample plots (with five line transects each) were included as a random factor in the analyses.

Results

We extracted 1300 points from all transect lines of 11 sample plots for analysis. For lynx, we found 35 occurrence points (one point had two occurrences); 116 points for moose (two occurrences at two sites); 86 points for roe deer (two occurrences at seven sites); 118 points for mountain hare (two occurrences at seven sites); and sable were recorded at 200 points (two occurrences at 14 sites).

Model selection

We found the five top generalized linear mixed models when only considering the effect of terrain and vegetation variables, and found three top models (without moose and roe deer) when incorporating other species' presence probability (P_i) in the second model, and calculated ω_i for each model. We presented the best supported generalized linear mixed models (i.e. those with $\Delta AIC \leq 2$) for the five species (Table 2).

On the first condition, when only environmental factors considered, we found five top generalized linear mixed models for the five species separately. For the moose, the most parsimonious resource model included two variables (river and random covariates; no. of model parameters $K = 2$, $\omega_i = 0.205$, Table 2). Roe deer's most parsimonious model consisted of three variables (shrub, coniferous and random covariate; $K = 3$, $\omega_i = 0.305$, Table 2). Mountain hare's most parsimonious resource model included two variables (river and random covariate; $K = 2$, $\omega_i = 0.246$, Table 2). Lynx's most parsimonious model had four variables (river, coniferous,

Table 2. Number of model parameters (K), differences in Akaike's information criterion ($\Delta AICc$) scores, and AICc weights (ω_i) for the eight most parsimonious generalized linear mixed models (with $\Delta AICc \leq 2$) for the five species in Greater Khingan Mountains, northeastern China.

Model	Logistic model	K	AIC _c	ΔAIC_c	ω_i
Moose	river + random variable	2	761.2	0.3	0.205
Roe deer	shrub + coniferous + random variable	3	610.0	0.2	0.305
Mountain hare	river + random variable	2	770.5	1	0.246
Sable	coniferous + shrub + random variable	3	1079.4	0	0.342
Lynx	river + coniferous + slope + random variable	4	296.4	1	0.183
Mountain hare	river + P_r + random variable	3	764.0	0.3	0.369
Lynx	coniferous + slope + P_h + random variable	4	292.4	0	0.378
Sable	shrub + P_h + random variable	3	1079.1	1.5	0.321

Notes: abbreviations of habitat variables are the same as in Table 1.

Table 3. Best generalized linear mixed models of five species habitat selection in Greater Khingan Mountains, northeastern China.

Model	Variable	Coeff.	95% CI
Moose	intercept	-2.556	-3.090 to -2.134
	river	-0.441	-0.707 to -0.189
Roe deer	intercept	-2.896	-3.583 to -2.343
	coniferous	0.2794	0.081 to 0.463
Hare	shrub	0.346	0.110 to 0.584
	intercept	-2.469	-2.895 to -2.098
Lynx	river	-0.330	-0.595 to -0.076
	intercept	-4.426	-5.445 to -3.688
Sable	river	-0.999	-1.652 to -0.428
	slope	0.469	0.070 to 0.882
	coniferous	0.396	0.060 to 0.680
	intercept	-1.831	-2.233 to -1.458
	coniferous	-0.213	-0.463 to -0.005
	shrub	0.161	-0.009 to 0.329

Notes: river, the distance to the nearest river; coniferous, the distance to the nearest coniferous patch edge; shrub, the distance to the nearest coniferous patch center; slope, the slope of the point; P_r , the presence probability of roe deer; P_h , the presence probability of mountain hare.

slope and random covariate; $K=4$, $\omega_i=0.183$, Table 2). The sable's most parsimonious model consisted of three variables (coniferous, shrub and random covariate; $K=3$, $\omega_i=0.342$, Tables 2–3) and we used it as its best resource selection model.

When considering the interspecies interactions, we found three top generalized linear mixed models for mountain hare, lynx and sable. But we didn't find the presence of moose and roe deer was significantly affected by other species in logistic regression model. For the mountain hare the most parsimonious interspecies interaction model included three variables (river, P_r , and random covariate; $K=3$, $\omega_i=0.369$, Table 4). For the lynx, the most parsimonious interspecies interaction model consisted of four variables (coniferous, slope, P_h , and random covariate; $K=4$, $\omega_i=0.378$, Table 4). For the sable, the most interspecies interaction parsimonious model included three variables (shrub, P_h , and random covariate; $K=3$, $\omega_i=0.321$, Table 4) interspecies interaction model.

Table 4. Best generalized linear mixed models of five species interspecies interaction in Greater Khingan Mountains, northeastern China.

Model	Variable	Coeff.	95% CI
Hare	intercept	-2.967	-3.505 to -2.486
	river	-0.361	-0.629 to -0.107
	P_r	6.890	2.368 to 11.301
Lynx	intercept	-6.107	-7.814 to -4.914
	slope	0.489	0.100 to 0.890
	coniferous	0.369	0.041 to 0.644
	P_h	20.537	11.323 to 33.109
Sable	intercept	-2.355	-2.983 to -1.741
	shrub	0.185	0.021 to 0.350
	P_h	5.950	0.353 to 11.464

Notes: river, the distance to the nearest river; coniferous, the distance to the nearest coniferous patch edge; shrub, the distance to the nearest coniferous patch center; slope, the slope of the point; P_r , the presence probability of roe deer; P_h , the presence probability of mountain hare.

Discussion

Effect of habitat factors on animal presence

Based on the top generalized linear mixed models selected for each species, we found that the most parsimonious resource selection model for moose included only one variable, river (Table 2), which meant that moose showed strong preference for areas near the rivers. More previous researches showed that moose were typical browsers and their habitat selection was affected by seasonal forage availability (Cederlund and Okarma 1988, Olsson et al. 2011, Van Beest et al. 2010), time of day, sex and reproductive status of the cow (Bjørneraas et al. 2011, 2012). In harsh winter, moose strongly selected young forest and wetter areas to obtain sufficient food resources, such as willow *Salix* spp., hazel *Corylus avellane*, and Siberian alder *Alnus hirsuta* var. *sibirica* that provided shoots to moose as winter food (Jiang et al. 2009). Moose also used watersheds in the summer as escape habitat and corridors for crossing between habitat patches in winter (Nicholson et al. 2014). In our study area, river valley is the most heterogeneous area, where plants such as willow *Salix* spp., Asian white birch *Betula platyphylla*, hazel *Corylus avellane* and Siberian alder *A. hirsuta* var. *sibirica* as well as many other broadleaf and shrub that provide sufficient annual new shoots as winter forage for moose. Moreover, in winter, the Siberian dwarf pine *Pinus pumila*, which is the dominant species on higher elevation, is buried by heavy snow, making it unavailable for moose and other larger body sized animal. And according to our surveys, the snow depth of areas with Siberian dwarf pine was usually more than 60 cm, so the dense branches and deep snow cover made it almost impossible for large and medium body sized animals to walking through it, and might be an important reason for the moose to choose river basin with high quality forage and suitable habitat complexity as its major winter home range.

The best resource selection model of roe deer included coniferous and shrub, both positively significant, which meant roe deer avoided coniferous patch edge and sparse shrub habitat (Table 2). Roe deer are medium body sized and have large mass-specific energy requirements to defend themselves from the harsh winter. They usually preferred sites with more abundant annual growth of browse plant species (Hofmann and Stewart 1972), dense forests that provided protective cover (Henry 1981), mature forest habitat of high quality, and avoided edge habitats (Mysterud et al. 1999). In our research area, the coniferous forest is characterized as mature forest, good canopy and no logging for several decades; which could provide enough food resource, sufficient bedding sites and shelters of high quality. The sparse shrub patches in the nature reserve are mostly composed of bare rock and under shrub habitat, which can hardly provide enough shelters and forage and bedding sites.

The resource selection model result showed that mountain hare also preferred areas near the river (Table 2). In Europe, the mountain hare was found predominantly in mixed forest (Naumov 1947), and it reached the highest densities in transition zone with open habitat (Lindlof et al. 1974), and in moorlands (Watson and Hewson 1973). As small herbivores, two main factors, namely food and shelter against predators decide the dense shrub layer to be the best habitat

selected for mountain hare (Hiltunen et al. 2004, Hiltunen and Kauhala 2006). Because in winter, the snow concealed lower herbs and shrubs, forcing hares to browse twig, and deciduous bushes (mainly birches *Betula* spp., rowan *Sorbus* spp. and willows *Salix* spp.), which dominated the hares' diet due to their availability above the snow cover (Angerbjörn and Flux 1995). The characteristics of habitat that mountain hare required were well met by areas near the river where there were abundant deciduous shrubs that could provide enough forage and shelter.

The lynx distribution was best explained by the combination of river, coniferous and slope (Table 2). In Norway, a research found lynx would select steep resting sites for safe hiding place in daytime (Sunde et al. 1998), which could be considered as a by-product of selection for less disturbed areas (Basille et al. 2008), meanwhile, researches and field observation had found moderately rugged terrain might be helpful for lynx to get higher prey catch ability (Krofel et al. 2007). The result suggested that lynx preferred the areas near river and with higher slope, but avoided coniferous patch edges. Lynx habitat selection had been studied in many countries and lynx were known to occur in areas with forest cover of greater than 40% (Niedziałkowska et al. 2006, Schadt et al. 2002, Mikusiński and Angelstam 2004). Podgórski et al. (2008) studied lynx's microhabitat selection and found that during both summer and winter, lynx selected sites characterized by high complexity, but large-scale approaches couldn't identify variation between different forest types in terms of the availability of specific environmental structures suitable as stalking cover or resting sites. In our study area, there is almost no human disturbance and either coniferous forest or deciduous forest could provide enough shelter, whereas shrub and swamp patch may be too open for lynx's predatory behavior. Lynx often used frozen rivers as long distance migration corridors, and herbivores prefer river areas for foraging (Jiang et al. 2009). Therefore, we predicted that lynx selected areas adjacent to rivers to improve stalking opportunities and used the river as a crossing path between habitat patches.

The resource selection result showed that sable preferred areas near the coniferous patch edge and avoided sparse shrub (Table 2). Sable are small sized forest carnivores selecting sites with a dense tree canopy, mixed dominant tree species, and high densities and diameters of larch tree boles (Buskirk et al. 1996). Certainly, sparse shrub could not provide enough cover in winter, whereas areas near coniferous patch edge usually were characterized with more tree species and densities, which well met the requirements of the survival of sable.

Effect of interspecies interactions

The most parsimonious interspecies interactions model of moose and roe deer that added the presence probability of other animals revealed that the presence of both species had no significant correlation with other animals so that the result was the same as their resource selection models (Table 2, 4). Indeed, lynx was one of the top predators in our study area, we once found an unsuccessful predation site, where a lynx failed to prey on an adult moose, and studies reported that lynx preyed on calves and disabled

moose (Swenson et al. 1999, Odden et al. 2006), but the main predation pressure came from bear, wolf and wolverine (Haglund 1974, Valdmann et al. 2005). Even though many studies revealed that roe deer were the dominating prey species for lynx in the winter (Okarma et al. 1997, Odden et al. 2006), we failed to detect such relationship, maybe because of the limited lynx occurrences (only 35 times) and different habitat requirements between lynx and roe deer in this area.

The most parsimonious interspecies interactions model of mountain hare contained two variables, river and $P_{[r]}$ (Table 4). Roe deer presence probability had a much more strong positive effect on mountain hare presence compared the effect of river. It was demonstrated theoretically that sympatric prey species which share predators usually had positive effects on each other's density (Abrams and Matsuda 1996). Roe deer and mountain hare are two most common distributed herbivores browsing on similar herbs in winter, but differ in body size and digestive systems, such as roe deer are ruminants but mountain hares are hindgut fermentors (Cederlund et al. 1980, Angerbjörn 1981, Pulliainen and Tunkkari 1987). As noted by Illius and Gordon (1992), smaller hindgut fermentors are more tolerant of poor-quality diets when competing directly with larger ruminants which have a more efficient digestive system, especially at times when quality and abundance of food resource reached its nadir in winter. In our study area, mountain hare and roe deer are sympatric species, and food resource utilization partitioning maybe one important reason for mitigating competing pressure in the harsh winter. Mountain hare should browse on the vegetation near the ground when compared to roe deer. At the beginning season, the forage resource is abundance and both species prefer twigs or smaller plants with smaller diameters, the easy digestible parts of plants (Palo et al. 1992). However, as the browsing season continues and vegetable resource becomes more limited at ground level, roe deer will be able to utilize the vegetation beyond the reach of the hare, and another effective way of acquiring grass plants for roe deer is from the bedding sites where they keep warm during the freezing nights (Mysterud et al. 1999). Mountain hares, on the other hand have no such refuge, will turn on the poor-quality forage, namely those twigs and plants with larger diameters (Hulbert and Andersen 2001).

The most parsimonious interspecies interactions model of lynx was best explained by coniferous, slope and $P_{[h]}$ (Table 4). Lynx showed preference to places with steep slope and avoided coniferous patch edge. In addition, lynx presence showed much more significant correlation with mountain hare presence other than coniferous and slope. The dietary composition and species preyed on by lynx depends on the configuration of herbivore community in the region (Okarma et al. 1997, Pedersen et al. 1999, Weber and Weissbrodt 1999, Koubek et al. 2001), and they tend to be an opportunistic generalist predator that has specialized on small ungulates (Jedrzejewski et al. 1993). In Europe, roe deer is the most widespread ungulates and the most common prey of lynx when they occur together (Jedrzejewski et al. 1993, Nowicki 1997, Belotti et al. 2015). The survey result showed that, in our study area, mountain hare (118 occurrence points) occurred more frequently than roe deer (86 occurrence points), as they were sympatric and mountain hare

preferred to use place where roe deer existed. Although we didn't find the direct linkage between lynx and roe deer, but the presence probability of lynx was significantly affected by the presence of mountain hare, which meant lynx preferred to use places with a higher presence probability of mountain hare, however, the presence of mountain hare was correlated with roe deer, indicating more chances for the lynx to meet with roe deer.

The most parsimonious interspecies interaction model of sable was best explained by shrub and $P_{[h]}$ (Table 2). Sable avoided shrub patches and selected place where mountain hare presence probability was higher. According to Miyoshi and Higashi (2005), the sable are small sized carnivores that prefer resting in dense forests to avoid predators (e.g. red fox) and strong wind and stalking in forests with abundant prey such as voles and mice. Sable mainly hunt for small animals, but it also preys on larger mammals such as chipmunks *Tamias sibiricus*, pikas *Ochotona*, squirrels *Sciurus* and *Pteromys*, muskrats *Ondatra*, marmots *Marmota*, mountain hares, and musk deer *Moschus moschiferus* (Moskov 1973, Khlebnikov 1977, Monakhov and Bakeyev 1981, Zirjanov et al. 2001, Chernikin 2006). Our results suggested sable preferred areas with higher mountain hare occurrence probability, and its impact was much stronger than shrub. As a small sized carnivore, sable are preyed on by many larger predator, such as brown bear *Ursus arctos*, wolf *Canis lupus*, red fox *Vulpes vulpes*, wolverine *Gulo gulo*, yellow-throated marten *Martes flavigula*, lynx *Lynx lynx* and some big birds, like eagle-owl *Bubo bubo*, golden eagle *Aquila chrysaetus*, raven *Corvus corax*, hawks: goshawk *Accipiter gentilis* and sparrow-hawk *Accipiter nisus*, and two owls: great gray owl *Strix nebulosa* and northern hawk owl *Surnia ulula* (Gusev 1966, Bakeyev et al. 2003). In our study area, lynx, wolverine and some other big birds might hunt sable, shelter was very important for sable and sparse shrub was too open for sable to escape from predation.

Conclusion

Our analysis result showed that food availability and shelter were most important factor deciding habitat use by the herbivores, and also the distribution of prey abundance and cover had a great impact on habitat selection of the carnivores. Different mammals chose different habitats to meet their needs for forage, shelter or escape. Areas near river was mostly favored by moose, mountain hare and lynx, while moose and mountain hare preferred river areas for browsing shoots, lynx's strong selection on river maybe the result of using river as a quick path to other habitat patches and there were more predation opportunities. Sparse shrub habitat was too open for mammals which could not provide enough shelter or cover to prevent them from predation or danger, so roe deer and sable showed strong avoidance for sparse shrub habitat. The interspecies interaction was studied in this research, and we found that the distribution of mountain hare was correlated with roe deer maybe because of the spatial separation of food resource during the harsh winter. Both lynx and sable preyed on mountain hare, and the strong relationship was detected by lynx and sable model when incorporating the occurrence probability into the models, which showed the importance of mountain hare in this area. Even though

we failed to find the direct correlation between lynx and roe deer, the occurrence of roe deer was positively correlated with mountain hare, which may enhance the probability of predation of roe deer by the lynx.

Acknowledgments – We thank staff of Hanma National Nature Reserve for help in driving and guiding during our field work.

Funding – This study was supported by Fundamental Research Funds for the Central Universities of China (2572014EA06; 2572015AA04), National Natural Science Foundation of China (NSFC 31272336; 31572285), and College students' innovative training program of Northeast Forestry University (201510225086).

Author contributions – K. Guo and H. Liu contributed equally to the study. GJ conceived and designed the experiments. JH, SW and WZ provided support on vehicle and guides in the field work. KG, HL and HB analyzed the data, KG and HL wrote and revised the manuscript.

Declaration of interest – The authors declare no conflict of interests. The authors alone are responsible for the content and writing of the paper.

References

- Abrams, P. A. and Matsuda, H. 1996. Positive indirect effects between prey species that share predators. – *Ecology* 77: 610–616.
- Adler, P. et al. 2001. The effect of grazing on the spatial heterogeneity of vegetation. – *Oecologia* 128: 465–479.
- Angerbjörn, A. 1981. Winter food as a limiting factor of dense mountain hare populations on islands, a comparative study. – *Proc. World Lagomorph Conf. Univ. of Guelph*, pp. 529–535.
- Angerbjörn, A. and Flux, J. E. C. 1995. *Lepus timidus*. – *Mamm. Spec.* 495: 1–11.
- Bakeyev, N. N. et al. 2003. The sable. – All-Russian Inst. of Hunting and Fur Farming Press, Vjatka Kirov, Russia, in Russian.
- Basille, M. et al. 2008. Assessing habitat selection using multivariate statistics: some refinements of the ecological-niche factor analysis. – *Ecol. Modell.* 211: 233–240.
- Batcheler, C. L. 1960. A study of the relations between roe, red and fallow deer, with special reference to Drummond Hill Forest, Scotland. – *J. Anim. Ecol.* 29: 375–384.
- Belotti, E. et al. 2015. Patterns of lynx predation at the interface between protected areas and multi-use landscapes in central Europe. – *PloS ONE* 10: e0138139.
- Beschta, R. L. and Ripple, W. J. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. – *Biol. Conserv.* 142: 2401–2414.
- Bjørneraas, K. et al. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. – *Wildl. Biol.* 17: 44–54.
- Bjørneraas, K. et al. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. – *Oecologia* 168: 231–243.
- Buskirk, S. W. et al. 1996. Winter habitat ecology of sables (*Martes zibellina*) in relation to forest management in China. – *Ecol. Appl.* 6: 318–325.
- Cederlund, G. N. and Okarma, H. 1988. Home range and habitat use of adult female moose. – *J. Wildl. Manage.* 52: 336–343.
- Cederlund, G. et al. 1980. Foods of moose and roe-deer at Grimsö in central Sweden. Results of rumen contents analyses. – *Swe. Wildl. Res.* 11: 170–247.

- Chernikin, E. M. 2006. Ecology of sable (*Martes zibellina*) in Barguzin Reserve. – Buryat State Univ. Press, Ulan-Ude, Russia, in Russian.
- Creel, S. et al. 2005. Elk alter habitat selection as an antipredator response to wolves. – *Ecology* 86: 3387–3397.
- Dussault, C. et al. 2005. Linking moose habitat selection to limiting factors. – *Ecography* 28: 619–628.
- Godvik, I. et al. 2009. Time scale, tradeoffs and functional responses in red deer habitat selection. – *Ecology* 90: 699–710.
- Gusev, O. K. 1966. Ecology and estimation of numbers in sable. – Lesnaja Promishlennost Publishing House, Moscow, Russia, in Russian.
- Haglund, B. 1974. Moose relations with predators in Sweden, with special reference to bear and wolverine. – *Nat. Can.* 101: 457–466.
- Henry, B. A. M. 1981. Distribution patterns of roe deer (*Capreolus capreolus*) related to the availability of food and cover. – *J. Zool.* 194: 271–275.
- Hiltunen, M. and Kauhala, K. 2006. Selection of sapling stand habitats by the mountain hare (*Lepus timidus*) during winter. – *Mamm. Biol.* 71: 183–189.
- Hiltunen, M. et al. 2004. Habitat use of the mountain hare *Lepus timidus* in summer: the importance of different vegetation layers. – *Acta Theriol.* 49: 479–490.
- Hofmann, R. R. and Stewart, D. R. M. 1972. Grazer or browser: a classification based on the stomach-structure and feeding habits of east African ruminants. – *Mammalia* 36: 226–240.
- Hulbert, I. A. and Andersen, R. 2001. Food competition between a large ruminant and a small hindgut fermentor: the case of the roe deer and mountain hare. – *Oecologia* 128: 499–508.
- Huston, M. A. 1994. Biological diversity: the coexistence of species. – Cambridge Univ. Press.
- Illius, A. W. and Gordon, I. J. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. – *Oecologia* 89: 428–434.
- Jedrzejewski, W. et al. 1993. Foraging by lynx and its role in ungulate mortality: the local [Białowieża Forest] and the Palaearctic viewpoints. – *Acta Theriol.* 38: 385–403.
- Jiang, G. et al. 2009. Multiple spatial-scale resource selection function models in relation to human disturbance for moose in northeastern China. – *Ecol. Res.* 24: 423–440.
- Jiang, G. et al. 2010. Multi-scale foraging habitat use and interactions by sympatric cervids in northeastern China. – *J. Wildl. Manage.* 74: 678–689.
- Khlebnikov, A. I. 1977. Ecology of the sable in West Sayan. – Nauka Publishing House, Novosibirsk, Russia, in Russian.
- Koubek, P. et al. 2001. How is the lynx (*Lynx lynx*) hunting strategy of ungulates in the Sumava Mountains (Czech Republic). – *Abst. 25th Int. Congre. of IUGB, Lemesos, Cyprus*: 32.
- Krofel, M. et al. 2007. Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. – *Nat. Sloveniae* 9: 25–36.
- Kuiters, A. T. et al. 2005. Facilitative and competitive interactions between sympatric cattle, red deer and wild boar in Dutch woodland pastures. – *Acta Theriol.* 50: 241–252.
- Lima, S. and Dill, L. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–649.
- Lima, S. L. and Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behaviour: the predation risk allocation hypothesis. – *Am. Nat.* 153: 649–659.
- Lindlof, B. et al. 1974. On activity, habitat selection and diet of the mountain hare (*Lepus timidus* L.) in winter. – *Viltrevy* 9: 27–43.
- Loyn, R. H. et al. 2001. Modelling landscape distributions of large forest owls as applied to managing forests in northeast Victoria, Australia. – *Biol. Conserv.* 97: 361–376.
- Menéndez, R. et al. 2007. Direct and indirect effects of climate and habitat factors on butterfly diversity. – *Ecology* 88: 605–611.
- Mikusiński, G. and Angelstam, P. 2004. Occurrence of mammals and birds with different ecological characteristics in relation to forest cover in Europe – do macroecological data make sense? – *Ecol. Bull.* 51: 265–275.
- Mittelbach, G. G. et al. 2001. What is the observed relationship between species richness and productivity? – *Ecology* 82: 2381–2396.
- Miyoshi, K. and Higashi, S. 2005. Home range and habitat use by the sable *Martes zibellina* brachyura in a Japanese cool-temperate mixed forest. – *Ecol. Res.* 20: 95–101.
- Monakhov, G. I. and Bakeyev, N. N. 1981. The sable. – Lesnaja Promishlennost Publishing House, Moscow, Russia, in Russian.
- Moskov, V. A. 1973. Sable and musk deer. – *Hunt Hunting Manage.* 4: 18–19, in Russian.
- Mysterud, A. et al. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? – *Can. J. Zool.* 77: 776–783.
- Naumov, S. P. 1947. Ecology of the snow hare *Lepus timidus* L.: theoretical foundations for the prognosis of the species' population. – Moscow Soc. Nat., Moscow.
- Nicholson, K. L. et al. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. – *J. Mammal.* 78: 483–504.
- Nicholson, K. L. et al. 2014. Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. – *Oecologia* 176: 69–80.
- Niedziałkowska, M. et al. 2006. Environmental correlates of Eurasian lynx occurrence in Poland – large scale census and GIS mapping. – *Biol. Conserv.* 133: 63–69.
- Nowicki, P. 1997. Food habits and diet of the lynx (*Lynx lynx*) in Europe. – *J. Wildl. Res.* 2: 161–166.
- Odden, J. et al. 2006. Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. – *Eur. J. Wildl. Res.* 52: 237–244.
- Okarma, H. et al. 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. – *Acta Theriol.* 42: 203–224.
- Olsson, M. et al. 2011. Space and habitat use of moose in southwestern Sweden. – *Eur. J. Wildl. Res.* 57: 241–249.
- Palo, R. T. et al. 1992. Digestibility, distribution of phenols, and fiber at different twig diameters of birch in winter. Implication for browsers. – *Oikos* 65: 450–454.
- Pedersen V. A. et al. 1999. Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. – *Wildl. Biol.* 5: 203–250.
- Podgórski, T. et al. 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. – *Acta Theriol.* 53: 97–110.
- Pulliamen, E. and Tunkkari, P. S. 1987. Winter diet, habitat selection and fluctuation of a mountain hare *Lepus timidus* population in Finnish forest Lapland. – *Ecography* 10: 261–267.
- Qi, J. et al. 2015. Spatial distribution drivers of Amur leopard density in northeast China. – *Biol. Conserv.* 191: 258–265.
- Ritchie, E. G. et al. 2012. Ecosystem restoration with teeth: what role for predators? – *Trends Ecol. Evol.* 27: 265–271.
- Schadt, S. et al. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. – *Ecol. Appl.* 12: 1469–1483.
- Siemann, E. et al. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. – *Am. Nat.* 152: 738–750.

- Street, G. M. et al. 2015. Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). – Can. J. Zool. 93: 813–821.
- Sunde, P. et al. 1998. Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. – Wildl. Biol. 4: 177–183.
- Swenson, J. E. et al. 1999. Effects of ear-tagging with radiotransmitters on survival of moose calves. – J. Wildl. Manage. 63: 354–358.
- Valdmann, H. et al. 2005. Winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Estonia and Latvia. – Acta Theriol. 50: 521–527.
- Van Beest, F. M. et al. 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. – J. Anim. Ecol. 79: 910–922.
- Watson, A. and Hewson, R. 1973. Population densities of mountain hares (*Lepus timidus*) on western Scottish and Irish moors and on Scottish hills. – J. Zool. 170: 151–159.
- Weber, J. M. and Weissbrodt, M. 1999. Feeding habits of the Eurasian lynx in the Swiss Jura Mountains determined by faecal analysis. – Acta Theriol. 44: 333–336.
- Wright, D. H. 1983. Species-energy theory: an extension of species–area theory. – Oikos 41: 496–506.
- Zirjanov, A. N. et al. 2001. About peculiarities of sable preying on musk deer. – In: Sokolov, G. A. (ed.), Rational use of sable resources in Russia. Krasnoyarsk State Univ. Press, Krasnoyarsk, Russia, pp.101–113, in Russian.