



Management and Conservation Article

Multi-Scale Foraging Habitat Use and Interactions by Sympatric Cervids in Northeastern China

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ABSTRACT Moose (*Alces alces*) and roe deer (*Capreolus pygargus*) are sympatric in the forest region of northeastern China. Using univariate analyses of feeding sign data, we found the 2 species were positively associated, but there were distinctions between their use of forage resources across landscape, patch, and microhabitat scales. We used resource selection function models to predict the influence of environmental covariates on moose and roe deer foraging; we detected covariate effects at the landscape and microhabitat scales but not at the patch scale. Forage resources used by the 2 species were similar, but moose used wetter areas and more low-visibility habitats than did roe deer, which strongly avoided areas with sparse vegetation. Both species were influenced by forage abundance and distribution at the microhabitat scale but exhibited differences in intensity of use of plant species and microhabitats. Moose used areas with deeper snow and avoided hiding cover; roe deer avoided areas with higher total basal areas of tree stems and preferred areas with high plant species richness. For moose, there was a trade-off in the use of concealment cover between the landscape and microhabitat scales. We detected avoidance by moose of roads where roe deer occurred. Roe deer exhibited more capacity for coping with human disturbance and interspecific interaction. In areas similar to our study area, road closures and suppression of roe deer near roads within 3–5 years postlogging may benefit moose. Furthermore, a mosaic of areas with different logging intervals may contribute to spatial separation of moose and roe deer and promote their coexistence.

KEY WORDS *Alces alces*, *Capreolus pygargus*, human disturbance, interspecific interaction, moose, roe deer.

Interactions among sympatric large herbivores are likely to influence their patterns of resource use. Sympatric species frequently display marked resource partitioning that presumably evolved as a consequence of past competition (Putman 1996). Demonstrating change in resource use by a species in the presence of another species (i.e., character displacement) is evidence of interspecific interaction. An understanding of habitat partitioning by herbivores at multiple scales can provide valuable information for development of management strategies (Collinge 2001). Because winter food availability may be a limiting factor for cervids, winter models can be particularly valuable (Dussault et al. 2005).

Deforestation is an ongoing disturbance throughout the world. Logging imposes sensory disturbance and can influence wildlife distribution and behavior (Mace et al. 1996; Jiang et al. 2006, 2007). Furthermore, human activity also may influence interspecific spatial distribution for ungulates (Jiang et al. 2008). Interspecific differences in responses to habitat factors by related species (Schweiger et al. 2000) can influence community structure in heterogeneous landscapes (Gabor et al. 2001).

In the Lesser Khingan Mountains forest region of northeastern China, moose (*Alces alces*) and roe deer (*Capreolus pygargus*) are sympatric, and the most recently available information suggests both species are declining (roe deer, Sheng et al. 1992; moose, Wang 1998). The study

of interactions between the 2 species has been limited to an investigation of dietary, habitat type, and foraging height overlap in northeastern China (Li et al. 1992). Both moose and roe deer are concentrate selectors and have similar forage requirements (Hofman 1989). However, differences in digestive system, forage selection, and morphology of the animal's mouth or other organs will affect feeding site selection (Voeten and Prins 1999). The moose is the largest cervid, but roe deer are small; therefore distinct differences in feeding site selection are expected. Based on an evolutionary point of view, we hypothesized that moose and roe deer would demonstrate resource partitioning, specifically that these species would select different feeding sites or use the same forage resources at different magnitudes.

We studied winter habitat preferences of moose and roe deer, forage selection, and ecological partitioning between the species during winter. Our goals were to 1) determine whether interspecific partitioning of foraging habitat exists in relation to multi-scale resource covariates, 2) assess the differential importance of resource covariates on selection of foraging habitats by moose and roe deer, 3) determine whether direct avoidance of one species' foraging behavior by the other species occurs, and 4) assess effects of human disturbance on selection of foraging habitats by the 2 species.

STUDY AREA

We conducted our study at the 20,661-ha Ekehe Forestry Farm (48°39'30"–48°48'21"N, 127°59'05"–128°15'19"E),

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along the northwestern slope of the Lesser Khingan Mountains in northeastern China. The forest farm was at an elevation of 420–465 m, with undulating terrain and slopes that ranged from 5° to 10°. A comprehensive drainage system merged to form a large area of forest wetland at the study site. Climate was characterized by long cold winters and short hot summers. Annual average temperature was -2°C , and average extreme temperatures ranged from -38.8°C to 34.3°C . Average annual precipitation ranged from 500 mm to 700 mm. The frost-free period was from late April to late September. Snow could persist from late November until the end of April. Vegetation in the study area consisted of coniferous, coniferous–deciduous, and deciduous forest. Dominant overstory tree species were Asian white birch (*Betula platyphylla*), Dahurian larch (*Larix gmelinii*), aspen (*Populus* spp.), willow (*Salix* spp.), Siberian alder (*Alnus sibirica*), Mongolian oak (*Quercus mongolica*), Chinese linden (*Tilia* spp.), Korean pine (*Picea koraiensis*), and Siberian fir (*Abies sibirica*). Dominant understory shrubs included hazel (*Corylus* spp.), rhododendron (*Rhododendron dauricum*), fire birch (*Betula fruticosa*), and lilac (*Syringa amurensis*), and dominant herbs included carex (*Carex* spp.) and nettle (*Urtica* spp.).

Most human presence in the forest was transient and occurred from mid-spring to mid-autumn. There were no villages in the forest, but there was a settlement occupied during winter by 4–5 forestry workers. A sparse network of open and closed roads (herein, trails) was associated with forestry operations. Logging, mostly selective, occurred for several decades and removed most mature trees while retaining young trees and some mature trees as seed sources.

METHODS

Collection of Habitat and Human Disturbance Data

We conducted field work from January to March during 2006 and 2007. We established plots along transects to measure habitat use by moose and roe deer. We established 28 transects, each 2.0–2.8 km in length, by randomly selecting the starting point for the first transect and extending the transect 2 km east. We established the remaining transects using an approximately parallel array at 2-km intervals extending south, traversing the whole study area, and covering all habitat types. Along these transects, we established 10×10 -m plots every 200 m (to avoid clustering) and recorded the Global Positioning System location at the center of each plot. At the 4 corners and center of each plot, we established $5 \times 2 \times 2$ -m subplots, yielding 613 plots and 3,065 subplots. To minimize pseudo-replication, we assessed plots within 7 days after heavy snowfall.

At each plot, we first looked for evidence of recent use by moose and roe deer based on fresh feeding sign (Lennart 2002, Jiang et al. 2006). We then recorded habitat covariates at microhabitat (plot), patch, or landscape scales. We used methods described in Li et al. (1992), Zhang and Xiao (1990), and Zhang (2001) to differentiate feeding sign left by the 2 species. If feeding sign of the species overlapped in height at the same feeding station, we ascribed the upper

half to moose and the lower half to roe deer. We were unable to differentiate use by gender.

We determined floristic and structural vegetation types using remote sensing. We generated digital forest cover and land use maps by visual interpretation of Spot-5 imagery (resolution: 2.5×2.5 m, volume: Network YZP0016533) taken on 21 September 2005. We used aerial photographs to build higher-resolution photo mosaics for classification of vegetation types. We scanned photographs and rectified mosaics with remote sensing software (ERDAS 2001); we then digitized scenes using ArcView Geographic Information System (GIS) Version 3.1 (Environmental Systems Research Institute 1996). We based classification of vegetation types primarily on categories established by the Zhanhe Forest Bureau forestry management map made in 2002. We identified 5 forest stands using an unsupervised classification with an iterative self-organizing data analysis technique and a supervised classification based on expert knowledge gained in the field (ERDAS 2001). The 5 forest types were birch stands, mixed deciduous broadleaf forest stands, tamarack forest stands, mixed coniferous and broadleaf forest stands, and low shrub and swamp (including areas of ice, which accounted for only 0.8% of the total study area).

For our analysis, we followed methods described in Johnson et al. (2004a) to evaluate aggregation and distribution of vegetation types at patch and landscape scales. We measured vegetation as the percentage of area per type at the patch scale and as mean density of patches in the region at the landscape scale. We then created map layers with a resolution of 100×100 m for both scales.

To measure distances (including distance to nearest settlement, roads, trails, rivers) and slope and aspect, we used the spatial analysis model in ArcView GIS Version 3.1. We also quantified logging intervals and mapped logged areas using ArcView GIS.

We used viewshed analysis to model visibility (Bowyer et al. 1999). Viewshed analysis determines areas visible and not visible on a grid or triangulated irregular network from one (e.g., a sample site) to many observation sites (Wang et al. 1996). Results are stored as a temporary integer grid where the value of each cell in the grid equals the number of sites from which it can be seen (Ormsby and Alvi 1999). Therefore, the higher viewshed value a site has, the more easily the site can be seen. We calculated the viewshed index of all survey plots using a software application within the 3D Analyst extension of ArcView GIS (Ormsby and Alvi 1999).

To measure forage availability at the landscape scale during late winter, we used greenness during September as a surrogate for vegetation quality and quantity (Cihlar et al. 1991). Greenness is highly correlated with leaf-area index (Crist and Cicone 1984, Cihlar et al. 1991). Thus, deciduous trees such as birch, aspen, willow, white alder, and Chinese linden can be expected to have greater coverage in areas of higher greenness (Mace et al. 1999); current annual shoots of these tree species are the main food for deer during winter (Yu et al. 1993). To indirectly assess concentrations of willows, we used wetness, a measure of soil moisture (Crist and Cicone 1984), and to assess openness, we used brightness, a measure

of bare soil surface reflectivity (Crist and Cicone 1984). We derived greenness, wetness, and brightness index values using a tasseled cap image transformation (Crist and Ciscone 1984) from the 2005 Spot-5 image.

We collected microhabitat covariate data within each plot; we sampled some covariates from the 5 subplots of one plot. We estimated hiding cover using a hiding-cover pole, following the method described by Griffith and Youtie (1988), and we recorded the number, stem cross-sectional area (tree basal area), and species of trees with diameter at breast height >5 cm and height >2 m in each plot. We then recorded number of fallen trees >10 cm diameter at breast height and classified species as conifers or deciduous trees within each plot.

We measured average snow depth (cm) and density of annual shoots as an index of forest productivity by counting, in the 5 subplots in each plot, the number of current annual growth shoots at heights below 175 cm for the 10 most common browse species, including aspen, willow, Asian white birch, hazel, fire birch, Chinese linden, rhododendron, Mongolian oak, willowleaf spiraea (*Spiraea salicifolia*), and Siberian alder (expressed as no./20 m²; Li et al. 1992, Andren and Angelstam 1993). We simultaneously recorded plant species richness for each subplot and calculated a Shannon–Wiener diversity index based on the number of shoots by species (Brewer 1979). We expressed availability of each of the main forage species as a proportion of total availability. To measure differential use of forage by the 2 deer species, we also quantified the number of shoots (expressed as no./20 m²) of each of the main forages browsed in the 5 subplots of each plot.

Scale Design

We based our analyses on associations between habitat characteristics at landscape, patch, and microhabitat scales and presence of either deer species, both species, or neither species. We extended the 2 scales of Johnson et al. (2004*b*; i.e., landscape and patch) into 3 scales (i.e., landscape, patch, and microhabitat). At the landscape scale, we quantified attributes of the whole region studied. We were unable to compare habitat characteristics within home ranges to the landscape scale because of the absence of home range data for both species in China. At the patch scale, we contrasted characteristics of vegetation patches (i.e., % area/vegetation type) with ungulate occurrence (WallisDeVries 1996). At the microhabitat scale, we examined differences in capacity for concealment, arboreal condition, forage abundance (i.e., food plant species diversity), barriers from fallen wood, snow depth, and feeding intensity on different plant species in the plots for both ungulate species.

We also considered human disturbance effects as landscape covariates that may impact resource selection at multiple scales. We analyzed effects of human disturbances on occurrence of foraging by each species separately and then considered interactions between the species.

Analyses and Modeling

For each covariate and scale, we initially used Mann–Whitney *U* tests for independent samples to examine

differences in habitat composition between plots where we detected moose and roe deer foraging. Due to the number of covariates (51) and scales (3), we applied the Dunn–Sidak adjustment (Sokal and Rohlf 1981) to ensure that all univariate tests were appropriately conservative (resulting $\alpha = 0.008$). We considered the *P* values, along with differences in means among compared groups, in describing relationships.

For each ungulate species, we used logistic regression to define a linear combination of vegetation and terrain covariates that best explained occurrence and distribution of each ungulate. We excluded human influence covariates until the next stage of analysis. We derived probabilistic resource selection functions (RSFs) to predict potential distribution of each species (Manly et al. 2002). Some covariates were highly skewed, so we normalized those using standard transformations (i.e., log transformation). We used a Pearson's correlation matrix to identify problematic collinearities among covariates (i.e., $r_s \geq 0.65$; Loyn et al. 2001). For correlated covariates, we retained the covariate that explained a greater portion of the model deviance.

We used a binomial distribution (feeding sign presence or absence) with a logit link function in generalized linear models using all possible subsets of covariates (Hayward et al. 2007). This represented an exploratory analysis given the scarcity of information available to define a clear set of a priori models. A logistic model can provide a better fit to the data if it demonstrates an improvement over the intercept-only model. An intercept-only model serves as a good baseline because it contains no predictors. Consequently, according to this model, all observations would be predicted to belong in the largest outcome category. An improvement over this baseline is examined by using inferential statistical tests (Menard 1995). We used Akaike's Information Criterion difference adjusted for small sample sizes (AIC_c) and Akaike model weights (w_i) to evaluate the models and identify the most parsimonious (i.e., fewest variables to explain the most variation). We assessed goodness-of-fit and predictive power using the Nagelkerke R^2 (R^2_N) and classification success (CS). We also calculated area under the receiver operating characteristic (AUC) curve, adopting the nonparametric assumption (Pearce and Ferrier 2000) or *c* statistic (Norusis 1999), which is the proportion of paired cases between the 2 groups in which a higher probability is assigned to cases where the event (i.e., detection of an independent deer feeding sign) has occurred. For each species, we applied the derived model within the GIS such that each pixel reflected occurrence probability. For different spatial scales, we followed methods of Johnson (2004*b*) to build the RSFs. The final predicted values, as opposed to true joint probabilities, represented relative probabilities of occurrence of species based on habitat covariates and were weighted by relative probabilities of occurrence across the larger study area (Johnson et al. 2004*b*).

To explore interspecific habitat partitioning, we first examined the relationship between the joint relative probability of potential distribution of moose and roe deer feeding sign detections at plots using a Spearman-rank

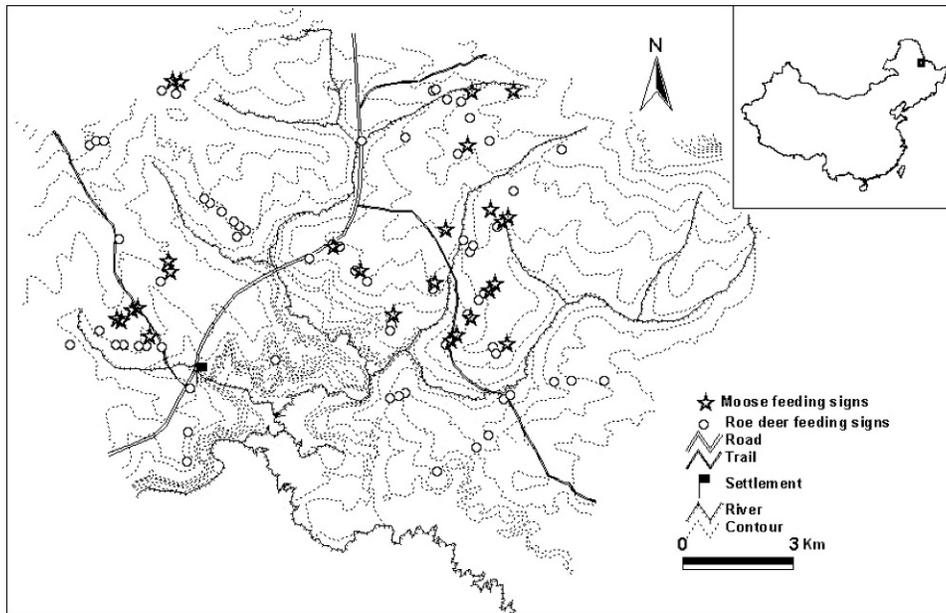


Figure 1. Distribution of moose and roe deer feeding sign presence locations in northwestern slope of Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). Contour lines are at 10-m intervals of altitude.

correlation coefficient. Then, we attempted to explain detection of each species beyond that predicted by its respective distribution-potential model by including detections of feeding sign of the alternate species as a potential covariate along with human influence variables. Finally, we evaluated the role of each species' potential distribution in predicting occurrence of the other, while accounting for covariation and direct interactions with human influence variables. We ran data analyses in the R statistical package using algorithms to calculate the AIC_c (Ihaka and Gentleman 1996).

RESULTS

Univariate Analyses

During January to March of 2006 and 2007, we detected moose and roe deer foraging in 26 and 67 of the 613 plots, respectively. Moose and roe deer used 14 and 31 plots, respectively, during January–March 2006, and 12 and 36 plots, respectively, during January–March 2007; 10 plots were used by both species simultaneously (Fig. 1). Mean snow depth at the 613 plots was 19.83 ± 0.75 cm.

Univariate results indicated that moose and roe deer responded similarly to most habitat characteristics. However, responses were different for 11 of 51 habitat covariates across the 3 spatial scales (Table 1). We detected moose more often than roe deer in landscapes characterized by high densities of patches of Asian white birch, which had low visibility (i.e., a low viewshed value) and reflected recent forest harvest. At the patch scale, we were more likely to detect moose than roe deer in low shrubs and swamp. At the microhabitat scale, moose were more tolerant of deep snow than roe deer, and we were more likely to detect moose in areas with a lesser basal area of Asian white birch, where there was a higher proportion of willow amongst the annual shoots, and where there was a lower density of fire birch annual

shoots. Moose browsed more annual shoots of hazel and willow and fewer Asian white birch shoots than did roe deer.

Model Selection

We found the top 5 logistic regression models by considering all resource and human disturbance variables at 3 scales and human disturbance and interspecific interaction, respectively, and calculated w_i for each model. We presented the best supported logistic regression models (i.e., those with $\Delta AIC_c \leq 2$) for moose (Table 2) and for roe deer (Table 3). Intercept-only models were not included in the best supported logistic regression model sets.

At the landscape scale for moose, the most parsimonious resource model consisted of 6 covariates (Asian white birch density, mixed coniferous and broadleaf density, greenness, wetness, elevation, and viewshed; no. of model parameters [K] = 8, $w_i = 0.420$). The second most parsimonious resource model incorporated slope ($K = 9$, $w_i = 0.280$; Table 2). At the patch scale, the best resource model had 2 covariates (Dahurian larch patch, and mixed coniferous and broadleaf patch; $K = 3$, $w_i = 0.401$). The next best resource model included the mixed deciduous broadleaf patch covariate ($K = 4$, $w_i = 0.315$; Table 2). At the microhabitat scale, the best resource model included 12 covariates (browsing intensity on fire birch, browsing intensity on willow, hiding cover, browsing intensity on Siberian alder, browsing intensity on aspen, rhododendron availability, browsing intensity on hazel, percent annual shoots of Asian white birch, percent annual shoots of willow, snow depth, hazel availability, and total basal area; $K = 13$, $w_i = 0.291$). The second best resource model removed rhododendron availability and hazel availability but included browsing intensity on rhododendron, percentage annual shoot number of hazel, and Siberian alder availability ($K = 14$, $w_i = 0.262$; Table 2). Considering human disturbance and interspecific interaction models, the best

Table 1. Differences in habitat variables between moose and roe deer winter foraging habitats at 3 spatial scales in the northwestern slope region of the Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). We show results for landscape, patch, and microhabitat (plot) scales. Differences (Mann–Whitney U tests) are indicated by + +/– ($P < 0.008$), +/– ($0.008 \leq P < 0.08$), or ns ($P \geq 0.08$) based on Monte Carlo 999 sampled. Sign indicates relationship of detection of moose foraging in the specified habitats relative to detection of roe deer foraging in the specified habitats.

Scale	Variables	Moose ($n = 26$)		Roe deer ($n = 67$)		Significance
		\bar{x}	SE	\bar{x}	SE	
Landscape	Asian white birch density	0.486	0.053	0.396	0.036	+
	Viewshed	45.477	6.688	57.385	4.422	–
	Logging interval	3.869	0.326	4.686	0.291	–
Patch	Low shrub and swamp patch	0.016	0.009	0.047	0.015	–
Microhabitat	Snow depth	21.192	0.833	19.589	0.528	+
	% basal area of Asian white birch	0.298	0.073	0.424	0.045	–
	% annual shoots of willow	0.151	0.054	0.044	0.020	++
	Browsing intensity on Asian white birch	3.846	1.682	8.000	1.869	–
	Browsing intensity on hazel	83.962	45.196	5.552	3.142	+
	Browsing intensity on willow	12.462	3.875	3.433	1.733	++
	Fire birch availability	103.846	78.394	197.985	78.055	–

Table 2. Number of model parameters (K), differences in Akaike’s Information Criterion (ΔAIC_c) scores, and AIC_c weights (w_i) for the most supported logistic regression models (with $\Delta AIC_c < 2$) for moose at 3 scales in Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007).

No.	Logistic model ^a	K	AIC_c	ΔAIC_c	w_i
Landscape scale					
1	AWB density + MCB density + greenness + wetness + elevation + elevation + viewshed	8	189.24	0.00	0.420
2	AWB density + MCB density + greenness + wetness + elevation + elevation + viewshed + slope	9	190.05	0.81	0.280
3	AWB density + MCB density + greenness + wetness + elevation + elevation + viewshed + slope + Dahurian larch density	10	191.26	1.98	0.153
Patch scale					
1	Dahurian larch patch + MCB patch	3	212.53	0.00	0.401
2	Dahurian larch patch + MCB patch + MDB patch	4	213.01	0.48	0.315
3	Dahurian larch patch + MCB patch + MDB patch + AWB patch	5	213.91	1.38	0.201
Microhabitat scale					
1	BI on fire birch + BI on willow + hiding cover + BI on Siberian alder + BI on aspen + rhododendron availability + BI on hazel + % ASN of AWB + % ASN of willow + snow depth + hazel availability + total basal area	13	125.40	0.00	0.291
2	BI on fire birch + BI on willow + hiding cover + BI on Siberian alder + BI on aspen + BI on rhododendron + BI on hazel + % ASN of AWB + % ASN of willow + snow depth + total basal area + % ASN of hazel + Siberian alder availability	14	125.61	0.21	0.262
3	BI on willow + hiding cover + BI on siberian alder + BI on aspen+ BI on rhododendron + BI on hazel + % ASN of AWB + % ASN of willow + snow depth + total basal area + % ASN of hazel + Siberian alder availability + Shannon–Wiener index	15	125.8	0.40	0.238
4	BI on fire birch + BI on willow + hiding cover + BI on Siberian alder + BI on aspen + BI on rhododendron + BI on hazel + % ASN of AWB + % ASN of willow + snow depth + total basal area + % ASN of hazel + Siberian alder availability + Shannon–Wiener index + AWB availability	16	126.9	1.50	0.138
Human disturbance and interspecific interaction model					
1	Logging interval ^b + logging interval + RSF_roe deer \times distance to road + (RSF_roe deer \times distance to roads) ^b + RSF_moose	6	86.11	0.00	0.412
2	Logging interval ^b + logging interval + RSF_roe deer \times distance to road + (RSF_roe deer \times distance to roads) ^b + RSF_moose + distance to human settlement ^b	7	86.58	0.47	0.326
3	Logging interval ^b + logging interval + RSF_roe deer \times distance to road + (RSF_roe deer \times distance to roads) ^b + RSF_moose + distance to human settlement ^b + distance to human settlement	8	87.89	1.78	0.169

^a AWB, Asian white birch; MCB, mixed coniferous and broadleaf forest stand; MDB, mixed deciduous broadleaf forest stand; BI, browsing intensity; ASN, annual shoot no.; RSF_roe deer, the roe deer potential-occurrence model; RSF_moose, the moose potential-occurrence model.

^b Squared second term for nonlinear Gaussian function.

Table 3. Number of model parameters (K), differences in Akaike's Information Criterion (ΔAIC_c) scores, and AIC_c weights (w_i) for the most supported logistic regression models (with $\Delta AIC_c < 2$) for roe deer at 3 scales in Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007).

No.	Logistic model ^a	K	AIC_c	ΔAIC_c	w_i
Landscape scale					
1	Elevation + elevation + AWB density + brightness	5	405.6	0.00	0.296
2	Elevation + elevation + AWB density + brightness + viewshed	6	405.77	0.17	0.272
3	Elevation + elevation + AWB density + brightness + viewshed + MCB density	7	406.24	0.64	0.215
4	Elevation + elevation + AWB density + brightness + viewshed + MCB density + slope	8	406.94	1.34	0.151
Patch scale					
1	AWB patch + Dahurian larch patch + low shrub and swamp patch	4	420.66	0.00	0.627
2	AWB patch + Dahurian larch patch + low shrub and swamp patch + MCB patch	5	422.32	1.66	0.273
Microhabitat scale					
1	Total basal area + % base area of AWB + plant species richness + % ASN of AWB + BI on willow + % ASN of hazel + BI on AWB + BI on fire birch + BI on rhododendron	10	250.45	0.00	0.323
2	Total basal area + % base area of AWB + plant species richness + % ASN of AWB + BI on willow + % ASN of hazel + BI on AWB + BI on fire birch + BI on rhododendron + BI on Siberian alder	11	250.58	0.13	0.302
3	Total basal area + % base area of AWB + plant species richness + % ASN of AWB + BI on willow + % ASN of hazel + BI on AWB + BI on fire birch + BI on rhododendron + BI on Siberian alder + hiding cover	12	251.03	0.58	0.241
4	Total basal area + % base area of AWB + plant species richness + % ASN of AWB + BI on willow + % ASN of hazel + BI on AWB + BI on fire birch + BI on rhododendron + BI on Siberian alder + hiding cover + BI on hazel	13	252.18	1.73	0.136
Human disturbance and interspecific interaction model					
1	Distance to road + distance to trail ^b + forest harvest interval ^b + RSF_moose \times logging interval + (RSF_moose \times distance to road) ^b + RSF_roe deer	7	257.1	0.00	0.377
2	Distance to road + distance to trail ^b + forest harvest interval ^b + RSF_moose \times logging interval + (RSF_moose \times distance to road) ^b + RSF_roe deer + distance to trail	8	257.64	0.54	0.288
3	Distance to road + distance to trail ^b + forest harvest interval ^b + RSF_moose \times logging interval + (RSF_moose \times distance to road) ^b + RSF_roe deer + distance to trail + distance to human settlement	9	258.26	1.16	0.211

^a AWB, Asian white birch; MCB, mixed coniferous and broadleaf forest stand; BI, browsing intensity; ASN, annual shoot no.; RSF_roe deer, the roe deer potential-occurrence model; RSF_moose, the moose potential-occurrence model.

^b Squared second term for nonlinear Gaussian function.

model consisted of 3 covariates for logging interval and its squared second term, the interaction between the potential occurrence of roe deer and roads (i.e., RSF_roe deer \times distance to road) and its squared second term, and potential occurrence of moose (i.e., RSF_moose; $K = 6$, $w_i = 0.412$). The second best model incorporated distance to human settlement and a squared second term ($K = 7$, $w_i = 0.326$; Table 2).

At the landscape scale for roe deer, the most parsimonious resource model consisted of 3 covariates (elevation, Asian white birch density, brightness; $K = 5$, $w_i = 0.296$). The next best resource model incorporated viewshed ($K = 6$, $w_i = 0.272$; Table 3). At the patch scale, the best resource model had 3 covariates (Asian white birch patch, Dahurian larch patch, and low shrub and swamp patch; $K = 4$, $w_i = 0.627$; Table 3). At the microhabitat scale, the best resource model consisted of 9 covariates (total basal area, percent base area of Asian white birch, plant species richness, percent annual shoots of Asian white birch, browsing intensity on willow, percent annual shoots of hazel browsing intensity on

Asian white birch, browsing intensity on fire birch, browsing intensity on rhododendron; $K = 10$, $w_i = 0.323$). The second best resource model added browsing intensity on Siberian alder ($K = 11$, $w_i = 0.302$; Table 3). Considering human disturbance and interspecific interaction models, the best model consisted of 6 covariates for distance to road, distance to trail with squared second term, forest harvest interval with squared second term, and squared second term for the interaction between potential occurrence of moose and forest harvest interval (i.e., RSF_moose \times logging interval), the interaction between potential occurrence of moose and road (i.e., RSF_moose \times distance to road), and potential occurrence of roe deer (i.e., RSF_roe deer; $K = 7$, $w_i = 0.377$). The second most parsimonious resource model incorporated distance to trail ($K = 8$, $w_i = 0.288$; Table 3).

Potential Species' Foraging Habitat Distributions

We generated 5,000 bootstrap samples at each scale. At the landscape scale, moose occurrence was best explained (R^2_N

Table 4. Best logistic regression model of moose feeding habitat potential distribution on northwestern slope of Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). We show model results for landscape, patch, and microhabitat scales.

Variable ^a	Coeff.	SE	95% CI
Landscape			
MCB density	-0.3983	0.2485	-0.9086 to 0.0715
Viewshed	-0.4154	0.2204	-0.8780 to -0.0059
Elevation	-43.4248	24.4749	-98.9887 to -14.8258
Elevation	61.491	33.503	20.4489 to 137.7266
Greenness	1.5137	0.4502	0.6648 to 2.4458
AWB density	0.7387	0.1997	0.3455 to 1.1363
Wetness	1.982	0.4498	1.1131 to 2.8930
Constant	-6.1810	1.3563	-9.2923 to -5.6451
Patch			
MCB patch	-0.3109	0.2314	-0.8189 to 0.1053
Dahurian larch patch	-0.9376	0.4474	-2.1117 to -0.2458
Constant	-3.3669	0.2768	-4.0373 to -2.8956
Microhabitat			
% ASN of willow	0.3745	0.2226	-0.1322 to 0.8022
Snow depth	0.5236	0.2886	-0.0747 to 1.0603
Hiding cover	-11.5973	5.8451	-24.3106 to -3.7269
BI on fire birch	0.3916	0.1341	0.0718 to 0.6598
Total basal area	-2.3384	1.142	-4.8786 to -0.2881
% ASN of AWB	0.8671	0.3236	0.2606 to 1.5840
Rhododendron availability	0.3618	0.136	0.1359 to 0.7242
Hazel availability	1.209	0.4294	0.4549 to 2.1919
BI on aspen	0.5489	0.17	0.2515 to 0.9079
BI on willow	0.5854	0.1884	0.2902 to 1.0368
BI on Siberian alder	0.6674	0.2469	0.3459 to 1.3118
BI on hazel	0.9116	0.2424	0.4959 to 1.5692
Constant	-6.0859	0.9112	-8.1893 to -5.6392

^a AWB, Asian white birch; MCB, mixed coniferous and broadleaf forest stand; BI, browsing intensity; ASN, annual shoot no.

= 0.224) by 6 characteristics from the suite of terrain, vegetation, and land-cover covariates (Table 4). The model successfully discriminated 95.8% (CS) of sample locations using a cut-point of $P = 0.50$ ($AIC_c = 189.24$, $\chi^2 = 41.978$, $df = 7$, $P < 0.001$, $AUC = 0.848$ [SE = 0.029]); roe deer occurrence was best explained by 3 of the resource covariates ($AIC_c = 405.56$, $R^2_N = 0.188$, $\chi^2 = 27.467$, $df = 4$, $P < 0.001$, $AUC = 0.716$ [SE = 0.032], CS = 89.1%; Table 5). At the patch scale, the best models for both moose and roe deer could not explain occurrence using our suite of covariates and had poor predictive power (moose: $AIC_c = 212.53$, $R^2_N = 0.047$, $\chi^2 = 8.680$, $df = 2$, $P = 0.013$, $AUC = 0.618$ [SE = 0.043], CS = 65%; roe deer: $AIC_c = 420.66$, $R^2_N = 0.034$, $\chi^2 = 10.363$, $df = 3$, $P = 0.016$, $AUC = 0.574$ [SE = 0.034], CS = 64.6%; Tables 4, 5). At the microhabitat scale, moose occurrence was best explained ($R^2_N = 0.581$) by 12 resource covariates (Table 4). The model successfully discriminated 97.4% (CS) of sample locations using a cut-point of $P = 0.50$ ($AIC_c = 125.402$, $\chi^2 = 115.814$, $df = 12$, $P < 0.001$, $AUC = 0.957$ [SE = 0.017]); roe deer occurrence was best explained by 9 resource covariates ($AIC_c = 250.45$, $R^2_N = 0.541$, $\chi^2 = 192.579$, $df = 9$, $P < 0.001$, $AUC = 0.936$ [SE = 0.014], CS = 93.8%; Table 5). For the 2-species models, the best models were all at the microhabitat scale. Models at the landscape scale were intermediate, and models at the patch scale were

Table 5. Best logistic regression model of roe deer feeding habitat potential distribution on northwestern slope of Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). We show model results for landscape, patch, and microhabitat scales.

Variable ^a	Coeff.	SE	95% CI
Landscape			
Elevation	-10.8949	7.2368	-27.6036 to 0.8024
Elevation	15.2816	9.7168	-0.3500 to 37.8141
AWB density	0.2570	0.1253	0.0057 to 0.4989
Brightness	-0.4705	0.1350	-0.7360 to -0.2051
Constant	-2.6932	0.3341	-3.4851 to -2.5693
Patch			
AWB patch	0.1535	0.098	-0.0583 to 0.3350
Low shrub and swamp patch	0.3465	0.1955	-0.0296 to 0.7538
Dahurian larch patch	-0.5714	0.2487	-1.1309 to -0.1435
Constant	-2.1874	0.1436	-2.4862 to -1.9194
Microhabitat			
Total basal area	-0.67647	0.44637	-1.6203 to 0.1178
% ASN of AWB	0.36132	0.18896	-0.0277 to 0.7237
% base area of AWB	0.41725	0.17233	0.0807 to 0.7604
% ASN of hazel	0.52573	0.20411	0.1317 to 0.9395
BI on willow	0.35346	0.09464	0.1676 to 0.5629
Plant species richness	0.72283	0.17478	0.3837 to 1.0750
BI on fire birch	0.60778	0.17218	0.3260 to 1.0457
BI on rhododendron	1.40565	0.3784	0.7721 to 2.3963
BI on AWB	1.73392	0.32334	1.1369 to 2.4110
Constant	-2.99616	0.26910	-3.5737 to -2.5111

^a AWB, Asian white birch; BI, browsing intensity; ASN, annual shoot no.

poor. Further, the same covariates had different effects on the 2 species.

Interspecific Relations

Among plots, frequency of independent deer detections was positively related between species ($r_s = 0.186$, $df = 612$, $P < 0.001$). There was a strong positive relationship between moose and roe deer based on the relative joint predictive probability of their distribution-potential models ($r_s = 0.704$, $df = 612$, $P < 0.001$), suggesting similar effects of spatial resources on their distributions.

Due to poor results at the patch scale, we only used the joint relative predictive probability of models at the landscape and microhabitat scales to predict the joint occurrence of the 2 species. Across the 2 scales, interactions between the roe deer distribution-potential model and human influence covariates explained distribution of moose better than did the moose distribution-potential model alone ($AIC_c = 86.11$, $\chi^2 = 141.101$, $df = 5$, $P < 0.001$, $R^2_N = 0.694$, $AUC = 0.985$ [SE = 0.008], CS = 98.2%; Table 6). Specifically, with increasing roe deer distribution potential, moose avoided areas along roadsides and preferred areas with forest harvest intervals of 2–3 year (Fig. 2a, b). Inclusion of human influence covariates also accounted for more variation in distribution of roe deer than did the roe deer distribution-potential model alone ($AIC_c = 257.09$, $\chi^2 = 179.936$, $df = 6$, $P < 0.001$, $R^2_N = 0.510$, $AUC = 0.896$ [SE = 0.026], CS = 94%; Table 7). With inclusion of the moose distribution-potential model, roe deer tended to avoid areas near trails, preferred areas near roads (but avoided those same areas if there was a low moose

Table 6. Best logistic regression model of moose feeding sign occurrence considering roe deer feeding sign occurrence and interactions with human influence variables. We collected data from field survey on the northwestern slope of Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). We accounted for variation explained by the moose potential-occurrence model (RSF_MS).

Variable ^a	Coeff.	SE	95% CI
RSF_roe deer × distance to road	−0.4607	0.2752	−0.9605 to 0.1351
RSF_roe deer × distance to roads ^b	−0.5751	0.2625	−1.3071 to −0.1372
Logging interval	5.7498	2.4867	1.5585 to 11.3281
Logging interval ^b	−6.0391	2.4769	−11.6288 to −1.8487
RSF_moose	6.1528	1.0576	4.3215 to 8.4979
Constant	−4.9324	0.6686	−6.5098 to −3.8546

^a RSF_roe deer, the roe deer potential-occurrence model; RSF_moose, the moose potential-occurrence model.

^b Squared second term for nonlinear Gaussian function.

distribution potential), and preferred areas with a logging intervals of about 3–6 years (Table 7; Fig. 2c–f).

DISCUSSION

Multiple-Scale Resource Use

Our data indicated that, at the landscape scale, foraging moose preferred heterogeneous areas with a high density of Asian white birch patches, high soil moisture (indicating likelier presence of willow), high greenness (indicating more productive vegetation), intermediate elevation, and low visibility (i.e., high concealment), and moose tended to avoid high densities of mixed deciduous broadleaf forest patches. Our findings are similar to the broad-scale habitat requirements of moose in interior Alaska (Maier et al. 2005). At the microhabitat scale, moose showed no avoidance of deep snow but exhibited avoidance of dense cover and high basal areas of tree stems, preferred areas with high proportions of annual shoots of Asian white birch and willow, and preferred areas with abundant annual shoots of hazel and rhododendron. The highest intensity of browsing by moose was on hazel, followed by Siberian alder, willow, aspen, and fire birch. At the landscape scale, roe deer also selected for a high density of Asian white birch patches and intermediate elevation, but unlike moose, roe deer strongly avoided areas with high brightness (i.e., sparse vegetation). At the microhabitat scale, roe deer shared the moose aversion to areas with high basal areas of tree stems and the moose preference for areas with high proportions of annual shoots of Asian white birch. Roe deer also preferred areas with high proportions of annual shoots of hazel, high basal areas of stems of Asian white birch, and high plant species richness. The highest intensity of browsing by roe deer was on Asian white birch, followed by rhododendron, fire birch, and willow.

Tufto et al. (1996) found that forest types characterized by high densities of food and low visibility inside home ranges were preferred by roe deer. We found that moose foraged in areas that offered concealment at the landscape scale but not at the microhabitat scale, perhaps because habitat features that provided concealment would also impede movements at the microhabitat scale. However, patches of Asian white birch offered security cover, should a threat be detected. The importance of availability of nearby refuges has been recognized; for example, Kolter et al. (1994) suggested that ibex (*Capra ibex*) minimize risk of predation by foraging

close to terrain that offers the potential for escape, such as extremely steep slopes or cliffs. Roe deer are territorial and often solitary, and it is possible that interference competition may occur because roe deer are intimidated by the larger moose (Dziciotowski 1979, Latham et al. 1996, Latham 1999). In the presence of predators, species may associate to enable mutualistic vigilance (e.g., de Boer and Prins 1990), but it has been recognized that a shorter species may be more of a commensal in this regard, presumably because of the greater field of vision of a taller species. For a smaller species it has been suggested that the advantage of predator avoidance may outweigh the disadvantage of forage competition (Bartos et al. 2002).

Moose are adapted to deep snow, but only up to 40 cm (Peek 1971, Telfer and Kelsall 1979). In our study area, long-term mean snow depths averaged about 40 cm, but there was a recent trend towards shallower depths, perhaps associated with global warming. Although our study revealed a tendency for moose to forage in areas with deeper snow than would roe deer, at a mean snow depth of about 20 cm, the difference between the species was slight. We expect that any competitive advantage that moose have over roe deer because of their capacity to forage in deeper snow will be lost if the trend toward shallower snow depths continues.

Winter is critical for deer species that live at high latitudes because of the limited abundance of preferred foods (Maizeret et al. 1989). Theory predicts that individuals should choose foraging strategies that maximize the rate of intake of energy or nutrients, and distribution of resources across the landscape has been shown to affect foraging patterns (Charnov 1976, Wallace et al. 1995, Morellet and Guibert 1999). Our results for moose and roe deer browsing were consistent with Li et al. (1992). The rank in importance of browsed plant species and differences in availability for both deer species may contribute to the species coexistence by mitigating interspecific competition for forage (Wiens 1993). Moose also often fed higher and on larger shoots than did roe deer. By browsing patchily and focusing on exposed trees in existing gaps, moose may suppress or redistribute preferred browse, thereby modifying the environment of roe deer (Edenius et al. 2002a, Jiang et al. 2009). That roe deer preferred areas where moose occurred may imply a mutualistic or commensal relationship.

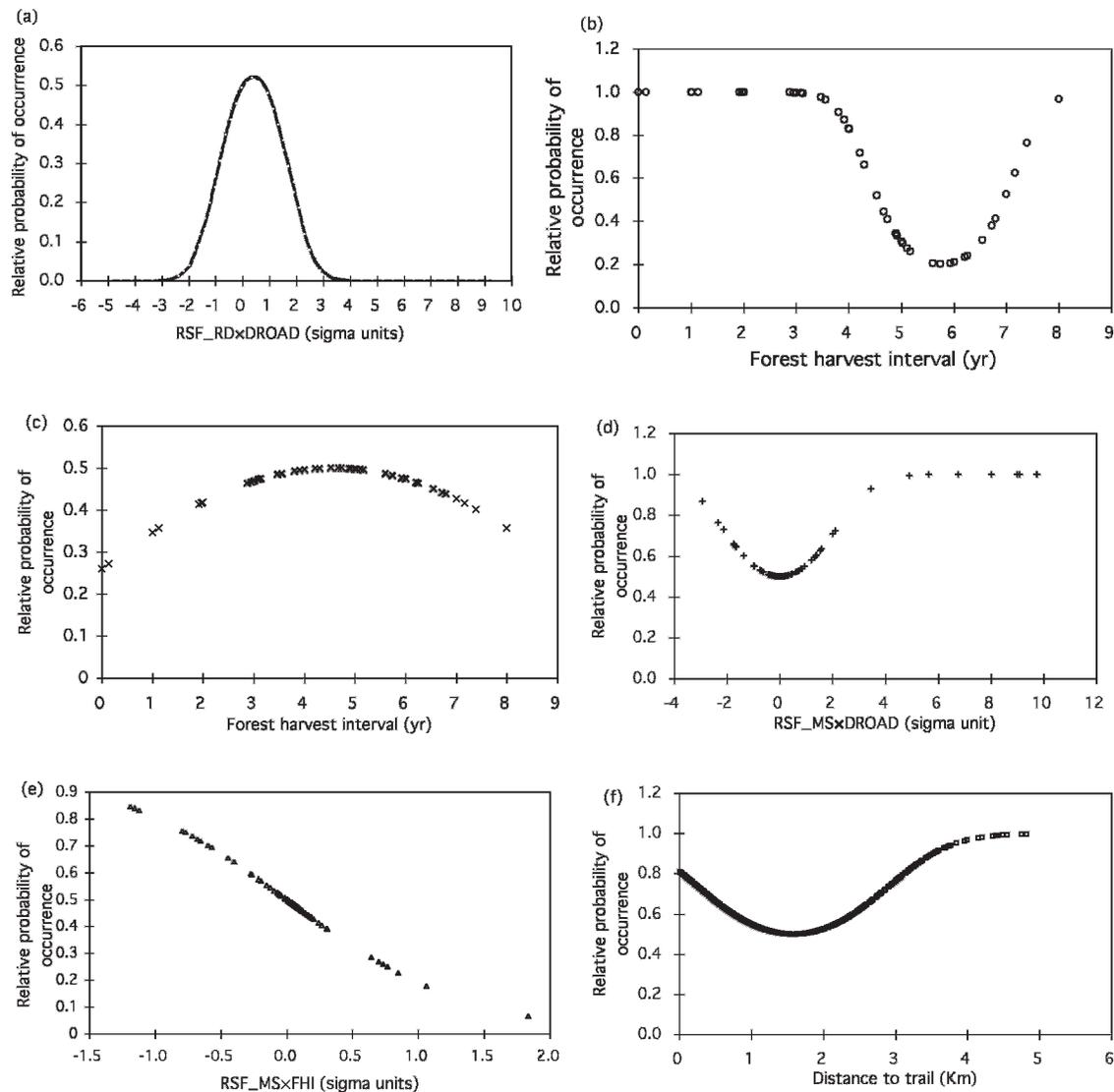


Figure 2. Relationship between relative probability of occurrence of moose feeding sign and predicted roe deer feeding sign occurrence (i.e., RSF_RD) and interactions with (a) distance to roads (i.e., DROAD) and (b) forest harvest interval, (c) relative probability of occurrence of roe deer feeding sign and forest harvest interval, (d) predicted moose feeding sign occurrence (i.e., RSF_MS) and interactions with distance to roads, (e) predicted moose feeding sign occurrence and interactions with forest harvest intervals (i.e., FHI), and (f) distance to trail. We took coefficients from the most parsimonious resource-selection-function model describing distribution of feeding habitat in northwestern slope of Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). We held the alternate variable at its mean.

Our failure to discriminate characteristics of foraging sites of the 2 species at the patch scale may have been because our definition of a patch was not congruent with ungulate foraging strategies. We defined patches based on uniformity of vegetation (i.e., forest stands), but Astrom et al. (1990) concluded that foraging ungulates perceive each tree as a patch, and Jiang et al. (2009) found that roe deer used clusters of aspen ramets as patches (a scale almost as fine as our microhabitat scale). Moose, on the other hand, may not perceive aspen stands as discrete patches, foraging instead on aspen ramets more in accordance with diet theory than with patch use theory (Edenius et al. 2002b). Species-specific plant productivity varies across landscapes and could cause pronounced ungulate aggregation on patches of high productivity (Fryxell 1991, Apps et al. 2001). Therefore, it seems likely that our botanically based definition of a patch

was inadequate as a criterion for defining an intermediate scale of analysis.

Interspecific Relationships and Human Disturbance

Bartos et al. (2002) noted complex interspecific behavior wherein there were tradeoffs between the disadvantage of interspecific competition and the greater advantage of interspecific cooperative vigilance; our work was premised on avoidance as the indicator of interspecific interaction or reaction to human disturbance. Applying predetermined RSF coefficients allowed us to easily assess the simple footprint (i.e., human activity facilities) impacts associated with human disturbance. Thus, we could explore the dynamics of the relative probability of occurrence as a function of change in disturbance or interspecific interaction intensity. Similar approaches were used to assess impacts of human activity on

Table 7. Best logistic regression model of roe deer feeding sign occurrence considering moose feeding sign occurrence and interactions with human influence variables. We collected data from field surveys on the northwestern slope of Lesser Khingan Mountains, northeastern China (Jan–Mar 2006 and Jan–Mar 2007). We accounted for variation explained by the roe deer potential-occurrence model (RSF_RD).

Variable ^a	Coeff.	SE	95% CI
Forest harvest interval ^b	0.3164	0.2034	−0.0864 to 0.7152
RSF_moose × distance to road ^b	−0.2178	0.1184	−0.4928 to 0.0086
RSF_moose × logging interval	1.4299	0.7389	0.0529 to 2.9989
Distance to trail ^b	−0.6213	0.2556	−1.1569 to −0.1515
Distance to road	0.4878	0.1668	0.1584 to 0.8159
RSF_ roe deer	1.9367	0.2265	1.5229 to 2.4121
Constant	−2.8554	0.2211	−3.3227 to −2.4506

^a RSF_ roe deer, the roe deer potential-occurrence model; RSF_moose, the moose potential-occurrence model.

^b Squared second term for nonlinear Gaussian function.

use of habitats by grizzly bears (*Ursus arctos horribilis*) in North America and by red deer (*Cervus elaphus xanthopygus*) in northeastern China (Suring et al. 1998, Jiang et al. 2007).

For ungulates, the most commonly described interaction has been either resource competition or interference competition (Birch 1957, Putman 1986). Illius and Gordon (1987) and Gordon and Illius (1989) concluded that smaller grazing animals are able to make better use of short grass swards than are larger animals, as demonstrated by male red deer leaving preferred feeding areas sooner than did smaller females. Li et al. (1992) suggested that the level of competition between moose and roe deer in northeastern China is low, based on the overlap of food items, the degree of overlap in foraging heights, and the degree of overlap in habitat use. However, Myrsterud (2000) cautioned that identification of overlap in space and diet is insufficient to demonstrate competition. We had no evidence of displacement of moose by roe deer, but our results suggested that roe deer potential distribution may have negatively influenced moose via an interaction with roads (Table 6; Fig. 2a). Although interaction of moose foraging and logging activity may directly benefit availability or quality of roe deer foraging habitat through effects on forest structure (Table 7; Fig. 2e), moose may not adapt as effectively as roe deer to human disturbance as evidenced by relative absence of moose from areas near roads where roe deer occurred. Jaeger et al. (2005) suggested that avoidance of roads by wildlife may indirectly result in habitat loss and fragmentation. In recent times, moose in the Greater Khingan Mountains and part of the Lesser Khingan Mountains have decreased by 46%, at an annual rate of decline of 6% (Wang 1998). Geographic distribution of moose declined toward the north and west by nearly 100 km and 200 km, respectively, resulting in 55,100 km² of lost habitat (Wang 1998). We further suggest that the rapidly decreasing number of moose and their shrinking distribution in northeastern China in the last 10 years may be the result of increasing human disturbance (i.e., construction of networks of forest roads) and potential presence of roe deer, whereas factors affecting distribution of roe deer may be more complex because of their stronger adaptive capability to interspecific interaction and human disturbances.

We found that roe deer preferred areas near roads (i.e., CI of coeff. > 0) and avoided foraging habitat with the interaction between occurrence of both moose and roads

(i.e., coeff. < 0, but CI of coeff. overlapped zero; Table 7; Fig. 2d; Manly et al. 2002). Jepsen and Topping (2004) suggested that roe deer are behaviorally plastic in that they aggregate and adjust their spatial distributions as antipredator strategies in habitats fragmented by human disturbances. Myrsterud et al. (1999) found that roe deer selected feeding sites closer to human settlement at night and as snow depth increased. Jiang et al. (2008) also suggested that roe deer coped with human disturbance better than did red deer in northeastern China.

Our results demonstrated that foraging roe deer preferred areas with 4–5-year logging intervals (Fig. 2c), whereas moose preferred areas with 1–3-year intervals and avoided areas with 4–7-year intervals (Fig. 2b), which indicated that forest succession after logging may have different effects on moose and roe deer. Rma et al. (1996) showed that forest succession after logging may affect cervid diets and perhaps habitat use. Reduced security cover or increased human disturbance from logging may alter both short- and long-term patterns of cervid movement (Stephenson et al. 1996). Moose prefer habitats containing early-successional woody browse, and this type of habitat is promoted by disturbances such as logging, floods, avalanches, and fire (Van Tighem 2001). Jiang et al. (2008) also suggested that human disturbance may contribute to observed patterns of habitat-based segregation by red deer and roe deer. In another study area, selective logging influenced tree species composition but did not change habitat classes (i.e., vegetation type); however, logging did alter the habitat structure, which could impact distribution of deer foraging sites (Rma et al. 1996). The spatial and temporal distribution of logging may produce areas of different successional stages preferred by foraging moose and roe deer and contribute to their partitioning of forage resources.

MANAGEMENT IMPLICATIONS

Given that the moose is a conservation priority in China, wildlife managers can promote moose populations by closing forest roads if feasible or by regulating density of roe deer in the vicinity of roads. Wildlife managers could reduce mixed coniferous and broadleaf forests, increase Asian white birch density, and promote riparian vegetation to improve quality of moose habitat. A mosaic of areas with different logging intervals may contribute to the spatial separation of moose and roe deer and promote their coexistence.

When applying these results, managers should focus on improving the landscape and microhabitat scale models by monitoring human disturbance and analyzing interspecific foraging relationship dynamics. Managers also should focus on increasing preferred forage availability, such as hazel willow, Asian white birch, and fire birch to benefit both species. Managers may promote roe deer use by improving forage diversity and increasing availability of rhododendron. Managers may benefit moose by promoting growth of Siberian alder and aspen.

Managers should assess foraging habitat relative to the patchiness of forest stands and consider planning for areas with high concealment cover at the landscape scale and low concealment cover at the microhabitat scale to maintain moose populations. Based on the inherent uncertainty in our models, managers should monitor spatial distributions of both species; researchers should evaluate multiple-scale habitat use characteristics and ecological effects of human disturbance on each species.

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