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Habitat use and separation between red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* in relation to human disturbance in the Wandashan Mountains, northeastern China

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Habitat use and separation in relation to human disturbance of two sympatric species, red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi*, were studied in the Wandashan Mountains, Heilongjiang Province, China. We measured 19 variables describing macrohabitat (e.g. distance to roads or forest type) and microhabitat (e.g. escape cover or snow depth) characteristics at each plot where red or roe deer occurred. Statistical analysis of macrohabitat characteristics for the two deer species identified a statistically significant difference in the distance to human disturbances, especially settlements, for sites utilised by red deer and roe deer. Despite range overlaps between red deer and roe deer in the study area, each species exhibited different patterns in microhabitat use. The two deer species do not seem to be impacted to the same degree by human disturbance. Red deer occurred at sites characterised by mature mixed coniferous and broadleaf stands, at higher elevations, and deeper snow cover. Additionally, red deer occurred at sites further from human settlement, cropland or logged areas than did roe deer. Conversely, roe deer occurred at sites with sparse forest cover and denser shrub cover, at lower altitudes, with less snow, and more abundant food of common plant species eaten by both deer. Overall, roe deer seemed to cope with human disturbance near settlements better than red deer. We suggest that human disturbance may be important in determining both species' utilisation of resources and thus may contribute to the observed patterns of red and roe deer habitat separation. Moreover, understanding any differential effects of human disturbance on the two species may contribute to understanding the population dynamics of these two species as human disturbance in China is expected to continue increasing.

Key words: Capreolus pygargus bedfordi, Cervus elaphus xanthopygus, coexistence, habitat selection, human disturbance, red deer, roe deer, spatial resource partitioning

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In the Helongjiang province of northeastern China and our study area in the Wandashan Mountains, red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* occur sympatrically (Li et al. 1992). In addition to being economically important species for their antlers and meat, both species of deer play an even more important role in shaping the structure and the composition of the forest ecosystems they inhabit for example through their feeding habits (Naiman 1988, Li & Yan 1989). Furthermore, red deer and roe deer are the primary prey species of the highly endangered Amur tiger *Panthera tigris altaica,* and their survival may be essential to the survival of the rare Amur tiger (Li et al. 2001).

Previous population estimates for *Cervus elaphus* in China range within 100,000 - 200,000 (Sheng & Ohtaishi 1993), but due to illegal hunting and habitat loss caused by human activities, populations have been declining. Sheng et al. (1992), referencing results of surveys conducted by Gu Jinghe and Gao Xingyi, Xiang Lihai in 1987, stated that red deer populations in the province of Xinjiang declined by 60% between 1970 and 1980. The distribution of *Cervus elaphus* once included the provinces of Shanxi and Hebei, but populations in these provinces were extirpated by the beginning of the 19th century. Despite a reduction in the previous range of 30-40% by 1975, some populations such as those in Heilongjiang had experienced a slight population increase. Range reduction due to habitat loss has led to the current distribution of *Cervus elaphus* being limited primarily to northeastern China (i.e. Heilongjiang, Nei Mongol and Jilin) and parts of the provinces of Ningxia, Xinjiang, Gansu, Qinghai, Sichuan and Tibet (Xu et al. 2000). Subsequently, *Cervus elaphus* is now listed as a category II protected species on Chinas National Protected Animals List (Wang 1998, Sheng et al. 1992). Historically, *Capreolus pygargus* occurred throughout China but is today primarily found in the provinces of Heilongjiang, Jilin, Liaoning, Shanxi, Hebei, Qinghai and Gansu. Previous population estimates, not including the province of Xinjiang, were just $< 650,000$ at the beginning of the 1990s and average estimated densities were $< 1/100$ ha. Chinese roe deer populations have been greatly impacted by hunting, particularly during the winter months, and have shown a very low annual index of potential reproduction (Sheng et al. 1992).

In northeastern China, red deer and roe deer had stable and higher population densities and there was considerable overlap in the distribution of the species, which are confronted by the same environmental pressure such as habitat loss and population isolation (Chang & Xiao 1988, Zhang & Xiao 1990), and the species share a number of behavioural and ecological characteristics (Zhang et al. 1992, Zhang & Zhang 1993, Zhang & Xu 2000). For example, Li et al. (1992) discovered considerable niche overlap in relation to forage plant species, height, diet and habitat utilised. In particular, the staple food species of both deer were poplar *Populus* spp., birch *Betula* spp. and willow *Salix* spp. Thus, red deer and roe deer exhibit superficially similar diets and habitat use. Both are fairly abundant in the Wandashan Mountains (Cheng et al. 1997), so our first objective was to identify the finer-scale characteristics of habitats utilised by red deer and roe deer to determine in which ways their habitat use might differ, a factor potentially important with respect to the conservation of both species in the face of continuous habitat loss. Our second objective was to understand how human disturbance may affect each species differently.

Methods

Study area

Our study was conducted at Wupao Forestry Farm (E 127°04'07"-127°16'45" and N 46°27'31"-46°38'60"; Fig. 1), located in the Wandashan Mountains, northeastern China, and covering an area of 155.6 km^2. The farm is located in the lower elevations of the Wandashan mountains at an altitude of 300-500 m a.s.l. The weather is characterised by long

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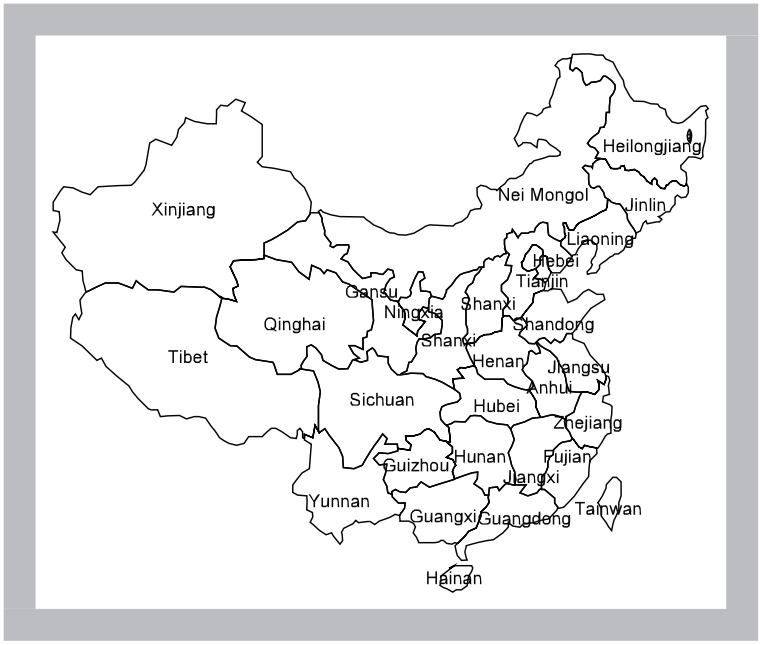


Figure 1. Location of the Wupao Forest Farm in the Wandashan Mountains, the province of Heilongjiang, northeastern China.

cold winters and short hot summers. Annual average temperature is 2.2°C, and extreme temperatures range within -34.8°C - 34.6°C. Average annual precipitation ranges within 500-800 mm. The frost-free period is 120 days, and it lasts from late April to late September. Snow accumulates in late November, persists until end of April, and total snowfall averages approximately 40 cm.

Major forest types in the study area are coniferous-deciduous and deciduous forest. Dominant overstory tree species are Korean pine *Pinus korainensis,* Manchurian ash *Fraxinus mandshurica,* amur linden *Tilia amurensis,* amur corctree *Phellodendron amurense,* elm *Ulmus* spp., poplar *Populus* spp., birch *Betula* spp., willow *Salix* spp., Korean larch *Larix olgensis* and mono maple *Acer mono.* Dominant understory shrub species include hazelnut *Corylus mandshurica*, largeflower deutzia *Deutzia grandifiora*, honeysuckle *Lonicera* spp., amur lilac *Syringa amurensis* and radix acanthopanacis senticosi *Acanthopanas senticosus*, and dominant herbaceous layer species include sedge *Carex* spp., nettle *Urtica* spp. and celery *Aegopodium alpestre*.

Field work was conducted over two separate years, i.e. during January-March 2003 and January-March 2004. A total of 716 10×10 m plots were placed every 100 m along 35 transects (Fig. 2). The 35 transects, each 2 km in length, were located by randomly selecting the starting point of the first transect and establishing the remaining transects at a parallel distance of 2 km from this first transect. The transects traversed the whole study area in a north - south direction south direction and covered all the habitat types. Within each 10 × 10 m plot, we established five 2 × 2 m subplots; the first one was located at the center of each 10 × 10 m plot, the GPS location recorded and the remaining plots were located in each of the four corners (see Fig. 2). Within each 10 × 10 m plot, the occurrence of red deer or roe deer was confirmed by the presence of tracks, feeding signs, faecal pellets and/or bedding sites (Latham et al. 1996, Gao et al. 1995). In plots that contained signs of red deer or roe deer occurrence, we collected data on the following microhabitat characteristics from each of the five 2 × 2 m subplots:

1) since red deer and roe deer forage on plant species ranging in height within 50-260 cm and within 20-180 cm, respectively (Li et al. 1992), we estimated food abundance in each 10 × 10 m plot by counting browse species ranging in height within 20-260 cm. We limited the browse species recorded to a list of 10 species identified in previous studies as commonly utilised by both deer species, including poplar *Populus* spp., willow *Salix* spp., birch *Betula* spp., Korean pine *Pinus koraienses,* amur linden, hazelnut *Corylus heterophlla,* amur lilac, oak *Qurcus mongolica,* spiraea *Spiraea* spp. and alnus *Alnus sibirica*,

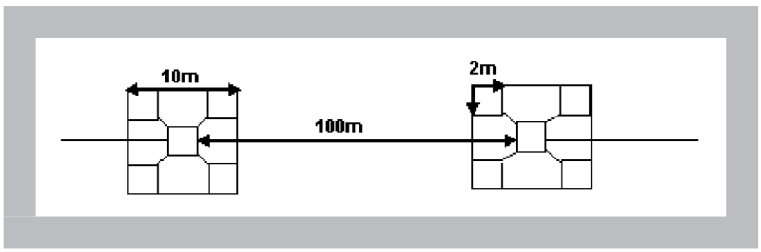


Figure 2. Diagramatic presentation of the survey transects, plots and subplots used in this study.

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all together plant species that the two deer species might be competiting for (Chen et al. 1998, Song et al. 2001, Li 2003).

2) Average snow cover was calculated from depth measurements taken in each of the five subplots.

3) Cover class (in %) expressed as concealment cover estimated by use of a 2.5 cm × 2.0 m hardwood cover pole (Griffith & Youtie 1988).

4) Altitude of each plot was recorded by a GPS fix centered on each plot, and slope position was recorded as upper, middle or down-slope position (Chang & Xiao 1988, Zhang & Xiao 1990).

Digital forest cover and land use maps were generated by visual interpretation of LANDSAT-5 TM imagery taken on 19 June 2003. Ground truthing of imagery was conducted by GPS along 5 km of the forest roads during field surveys. Aerial photographs were used to build more sensitive photo mosaics for classification of vegetation type. Photographs were scanned and mosaics were rectified with remote sensing software (ERDAS Inc. ERDAS IMAGINE 8.5 Tour Guides 2001a) and then digitised using Arcview GIS Version 3.1 (ESRI Inc. 1996). Due to the high relative relief, > 3 ground control points were used for each image along with a thin plate spline rectification model. Classification of vegetation types was based primarily on categories previously established by the Yinchun Forest Bureau (2000). Five forest and land cover types were identified using a unsupervised classification with an iterative self-organising data analysis technique and a supervised classification based on expert knowledge gained in the field (ERDAS Inc. IMAGINE Subpixel-Classifier 8.5 User Guides 2001b). The five cover types are coniferous forest (including planted forest), mature mixed coniferous and broadleaf forest, immature mixed coniferous and broadleaf forest, mature deciduous broadleaf forest, and shrub stands (including cropland which accounted for only 0.6% of the total study area and therefore it was too small to be analysed as a discrete habitat type). The produced maps were used to identify the vegetation type of each survey plot by inputting the GPS coordinate of each 10 × 10 m plot.

Differences in the availability of geographical features such as slope, aspect, altitude and distance to human disturbance may cause bias in assessment of red deer and roe deer distribution if unconsidered. We therefore utilised the spatial analysis function provided in Arcview GIS Version 3.1 to create feature maps which we then used to estimate availability of each geographical feature throughout the study area. Feature maps were generated from TIN calculated with 1:25,000 topographical maps and 10-m contour intervals. To analyse the different levels of disturbance relative to each plot, we measured the distance to settlements, cropland, forest roads, logging sites and abandoned logging roads using the same 1:25,000 topographic map of the study area (ESRI Inc. 1996).

In order to statistically analyse our data, we first utilised quantification theory to convert each qualitative variable, such as vegetation type or slope position, into quantitative variables (Liu et al. 2004, Chang & Xiao 1988, Zhang & Xiao 1990). Levene's test was used to evaluate the homogeneity of variance for each variable between red deer and roe deer locations. One-way analysis of variance and Mann-Whitney U-tests were used to test whether habitat variables differed between deer species, and discriminant function analysis was used to examine habitat separation (Morgan & Griego 1997). This methodology is frequently utilised in animal systematics and has been moderately widely used in ecological studies to measure differences in habitat utilisation patterns of different species (Stancanipiano & Schnell 2004, Pavlacky & Anderson 2004, Traylor et al. 2004). Moreover, the stepwise method of discriminant function analysis was applied because it can be used as an exploratory tool to identify predictor variables from potentially useful parameters (Marnell 1998, Segurado & Araújo 2004, Olden & Jackson 2002). To carry out this approach, we entered variables into the discriminant function analysis individually, choosing variables which had not correlated with each other significantly and minimised the overall Wilks' lambda for the function at each step. Variable selection ended when no additional increase in the accuracy of the discriminant function was achieved (Morgan & Griego 1997). This approach allowed us to select only those variables which best discriminate significant differences in habitat variables between sites of both deer species. All statistical analyses were performed using SPSS for Windows (Morgan & Griego 1997).

Results

The mean and SD of the 19 habitat variables indicated some differences between the two species (Table 1). Levene's univariate of homogeneity of variance test indicated that variances of 11 of the 19

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Table 1. Mean ($\bar{x}$), standard deviation (SD) and Levene's univariate of homogeneity of variances tests of habitat selection variables between red deer (N = 111) and roe deer (N = 61).

	Red deer		Roe deer		Levene's test	
Habitat variables	$\bar{x}$	SD	$\bar{x}$	SD	F	P
Food abundance (twig number/m^2)	11.06	6.04	15.10	9.96	5.401	0.021
Snow depth (cm)	52.78	13.75	49.77	12.74	0.415	0.521
Cover class (concealment cover)	0.52	0.20	0.49	0.19	0.138	0.711
Slope	23.55	21.92	23.15	19.97	0.775	0.380
Aspect	134.35	107.04	98.06	100.87	0.226	0.635
Altitude (m)	278.49	69.01	227.25	57.88	4.769	0.030
Distance to settlement (m)	7013.02	2173.14	3898.69	2450.35	0.584	0.446
Distance to logging site (m)	2252.43	1388.49	1600.41	1254.67	0.558	0.456
Distance to crop field (m)	5614.59	2139.43	3115.43	2309.33	0.395	0.530
Distance to forest road (m)	1132.14	628.45	888.30	548.26	2.252	0.135
Distance to abandoned logging road (m)	1625.93	1178.32	3638.08	1870.79	12.312	0.001
Coniferous stands	0.26	0.44	0.03	0.18	105.944	<0.001
Mixed coniferous and broadleaf mature stands	0.17	0.38	0.18	0.39	0.090	0.765
Mixed coniferous and broadleaf young stands	0.12	0.32	0.26	0.44	23.121	<0.001
Deciduous broadleaf mature stands	0.34	0.48	0.21	0.41	15.095	<0.001
Shrub	0.11	0.31	0.31	0.47	44.219	<0.001
Upper slope position	0.29	0.46	0.26	0.44	0.541	0.463
Middle slope position	0.49	0.50	0.44	0.50	1.185	0.278
Down slope position	0.23	0.42	0.30	0.46	3.766	0.054

variables were equal, whereas eight were unequal (see Table 1). Although homogeneity of variance is an underlying assumption for analysis of variance, violation of this assumption is typical for ecological data and does not necessarily negate the derivation of biologically meaningful results from such analyses (Reinert 1984).

Because data had non-normal distributions, parametric and nonparametric tests were applied to compare results. One-way analysis of variance detected that 10 of 19 variables differed significantly between red deer and roe deer ($P < 0.05$; Table 2). The Mann-Whitney U-test detected that 12 of 19 variables differed significantly between species

Table 2. One-way analysis of variance (ANOVA) and Mann-Whitney U-test for differences in habitat selection variables between red deer and roe deer.

	ANOVA (df = 1,171)		Mann-Whitney U-test	
Habitat variables	F	P	U	P
Food abundance (twig numbers/m^2)	1.019	0.485	2516.5	0.005
Snow depth (cm)	1.989	0.160	2779.0	0.049
Cover class (concealment cover)	0.944	0.333	3115.0	0.362
Slope	0.014	0.907	3282.5	0.742
Aspect	4.713	0.031	2754.5	0.043
Altitude (m)	24.243	<0.001	1991.5	<0.001
Distance to settlement (m)	73.782	<0.001	1058.0	<0.001
Distance to logging site (m)	9.282	0.003	2456.0	0.003
Distance to crop field (m)	50.759	<0.001	1360.5	<0.001
Distance to forest road (m)	6.473	0.012	2635.0	0.016
Distance to abandoned logging road (m)	74.701	<0.001	1365.5	<0.001
Coniferous stands	14.956	<0.001	2612.0	<0.001
Mixed coniferous and broadleaf mature stands	0.023	0.881	3354.5	0.880
Mixed coniferous and broadleaf young stands	6.059	0.015	2894.0	0.015
Deciduous broadleaf mature stands	3.173	0.077	2948.0	0.077
Shrub	11.637	0.001	2697.0	0.001
Upper slop position	0.027	0.131	3297.5	0.717
Middle slop position	0.301	0.584	3237.0	0.582
Down slop position	1.019	0.314	3149.0	0.313

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($P < 0.05$). Results of parametric and nonparametric tests were almost the same relative to variables and level of probability, revealing that both species used different microhabitats.

The discriminant function analysis of the two species was significant (eigenvalue = 1.073, Wilks' lambda = 0.482, $\chi^2 = 121.406$, df = 7, $P < 0.001$), which suggested that the two deer species exhibited different patterns in habitat use. The discriminant function analysis correctly classified 86.6% (149 of 172 samples) of the overall habitat samples, and by species 87.4% (97 of 111 samples) for red deer and 85.2% (52 of 61 samples) for roe deer. Although parametric and nonparametric tests detected 10 and 12 variables predictive of red deer and roe deer sites, respectively, the stepwise approach only identified seven variables that appeared to be the most significant in discriminating sites of both species (Table 3).

Standardised canonical discriminant function coefficients and correlations between discriminating variables and canonical discriminant functions can be used to judge the relative contribution to the power of discriminant function. Larger absolute values of correlations or coefficients indicate stronger contribution to the power of the function (Cooley & Lohnes 1971). Correlations of the seven indicator variables identified by discriminant function analysis fell within a range of absolute values of 0.011-0.636 (see Table 3). Distance to settlements contributed most to the power of the discriminant function, and the forest type mature mixed coniferous and broadleaf forest contributed least. Standardised coefficients of the seven selected variables fell between 0.23 and 2.60. Again, distance to settlements contributed most to the power of the function, but the forest type mature mixed coniferous and broadleaf forest contributed least. Although the results of three coefficients differed in variable rank analyses, some others ranked the same, especially the maximum and the minimum (see Table 3). Correlations and coefficients for each of the seven variables were similar and therefore seem to contribute equally to the power of the discriminant function subsequently allowing us to treat each variable as an indicator of sites utilised by red deer and roe deer.

Red deer often occurred at higher altitude sites in mature mixed coniferous and broadleaf forest and with deep snow cover. Additionally, red deer sites were typically far from human settlements, cropland and logging sites. Conversely, roe deer often occurred at lower elevation sites in shrub, less cover class and a more abundant food source. Roe deer sites, compared with red deer sites, were nearer to human settlements, cropland and logging sites.

Table 3. Stepwise discriminant functional analysis for significantly different habitat variables of red deer and roe deer (maximum significance of F to enter 0.05, minimum significance of F remove 0.1), expressed as standardised canonical discriminant function coefficients (Scdfc) and correlation between discriminating variables and canonical discriminant functions (Cdvacdf).

Habitat variables	Scdfc	Cdvacdf
Food abundance	0.338	0.214
Snow depth	0.484	0.104
Altitude	0.364	0.365
Distance to settlement	2.596	0.636
Distance to abandoned logging road	0.323	0.226
Distance to crop field	-1.861	0.527
Mixed coniferous and broadleaf mature stands	-0.232	-0.011

Discussion

Adaptability to human disturbance

Anciaux et al. (1991) suggested that red deer presence influences roe deer habitat utilisation. Additionally, studies of red deer suggest that they are sensitive to human activities (Edge & Marcum 1985, Lyon 1983). In today's ecosystems, in which humans have eliminated large carnivores, predation risk effects may occur because of past natural selection or human sport hunting (human as predators; Ripple & Beschta 2004). For example, in Montana, St. John (1995) concluded that elk adjusted their foraging behaviour by browsing far from roads to avoid human contact and possible predation. Prey species will alter their use of space according to the extent to which these features affect risk of predation (e.g. avoid sites with high predation risk and forage or browse less intensively at high-risk sites; Ripple & Beschta 2004). In landscapes with both open and closed habitat structures, ungulates may use a strategy of hiding in forest cover to lower predator encounter rates, or they may seek open terrain to see predators from a long distance (Kie 1999). Our results revealed that each deer species utilised resource space away from human disturbances (human settlements, logging sites and cropland). For example, the mean distance to human settlements, logging sites and cropland of both deer species were all >3 km, 1.5 km and 3 km, respectively. However,

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both deer species utilised resource space (distance to human settlements, logging sites and cropland) differently ($P < 0.01$) and thus exhibited some spatial separation. Additionally, the area in which both deer can coexist is also likely diminishing (see Kie 1999). For example, roe deer are smaller, inferior competitors to red deer and seem to find escape cover near human settlements more easily, whereas the opposite seems to hold for red deer (the distances to settlements of red deer were almost the double of those of roe deer). Consequently, we conclude that while both deer species may be negatively affected by the continued growth of the human population that is expected, the areas where both species can coexist will decrease, and it is red deer that will be impacted most negatively.

Behavioural responses to food and vegetation types

It has been argued that large-sized ruminants have relatively low mass-specific energy requirements and thus are adapted to feed on less energy-dense and low quality food items (Bell 1971, Jarman 1974, Gordon & Illius 1996). Red deer, an intermediate feeder (Hofmann & Stewart 1972, Hofmann 1985) with a large body size, occurred in sites with lower food abundance in mature mixed coniferous and broadleaf forest and with less human disturbance. During late winter, red deer body condition is at its lowest as food resources are scarce (Jiang & Robert 1996, Zhang & Xiao 1990), and hunting pressure from nearby human settlements are at their highest. Energy conservation, particularly during the winter, is very important to red deer and therefore feeding and movement in the more open habitats could reduce energy expenditures. In contrast, roe deer are smaller, with larger mass-specific energy requirements, and therefore usually prefer sites with more abundant annual growth of browse species (Hofmann & Stewart 1972, Hofmann 1985) as well as dense forests, which provide greater protective cover (Henry 1981). This may explain why roe deer in our study used microhabitats with more abundant food resources and avoided the mature mixed coniferous and broadleaf forest, which offers less protective cover.

Effect of snow depth and altitude

Snowpack conditions can greatly influence ungulates' access to vegetation and thus their energy budgets or even starvation rates. Variations in snow depth can also affect the ability of ungulates to escape predators (Crête & Manseau 1996). Large snowpack accumulations in broken terrain may preclude elk foraging and affect herd distributions, whereas more open landscapes offer opportunities for snow to melt or blow away from foraging areas. Such open areas also offer good visibility and provide escape terrain with little snow to slow ungulates fleeing from predators. In mountainous terrain, winters with little snowfall may allow ungulates to remain at higher elevations, thus resulting in reduced levels of browsing on woody species in valley bottoms. Conversely, high-snowfall winters are likely to increase browsing pressure on low-elevation plant communities (Ripple & Beschta 2004). In recent years, average winter temperatures and average cumulative snow fall in the study area have increased making winter locomotion increasingly more difficult and energetically costly for deer. Pauley et al. (1993) pointed out that basal metabolic rates of white-tailed deer *Odocoileus virginianus* were depressed when snow depths exceeded 40 cm, but were elevated when snow depths did not exceed 30 cm. Additionally, Zhang & Xiao (1990) found evidence that snow depths exceeding 40 cm influenced winter habitat selection by roe deer. Therefore, the smaller-bodied roe deer may select sites with less snow than red deer, which due to their larger body size, can move more freely and with less energetic expenditures in deeper snow. Additionally, vegetative cover varies with altitude and selection of food resources by each species reflected these altitudinal differences, with red deer utilising vegetation types present at higher altitudes and roe deer utilising vegetation types present at lower altitudes. Overall, we conclude that snow depth and altitude differ between the habitats selected by the two deer species, and that this may contribute to habitat separation and coexistence of red deer and roe deer during late winter (Loison & Langvatn 1998, Chang & Xiao 1988, Zhang & Xiao 1990).

Conclusion

We found that the red deer often occurred at sites in mature mixed coniferous and broadleaf forest with higher altitude and deeper snow cover. These sites were also further from human settlements, cropland and logging sites than those utilised by roe deer. Conversely, roe deer often preferred sites in shrub with lower altitude and more abundant food resources.

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Our analysis revealed that habitat selection with respect to human disturbance is greater at finer spatial scales than that of other natural factors. Roe deer showed less use of open mature mixed coniferous and broadleaf forest, avoidance of deeper snow, and significant preference throughout the two late winters for areas with a more abundant food resource. In comparison to previous work, we found considerable differences in habitat selection by sympatric red deer and roe deer. Differences in habitat selection were greatest in late winter, when disturbance from human activities (e.g. hunting) was greater. These results suggest that human settlements and disturbances may contribute to habitat loss for both species, but that red deer may suffer most if the human population and disturbance continue to increase. Moreover, we suggest that understanding any differential effects of human disturbance may be important to understand the future population dynamics of these two species as human disturbance in China is expected to keep increasing as the human population grows.

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