

## Seasonal habitat selection of the red deer (*Cervus elaphus alxaicus*) in the Helan Mountains, China

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**ABSTRACT.** We studied the seasonal habitat selection of the red deer, *Cervus elaphus alxaicus* Bobrinskii & Flerov, 1935, in the Helan Mountains, China, from December 2007 to December 2008. Habitat selection varied widely by season. Seasonal movements between high and low elevations were attributed to changes in forage availability, alpine topography, the arid climate of the Helan Mountains, and potential competition with blue sheep, *Pseudois nayaur* (Hodgson, 1833). The use of vegetation types varied seasonally according to food availability and ambient temperature. Red deer used montane coniferous forest and alpine shrub and meadow zones distributed above 2,000 m and 3,000 m in summer, alpine shrub and meadows above 3,000 m in autumn, being restricted to lower elevation habitats in spring and winter. The winter habitat of *C. elaphus alxaicus* was dominated by *Ulmus glaucescens* Franch. and *Juglans regia* Linnaeus, deciduous trees, and differed from the habitats selected by other subspecies of red deer. *Cervus elaphus alxaicus* preferred habitats with abundant vegetation coverage to open habitats in winter, but the reverse pattern was observed in summer and autumn. Red deer preferred gentle slopes (<10°) but the use of slope gradient categories varied seasonally. Red deer avoidance of human disturbance in the Helan Mountains varied significantly by season. Information on red deer habitat selection can help understand the factors affecting seasonal movements and also support decision making in the management and conservation of red deer and their habitats.

**KEY WORDS.** Habitat use; migration; seasonal movement; ungulates.

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The red deer, *Cervus elaphus alxaicus* Bobrinskii & Flerov, 1935 is an endemic subspecies in China, distributed in the central region of the Helan Mountains, which range from the border between Alxa League of the Inner Mongolia Autonomous Region to the Ningxia Hui Autonomous Region in west-central China. The Helan Mountains support the only known population of this subspecies (WANG *et al.* 1999). Its population is small and is isolated from other subspecies of red deer (ZHANG *et al.* 1999). Historically, the survival of *C. e. alxaicus* has been threatened by the deterioration of habitats on the Alxa Plateau, and its reduced population has since been isolated in the relatively poor ecological environment of the Helan Mountains for a long period. Population estimates for *C. e. alxaicus* in the Helan Mountains ranged from 850 to 1,060 in 1983, increasing to 1,705 ± 523 in 2005, after the creation of the Ningxia Helan Mountain Nature Reserve in 1982 (ZHANG *et al.* 2006). While *C. e. alxaicus* is a threatened subspecies, *C. elaphus* is categorized as a species of Least Concern in the World Conservation Union's Red List of Threatened Animals (LOVARI *et al.* 2008).

Habitat selection by animals is considered as an optimization process that involves factors such as food supply, conspecific population density, body size, competitors, predators, and landforms (MORRISON *et al.* 1998). Information on which resources are preferred or avoided by organisms improves our understanding of how they meet their requirements for survival and reproduction (MANLY *et al.* 2002). The distribution and availability of trophic resources are important factors that affect habitat selection. In most temperate habitats, food is scarce during the winter months and abundant in spring and early summer (MOEN 1976, SCHMITZ 1991). This forces animals in temperate regions to adapt to seasonal changes in food supply. Ungulates that inhabit temperate and boreal regions often exhibit cyclical seasonal movements between summer and winter ranges in response to environment factors (e.g., snow conditions, food availability), social constraints and predation risk (FRYXELL & SINCLAIR 1988, PÉPIN *et al.* 2008). Regular, round-trip movements between seasonal home ranges (WHITE & GARROTT 1990) have evolved to enable animals to avoid undesirable conditions at a particular

time of the year (VAUGHAN *et al.* 2000). Generally, seasonal movement patterns of ungulates include short-distance movements, dispersal, and migration (GROVENBURG *et al.* 2009). Seasonal migration of cervids involves dispersal to areas of lower elevation, particularly in winter, when the environment is less hospitable at higher elevations (ALBON & LANGVATN 1992, IGOTA *et al.* 2004, PÉPIN *et al.* 2008). Mixed strategies of migration have, however, been found among cervids that inhabit temperate and boreal mountainous regions (IGOTA *et al.* 2004, BRINKMAN *et al.* 2005, GROVENBURG *et al.* 2009).

Despite numerous studies of other subspecies of red deer, little is known about the seasonal habitat use or movement patterns of *C. e. alxaicus* during different seasons. The objective of this study was to: 1) compare habitats used by *C. e. alxaicus* during different seasons to document differences in habitat selection; and 2) examine environmental variables that affect the seasonal movement of *C. e. alxaicus*.

## MATERIAL AND METHODS

This study was conducted over four seasons from December 2007 to December 2008 in the Helan Mountain region, which is located between the eastern Yinchuan plain in Ningxia Hui Autonomous Region and the western Alxa Plateau in Inner Mongolia Autonomous Region (105°44'-106°42'E, 38°21'-39°22'N) (Fig. 1). The Helan Mountain region, located in north-western China, is on the transitional zone between steppe and desert regions of central Asia (TAKHTAJAN 1986). It generally lies at 2,000-3,000 masl, with a maximum elevation of 3,556 masl. It covers an area of 2,740 km<sup>2</sup> [including Ningxia Helan Mountain National Nature Reserve (2,063 km<sup>2</sup>) and Inner Mongolia Helan Mountain National Nature Reserve (677 km<sup>2</sup>, Fig. 1)], with a north-south length of about 250 km and an east-west width of about 20-40 km (Z.S. Liu unpublished data).

The region has a typical continental climate, characterized by cool and dry conditions, with annual mean temperature of -0.9°C and mean annual rainfall of 420 mm. The local climate is influenced by the topography of the Helan Mountain, the low temperature center of the northern Ningxia. The maximum monthly mean temperature is 11.9°C, in July, and the minimum is -14.2°C, in January, 8.8 ~9.8°C lower than in Yinchuan, the capital city of Ningxia Hui Autonomous Region. Precipitation varies seasonally, with 62% falling as rain in summer. There is little precipitation in winter, about 10.1% of the annual total. Snow cover is limited in the Helan Mountains (GENG & YANG 1990). The vegetation distribution is strongly influenced by moisture conditions. The elevation differential between the Helan Mountains and the plains to the south and east is about 2100 m, which creates an elevational climatic gradient that results in the formation of four elevational vegetation zones. The mountain steppe zone (MS) occurs at 1,400-1,600 masl and covers an area of 1,241 km<sup>2</sup> dominated by *Stipa breviflora* Griseb., *Ajanía fruticulosa* (Ledeb.) Poljak,

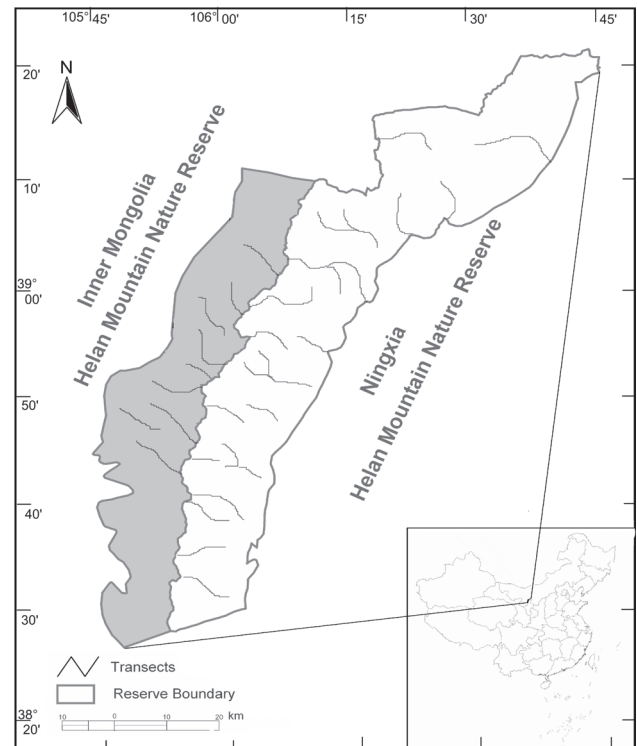


Figure 1. Location and distribution of the study area and transects in the Helan Mountain region, China. Grey shading represents Helan Mountain Nature Reserve in Inner Mongolia Autonomous Region, while the unshaded area represents the reserve in Ningxia Hui Autonomous Region.

*Ptilagrostis pelliottii* (Danguy) Grubov.), *Oxytropis aciphylla* Ledeb.), *Convolvulus gortschakovii* Schrenk ex Fisch. & C.A. Mey., and *Salsola laricifolia* Turcz. ex Litv. The open mountain forest and steppe zone (MOFS) (1,600-2,000 masl, 1,155 km<sup>2</sup>) is dominated by *Ulmus glaucescens* Franch., *Prunus mongolica* Maxim., *Stipa grandis* P.A. Smirn., and *S. bungeana* Trin. The mountain coniferous forest zone (MCF) (1,900-3,000 masl, 319 km<sup>2</sup>) is dominated by *Picea crassifolia* Kom., *Pinus tabulaeformis* Carrière, *Juniperus rigida* Siebold & Zucc., and *Potentilla parvifolia* Fisch. ex Lehm. The alpine shrub and meadow zone (ABM) (3,000-3,556 masl, 23 km<sup>2</sup>) is dominated by *Salix cupularis* var. *lasilogyne* Rehd., *Caragana jubata* (Pall.) Poir., *Kobresia* spp., *Polygonum viviparum* Linnaeus and *Arenaria* spp. (JIANG *et al.* 2000, DI 1986). Mammals found in the area include insectivores: Daurian hedgehog, *Mesochinus dauuricus* (Sundevall, 1842); carnivores: red fox, *Vulpes vulpes* (Linnaeus, 1758); artiodactyls: blue sheep, alpine musk deer: *Moschus chrysogaster* (Hodgson, 1839); lagomorphs: Daurian pika, *Ochotona dauurica* (Pallas, 1776); and chiropterans and rodents. Blue sheep and *C. e. alxaicus* are the two dominant ungulate species in the Helan Mountain region (LIU 2009).

From December 2007 to December 2008, we carried out four surveys, one per season, to determine the distribution of *C. e. alxaicus* throughout the Helan Mountain area. Each seasonal survey sampled 32 line transects established along the valleys and each survey took about one month to sample all topographic types. Differences in topographic relief prevented walking along the transects at the same velocity and length, therefore, transects ranged in length from 4.5 to 8.5 km, for a total of 350 km traversing the whole study area and covering all four elevational vegetation zones. The distance between any two transects was at least 2 km, to ensure the independence of each transect.

Because of the rarity of *C. e. alxaicus* in the area and their high sensitivity to anthropogenic disturbance (JEPPESEN 1987), we documented habitat use mainly by recording fresh signs, such as evidence of bedding or the presence of feces. We also observed deer in order to record their activities. It was easy to differentiate the signs left by *C. e. alxaicus* from those of other ungulates (e.g., *P. nayaur*, *M. chrysogaster*) in the Helan Mountains, because *C. e. alxaicus* is larger than *P. nayaur* and *M. chrysogaster*, and the size and shape of their feces are different (CHANG & XIAO 1988). To ensure the accu-

racy of data, we recorded fresh feces only (3-5 days old as estimated by the color and water content). When deer were observed during line transect surveys, we first used telescopes to observe their feeding or bedding behavior, without disturbing the animals. After deer had departed the area, we carried out detailed sampling.

We recorded terrestrial coordinates according to a Global Positioning System (GPS) after a feeding or bedding habitat was identified. We then established a plot with five sample quadrants (Fig. 2) to collect data of 18 topographic and biological variables (Table I) using the methods described by LIU *et al.* (2002). The distance between any two plots was at least 500 m to ensure the independence of each plot (Fig. 2).

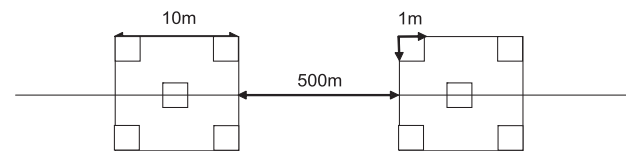


Figure 2. Diagrammatic presentation of the survey transects, plots and sample quadrats used in this study.

Table I. Variables collected in feeding and bedding habitat plots used by *Cervus elaphus alxaicus* in the Helan Mountain region, China.

Variables	Categorization and Criterion	Abbreviation
Altitude (m)	The altitude of the plot accorded to GPS	AL
Vegetation types	Mountain steppe zone (MS); Mountain open forest and steppe zone (MOFS); Mountain coniferous forest zone (MCF); Alpine bush and meadow zone (ABM)	VT
Topography	Categorized by the slope and fault of a hillside, divided into 5 levels: Smooth undulating slope; Moderately broken slope; Distinctly broken slope; Scree/landslide; Cliff	TO
Dominant tree	The tree covers 70% of the density in the 10×10 m plot. It usually was <i>Ulmus glaucescens</i> , <i>Ziziphus jujube</i> , <i>Salix</i> spp., <i>Juniperus rigida</i> , <i>Pinus tabulaeformis</i> , <i>Picea crassifolia</i> Mixture or Open land with no tree	DT
Tree density (trees/100 m <sup>2</sup> )	The total number of trees in the 10×10 m plot	TD
Tree height (m)	The mean height of trees in the 10×10 m plot	TH
Distance to the nearest tree (m)	Distance from the center of the 10×10 m plot to the nearest tree	DtT
Shrub density (trees/100 m <sup>2</sup> )	The number of shrubs in the 10×10 m plot	SD
Shrub height (m)	The mean height of shrubs in the 10×10 m plot	SH
Distance to the nearest shrub (m)	Distance from the center of the 10×10 m plot to the nearest shrub	DtS
Herb coverage (%)	The mean herb coverage of the 5 sample quadrats in the 10×10 m plot	HC
Slope gradient (°)	Slope gradient of the hillside where the spot located measured with military compass	SG
Slope location	A visual assessment of the site location relative to the macroslope which is usually from valley bottom to ridge top, classed as: lower slope (includes valley bottom and flat), middle slope and upper slope (includes ridge top)	SL
Slope aspect	Aspect was surveyed to eight compass points, translated as 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315° from North, as 0° is equivalent to 360°. And the slope aspect was grouped into 3 main directions: sunny slope (135°~225°), partial shade slope (45°~135° and 225°~315°) or shady slope (315°~45°)	SA
Distance to water resource (m)	The distance from the spot to the nearest water resource	DtW
Distance to human disturbance (m)	The distance from the spot to the nearest place of human activity such as highway, road and shelter forest station, etc	DtH
Distance to bare rock (m)	The distance from the spot to the nearest bare rock	DtR
Hiding cover (%)	The coverage of the hiding conditions. Percent hiding cover was determined by visually estimating the percent of a deer or a substitute (a 1 m stick) obscured at 30 m in the four cardinal directions (KUNKEL & PLETSCHER 2001)	HiC

Generally, research on resource selection requires a comparison of the habitats used by *C. e. alxaicus* (observed plots) with those that are available (expected plots, assuming no differential selection by deer). To provide comparison plots for the analysis of habitat selection, 617 randomly located plots were surveyed. The random plots were established along the survey transects, in areas with no obvious evidence of *C. e. alxaicus* use. The distance between random plots and occupied plots or any two random plots was at least 500 m to reduce the possibility of overlap between used and unused plots. Comparison plots were surveyed in each vegetation zone according to the proportion of used plots in each zone. Data were recorded for comparison plots using the same methods used in the occupied plots.

Data were analyzed to quantify habitat selection by *C. e. alxaicus* by season. To assess seasonal differences between the 18 factors recorded at used plots and comparison plots, we used a chi-square goodness-of-fit test within classified categories for each variable (MARCUM & LOFTSGAARDEN 1980). P-values less than 0.05 were considered statistically significant. Bonferroni confidence intervals were calculated by the following formula to identify variables that indicate preference or avoidance, following the method developed by NEU *et al.* (1974) and BYERS *et al.* (1984).  $(p_i - r_i) \pm Z_{1-\alpha/2k} \times \sqrt{p_i(1-p_i)/n_i + r_i(1-r_i)/m_i}$ ; where,  $n_i$  is the number of comparison plots in category  $i$ , and  $p_i$  is the proportion of the comparison plots that fall in category  $i$ ;  $m_i$  is the total number of plots used by *C. e. alxaicus*,  $r_i$  is the proportion of plots used by *C. e. alxaicus* in category  $i$ ;  $Z_{1-\alpha/2k}$  is the upper standard normal table value corresponding to a probability tail area of  $1-\alpha/2k$ ;  $\alpha$  is the level of significance; and  $k$  is the number of categories tested. The confidence intervals indicated that *C. e. alxaicus* showed avoidance (marked "-") of category  $i$  when  $(p_i - r_i) - Z_{1-\alpha/2k} \times \sqrt{p_i(1-p_i)/n_i + r_i(1-r_i)/m_i} > 0$ ; whereas *C. e. alxaicus* showed preference (marked "+") for category  $i$  when  $(p_i - r_i) + Z_{1-\alpha/2k} \times \sqrt{p_i(1-p_i)/n_i + r_i(1-r_i)/m_i} < 0$ ; and *C. e. alxaicus* showed no obvious selection (marked "=") for category  $i$  when  $(p_i - r_i) - Z_{1-\alpha/2k} \times \sqrt{p_i(1-p_i)/n_i + r_i(1-r_i)/m_i} < 0$  and  $(p_i - r_i) + Z_{1-\alpha/2k} \times \sqrt{p_i(1-p_i)/n_i + r_i(1-r_i)/m_i} > 0$ .

Data for non-numeric ecological factors (VT, TO, DT, SL and SA; see Table I) were examined with chi-square tests. Data for the remaining numeric ecological variables were initially analyzed with one-sample Kolmogorov-Smirnov tests to determine if they were normally distributed. The normally distributed data were analyzed with independent-samples t-tests, while the non-normally distributed data were analyzed with Kruskal-Wallis H tests.

## RESULTS

A total of 602 plots used by *C. e. alxaicus* (observed plots) were recorded and compared among the four vegetation zones

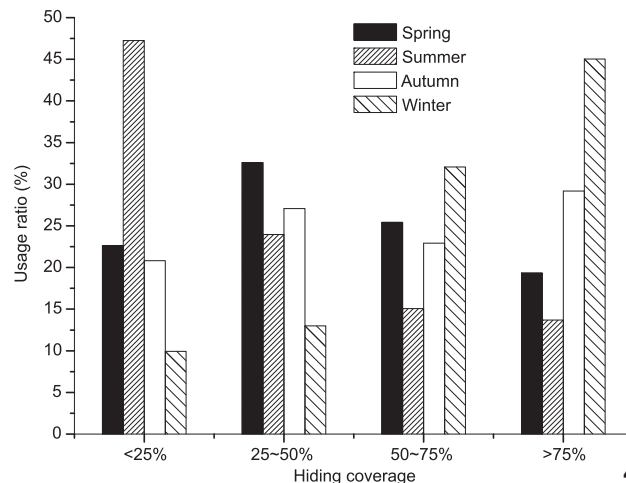
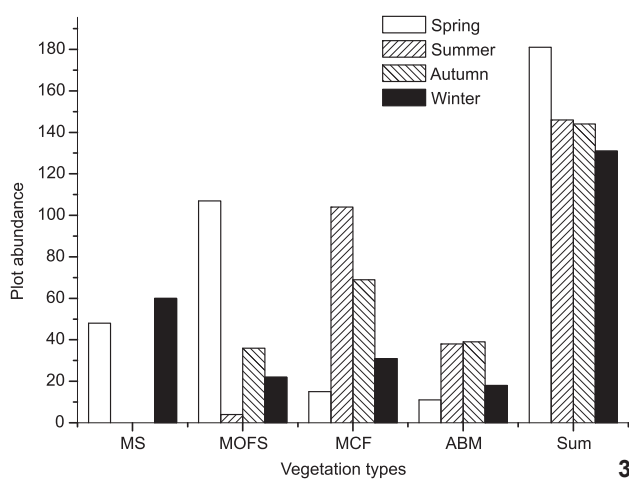
(Fig. 3). Across the whole study period, 209 used plots in the coniferous forest mountain zone were measured, and this type was the most common vegetation type, followed by open mountain forest and steppe zone of 169 plots, mountain steppe zone of 108 plots and alpine shrub and meadow zone of 106 plots (Fig. 3).

Across the entire study area in spring, we sampled 181 plots used by deer (Fig. 3) and 181 comparison plots (Appendix 1). Deer selected habitats characterized by gentle ( $<10^\circ$ ), undulating, sunny slopes in spring. Deer preferred habitats with 4-6 m high trees, near dense shrubs ( $> 10$  trees/100 m<sup>2</sup>) taller than 1.3 m, with high herb coverage of more than 50%, good hiding conditions (hiding cover lower than 50%) (Fig. 4), and distant from bare rock. However, no significant preference was shown during spring with respect to dominant tree species ( $\chi^2 = 9.65$ ,  $df = 10$ ,  $p > 0.05$ ), distance to the nearest tree ( $\chi^2 = 4.02$ ,  $df = 2$ ,  $p > 0.05$ ), altitude ( $\chi^2 = 0.59$ ,  $df = 3$ ,  $p > 0.05$ ), distance to water resource ( $\chi^2 = 0.59$ ,  $df = 2$ ,  $p > 0.05$ ), or distance to human disturbance ( $\chi^2 = 0.00$ ,  $df = 2$ ,  $p > 0.05$ ) (Appendix 1).

In summer, 146 plots were used by deer (Fig. 3) and 167 comparison plots (Appendix 1) were surveyed. Deer preferred habitats with gentle, undulating slopes ( $<20^\circ$ ) on the south side of the MCF zone above 2,000 m and the ABM zone above 3,000 m, respectively, during summer. Habitats used in summer were on lower slopes near dense stands of trees ( $> 4$  tree/100 m<sup>2</sup>) with mixed tree species of 4-6 m height, near dense shrub stands ( $> 10$  tree/100 m<sup>2</sup>) taller than 1.3 m, with high herb coverage ( $> 80\%$ ), good hiding condition (hiding coverage lower than 50%) (Fig. 4) and far from bare rock ( $> 50$  m). Distance to human disturbance did not affect habitat use by deer in summer (Appendix 1).

A total of 144 plots used by deer (Fig. 3) and 138 comparison plots (Appendix 1) were surveyed in autumn. Autumn habitat use was similar to that during summer: *C. e. alxaicus* preferred habitats with gentle ( $<10^\circ$ ), undulating and partially shaded slopes in the ABM zone, at elevations above 3,000 m in autumn. They also preferred habitats with more gentle slopes, high tree density ( $> 4$  trees/100 m<sup>2</sup>), mixed tree species of 4-6 m height, dense shrubs ( $> 10$  trees/100 m<sup>2</sup>), high herb coverage ( $> 80\%$ ) good hiding condition (hiding coverage lower than 50%) (Fig. 4), and distant from bare rock ( $> 100$  m). There was no significant difference between the used plots and comparison plots in autumn with respect to distance to the nearest tree ( $\chi^2 = 0.36$ ,  $df = 2$ ,  $p > 0.05$ ), shrub height ( $\chi^2 = 4.00$ ,  $df = 2$ ,  $p > 0.05$ ), distance to water resource ( $\chi^2 = 2.95$ ,  $df = 2$ ,  $p > 0.05$ ), or distance to human disturbance ( $\chi^2 = 5.41$ ,  $df = 2$ ,  $p > 0.05$ ) (Appendix 1).

131 plots used by *C. e. alxaicus* (Fig. 3) and 131 comparison plots (Appendix 1) were surveyed in winter. Deer preferred winter habitats with gentle ( $<10^\circ$ ), undulating, sunny slopes, lower slopes with high herb coverage ( $> 50\%$ ), and average hiding condition (hiding coverage lower than 75%) (Fig. 4). However, deer maintained a distance of more than 1.5 m from shrubs



Figures 3-4. (3) Abundance and proportion of plots used by *Cervus elaphus alxaicus* in different vegetation type zones among four seasons, in the Helan Mountain region, China. (MS) Mountain steppe zone, (MOFS) Mountain open forest and steppe zone, (MCF) Mountain coniferous forest zone, (ABM) Alpine bush and meadow zone. (4) Seasonal changes in the usage ratio of hiding coverage on *C. e. alxaicus* in the Helan Mountain region, China.

and 50-100 m from bare rock. Deer showed no significant preference with respect to vegetation type ( $\chi^2 = 0.90$ ,  $df = 3$ ,  $p > 0.05$ ), shrub height ( $\chi^2 = 2.40$ ,  $df = 2$ ,  $p > 0.05$ ), altitude ( $\chi^2 = 1.59$ ,  $df = 3$ ,  $p > 0.05$ ), distance to water source ( $\chi^2 = 0.14$ ,  $df = 2$ ,  $p > 0.05$ ), or distance to human disturbance ( $\chi^2 = 2.13$ ,  $df = 2$ ,  $p > 0.05$ ) (Appendix 1).

There were statistically significant differences in the use of five non-numeric ecological factors by season. *Cervus elaphus alxaicus* selected habitats by season based on vegetation type ( $\chi^2 = 58.611$ ,  $df = 3$ ,  $p < 0.001$ ), topography ( $\chi^2 = 969.841$ ,  $df = 3$ ,  $p < 0.001$ ), dominant tree species ( $\chi^2 = 820.947$ ,  $df = 10$ ,  $p < 0.001$ ), slope aspect ( $\chi^2 = 74.355$ ,  $df = 2$ ,  $p < 0.001$ ) and slope location ( $\chi^2 = 143.096$ ,  $df = 2$ ,  $p < 0.001$ ). There were also statistically significant differences in the use of 13 numeric ecological factors by season (Table II).

## DISCUSSION

*Cervus elaphus alxaicus* in the Helan Mountains displayed a pattern of seasonal elevational migration similar to that of other red deer subspecies in mountainous areas (ALBON & LANGVAIN 1992, JARNEMO 2008, PÉPIN *et al.* 2008). However, we observed differences between the habitat selection of *C. e. alxaicus* and that of other subspecies. HUTTO (1985) described the mechanisms determining habitat selection as: geographic restrictions, genetic evolution, influence of experience, and settlement decisions following exploration.

Vegetation type determines the composition and distribution of deer forage, and is determined by soil type, climate, sunlight, topography, landform and many microhabitat factors. The heterogeneous distribution of biotic and abiotic fac-

tors in environments leads to spatial heterogeneity in vegetation types. Physiological and ecological requirements of deer are met to varying degrees by different vegetation types. Thus the geographic and seasonal variation in vegetation types affect red deer habitat selection. In the Helan Mountains, *C. e. alxaicus* range annually from the mountain steppe zone below 1,600 m to alpine shrub and meadow zone above 3,000 m (LIU 2009). Deer preferred habitats in the montane coniferous forest zone (> 2,000 masl) and alpine shrub and meadow zone (> 3,000 masl), in summer, and those in the alpine shrub and meadow zone (> 3,000 m) in autumn. Deer showed no preference for any vegetation type in spring or winter (Appendix 1), using habitats in proportion to their availability during those seasons. IGOTA *et al.* (2004) reported that deer rarely change their summer home ranges for breeding and nursing of offspring. We predicted that some *C. e. alxaicus* might migrate down from the alpine shrub and meadow zone during winter and spring, while some might stay at high altitude. Further study with GPS collars on *C. e. alxaicus* has been conducted to test the prediction.

CUI *et al.* (2007) and CHANG *et al.* (2010) reported that *U. glaucescens*, *Populus davidiana* Dode, *P. mongolica*, *Potentilla* spp., Graminoids (*Stipa* spp., *Poa* spp.), *Caragana* spp. were important in the winter diet of *C. e. alxaicus*. In summer, *C. e. alxaicus* ate 18 plant species of 11 families, which were mostly *Salix microstachya* var. *bordensis* (Nakai) C.F. Fang, *P. davidiana*, *U. glaucescens* and *Agropyron cristatum* (L.) Gaertn. which were mainly distributed in the mountainous open forest and steppe zone, ranging from 1,600 m to 2,000 m altitude, and *C. e. alxaicus* of migratory group migrated down from alpine shrub and meadow zone during winter and spring (Table II) as the

amount of food resources declined. Food availability is clearly critical for the nutrition of ungulates, especially for fawns and females (PETTORELLI *et al.* 2005). Adaptation to varying feeding conditions throughout seasons or years was also confirmed by GROOT & HAZEBROEK (1995).

Habitat selection by deer is determined by the presence of both food and hiding cover (BORKOWSKI & UKALSKA 2008). The role of hiding cover in habitat use may be especially important in winter, when cervids reduce their food intake and survive, to a large extent, using their fat reserves (PUTMAN 1988). PEEK *et al.* (1982) studied the role of cover in habitat selection. Two cover types were recognized: thermal cover, in which a forest overstory protects against weather and sun, and hiding (security) cover used to escape and avoid predators and humans. *C. e. alxaicus* in the Helan Mountains preferred habitats near cover to open habitats in winter, but the reverse was found in summer and autumn (Fig. 4). Habitats dominated by *U. glaucescens* and *Juglans regia* Linnaeus were frequently used in winter (Appendix 1). *C. e. alxaicus* are likely to be under low predation risk except from poaching in the Helan Mountains. Therefore, selection of habitat by deer mainly reflects their food requirements and need for protection against severe weather. The habitat selection process presumably results from demands to maximize their energy efficiency while minimizing their movements when searching for food, water and cover (QIAO *et al.* 2006). It differed from other subspecies of red deer, such as *Cervus elaphus xanthopygus* Milne-Edwards, 1867 in northeast China and *Cervus elaphus nelsoni* (Bailey, 1935) in the Rocky Mountains, which preferred coniferous forest and sapling trees and shrubs, feeding on shrub and epicormics in winter (UNSWORTH *et al.* 1998). *C. e. alxaicus* preferred montane coniferous forest and alpine shrub and meadow zones in summer and autumn, but preferred mountain steppe and mountain open forest and steppe zones in winter and spring, similar to *Cervus elaphus scoticus* Lönnerberg, 1906 (WELCH *et al.* 1990).

The special alpine topography and arid climate in the Helan Mountain region were the two important factors explaining the habitat selection of *C. e. alxaicus*. Given that precipitation is low in the Helan Mountain region, especially in winter, and the snow coverage is also very low (GENG & YANG 1990), the snow depth and coverage are not important factors initiating the habitat selection and movement of *C. e. alxaicus*. The local population of blue sheep is widespread and numbers more than 10,000 (LIU 2009, LIU *et al.* 2007b). Blue sheep inhabit the mountain open forest and steppe zone, and probably compete with deer for forage, especially in winter and early spring, when food is scarce (LIU *et al.* 2007a). We recorded migration of *C. e. alxaicus* during winter and early spring to the mountain open forest and steppe zone from higher altitude areas (Appendix 1). A reasonable assumption is that blue sheep density, to a certain degree, has a negative influence on *C. e. alxaicus* density, which might also explain deer movements to higher el-

evations in summer. Further study on the niche overlap between blue sheep and *C. e. alxaicus* is underway. AGER *et al.* (2003) reported sympatric populations of Rocky Mountain elk (*C. e. nelsoni*) and mule deer, *Odocoileus hemionus* (Rafinesque, 1817), in northeastern Oregon, where elk exhibited strong daily and seasonal patterns of movements and habitat use under competition from mule deer.

Topography and slope gradient were important factors affecting habitat selection by *C. e. alxaicus*. Generally, deer preferred gentle (<10°), undulating slopes (Appendix 1), but this varied seasonally according to food availability and temperature (Fig. 5). Deer selection of lower slopes was also caused by the predominantly steep topography of the Helan range, which includes only a small proportion of the total area as gentle slopes (DI 1986). *C. e. alxaicus* preferred sunny slopes with direct solar radiation, especially during the cold winter and spring (Fig. 5).

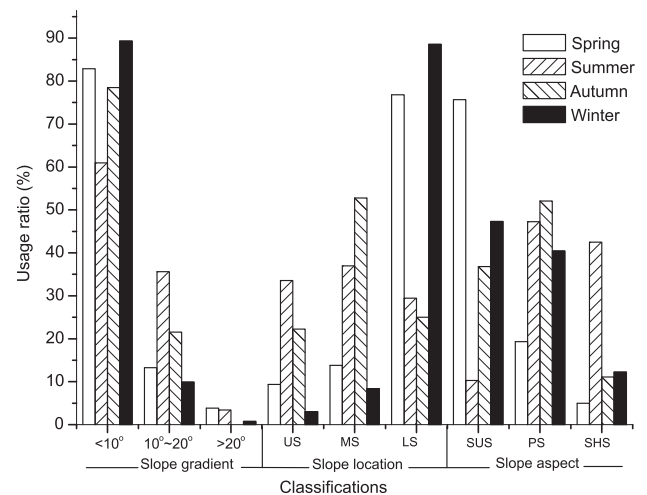


Figure 5. Seasonal changes in the effect of slope characteristics on *Cervus elaphus alxaicus*. (US) Upper Slope, (MS) Middle Slope, (LS) Lower Slope, (SUS) Sunny Slope, (PS) Partial shade slope, (SHS) Shady slope.

Pressure from predators and human disturbance are often considered to be important factors that influence ungulate behavior and habitat selection (BONENFANT *et al.* 2004, BORKOWSKI 2004). However, historically, the main predators of *C. e. alxaicus*, the snow leopard, *Uncia uncia* (Schreber, 1775); the gray wolf, *Canis lupus* Linnaeus, 1758; and lynx, *Lynx lynx* (Linnaeus, 1758), became extinct during the 1980s in the Helan mountain region (WANG & SCHALLER 1996). Numerous studies have demonstrated that deer behavior and habitat use are mostly influenced by humans (BORKOWSKI & UKALSKA 2008), including hunting, other human activities (LICOPPE 2006), travel routes

and road traffic (YOST & WRIGHT 2001). JIANG *et al.* (2007) reported that *C. e. xanthopygus* in northeastern China showed some behavioral plasticity in response to human influences, and the effect of habitat loss or fragmentation caused by human activities are expected to be great (JAEGER *et al.* 2005). However, in the Helan Mountain region, we found that the deer neither preferred nor avoided human disturbance ( $p > 0.05$ ) (Appendix 1), and they profited from the programs of Forest-Grass Conservation Project and Shelterbelt Forestry Project and Returning Husbandry to Forestry (Grass) launched in 1996 (ZHAO *et al.* 2000) and 1999 (ZHAO *et al.* 2004), respectively. Wild animal hunting and livestock grazing have been forbidden in most of the Helan Mountain region and habitats are generally well-preserved. Therefore, *C. e. alxaicus* has not suffered much human disturbance, apart from regular ranger, activities whose impact is probably negligible. However, in our data, there was a significant amount of seasonal variation in deer avoidance of human disturbance in the Helan Mountains (Table II). The migration of *C. e. alxaicus* individuals to lower altitudes for foraging in winter and spring has brought deer closer to areas that are impacted by humans. Deer preferred habitats far from human disturbance at higher elevations during summer and autumn. During our survey, human-related *C. e. alxaicus* fatalities were low compared to those of other studies (LICOPPE 2006, PÉPIN *et al.* 2008); therefore, limited persecution and food availability may have facilitated and encouraged *C. e. alxaicus* individuals to use human-impacted areas in winter and spring.

Many studies on ungulate seasonal movement and habitat selection are based on data provided by GPS-collars or radio-collars, which are very precise. However, because of the difficulties involved in capturing *C. e. alxaicus* and the rugged topographic conditions in the Helan Mountains, we conducted our surveys by comparing use versus availability of habitats to

quantify the seasonal habitat selection of *C. e. alxaicus*. This study was based on several years of observation and one year of data collection, but the biodiversity and natural conditions in the Helan Mountains have remained stable for years due to its continental climate. Understanding habitat selection by the red deer and its strategies of seasonal movement can be used for decision making on appropriate management and conservation measures (GUISAN & THUILLER 2005) for *C. e. alxaicus* and its habitat.

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Table II. Characteristics of 13 ecological factors in the habitats used by *Cervus elaphus alxaicus* during the year in the Helan Mountain region, China. Significant P-values: \*  $p \leq 0.001$ .

Ecological factors	Spring (mean $\pm$ SE)	Summer (mean $\pm$ SE)	Autumn (mean $\pm$ SE)	Winter (mean $\pm$ SE)	Kruskal-Wallis H Test $\chi^2$
TD (individuals/100 m <sup>2</sup> )	2.06 $\pm$ 5.065	8.89 $\pm$ 10.258	3.13 $\pm$ 5.634	2.90 $\pm$ 4.642	58.051*
TH (m)	1.91 $\pm$ 2.050	3.09 $\pm$ 2.561	1.66 $\pm$ 2.423	1.90 $\pm$ 1.879	3.319*
DtT (m)	13.28 $\pm$ 11.243	9.83 $\pm$ 11.437	17.01 $\pm$ 10.845	12.81 $\pm$ 11.129	60.433*
SD (individuals/100 m <sup>2</sup> )	12.08 $\pm$ 10.954	19.20 $\pm$ 13.947	12.29 $\pm$ 11.127	6.70 $\pm$ 10.808	76.191*
SH (m)	0.95 $\pm$ 1.012	0.90 $\pm$ 0.567	0.64 $\pm$ 0.611	0.64 $\pm$ 3.499	71.366*
DtS (m)	3.24 $\pm$ 3.782	1.51 $\pm$ 2.143	3.29 $\pm$ 3.795	6.30 $\pm$ 4.252	78.617*
HC (%)	67.84 $\pm$ 23.194	82.40 $\pm$ 23.873	88.56 $\pm$ 17.755	66.98 $\pm$ 24.664	126.156*
SG (°)	5.55 $\pm$ 6.151	10.21 $\pm$ 10.977	6.40 $\pm$ 3.350	4.61 $\pm$ 6.081	75.136*
AL (m)	1,903.62 $\pm$ 427.717	2,512.13 $\pm$ 375.169	2,512.46 $\pm$ 493.990	1,890.61 $\pm$ 570.243	203.163*
DtW (m)	1,060.92 $\pm$ 1351.187	1,176.24 $\pm$ 863.845	1,510.63 $\pm$ 1221.745	1,327.50 $\pm$ 1431.247	26.920*
DtH (m)	2,933.31 $\pm$ 1907.579	5,380.26 $\pm$ 3124.869	7,255.49 $\pm$ 3343.345	3,134.27 $\pm$ 1913.725	158.822*
DtR (m)	120.04 $\pm$ 185.693	186.05 $\pm$ 168.370	247.47 $\pm$ 222.321	75.61 $\pm$ 217.001	178.969*
HiC (%)	47.36 $\pm$ 27.710	35.80 $\pm$ 28.239	52.68 $\pm$ 27.888	67.25 $\pm$ 24.434	86.234*

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Appendix 1. The proportion of 18 ecological factors in used (Obs) plots by *Cervus elaphus alxaicus* and comparison (Exp) plots during different seasons in the Helan Mountain region, China. Selection was determined according to the method of BYERS *et al.* (1984). Factors: (AL) Altitude, (VT) Vegetation types, (TO) Topography, (DT) Dominant tree, (TD) Tree density, (TH) Tree height, (DtT) Distance to the nearest tree, (SD) Shrub density, (SH) Shrub height, (DtS) Distance to the nearest shrub, (HC) Herb coverage, (SG) Slope gradient, (SL) Slope location, (SA) Slope aspect, (DtW) Distance to water resource, (DtH) Distance to human disturbance, (DtR) Distance to bare rock, (HiC) Hiding cover.

Factors	Item	Spring			Summer			Autumn			Winter		
		Obs	Exp	$\chi^2$ (Sig)	Obs	Exp	$\chi^2$ (Sig)	Obs	Exp	$\chi^2$ (Sig)	Obs	Exp	$\chi^2$ (Sig)
VT	MS	48(=)	45	$p < 0.05$	0(-)	45	$p < 0.01$	0(-)	26	$p < 0.01$	60(=)	56	$p > 0.05$
	MOFS	107(=)	108		4(-)	28		36(=)	47		22(=)	26	
	MCF	15(=)	17		104(+)	71		69(=)	48		31(=)	31	
	ABM	11(=)	11		38(+)	23		39(+)	17		18(=)	18	
TO	Smooth undulating slope	156(+)	12	$p < 0.01$	82(+)	8	$p < 0.01$	120(+)	7	$p < 0.01$	112(+)	44	$p < 0.01$
	Moderately broken slope	19(-)	42		64(+)	16		24(+)	5		18(-)	43	
	Distinctly broken slope	6(-)	70		0(-)	97		0(-)	83		0(-)	36	
	Scree/landslide	0(-)	26		0(-)	10		0(-)	21		0(=)	5	
	Cliff	0(-)	31		0(-)	36		0(-)	22		1(=)	3	
DT	<i>Ulmus glaucescens</i>	54(=)	54	$p > 0.05$	0(-)	23	$p < 0.01$	9(=)	17	$p < 0.01$	47(=)	54	$p < 0.01$
	<i>Ziziphus jujuba</i> var. <i>spinosa</i> (Bunge)Hu	2(=)	0		0(=)	0		0(=)	1		5(=)	0	
	<i>Salix babylonica</i> Ⓞ	3(=)	0		0(=)	1		0(=)	1		2(=)	0	
	<i>Juniperus rigida</i>	11(=)	16		20(=)	19		11(=)	12		8(=)	8	
	<i>Pinus tabulaeformis</i>	1(=)	3		1(=)	4		3(=)	1		2(=)	9	
	<i>Picea crassifolia</i>	4(=)	8		32(=)	27		18(=)	13		0(-)	10	
	<i>Prunus armeniaca</i>	2(=)	0		0(=)	0		0(=)	0		8(=)	2	
	<i>Juglans regia</i>	3(=)	0		0(=)	0		0(=)	0		59(=)	48	
	<i>Salix microstachya</i>	0(=)	0		0(=)	0		0(=)	0		0(=)	0	
	No tree	86(=)	100		49(-)	91		92(=)	92		0(=)	0	
	Mixture	15(=)	0		43(+)	2		11(+)	1		0(=)	0	
TD	<2 tree/100 m <sup>2</sup>	114(=)	123	$p < 0.05$	51(-)	107	$p < 0.01$	96(=)	103	$p < 0.01$	75(+)	59	$p < 0.01$
	2-4 tree/100 m <sup>2</sup>	43(=)	46		10(-)	31		10(=)	18		31(=)	42	
	> 4 tree/100 m <sup>2</sup>	24(=)	12		85(+)	29		38(+)	17		21(=)	30	
TH	<4 m	148(-)	172	$p < 0.01$	72(-)	129	$p < 0.01$	113(=)	119	$p > 0.05$	116(=)	113	$p < 0.01$
	4-6 m	30(+)	7		53(+)	31		21(=)	14		13(=)	18	
	> 6 m	3(=)	2		21(+)	7		10(=)	5		2(=)	0	
DtT	<1 m	3(=)	1	$p > 0.05$	23(+)	2	$p < 0.01$	2(=)	0	$p > 0.05$	4(=)	9	$p < 0.05$
	1-3 m	64(=)	65		69(=)	70		37(=)	39		42(=)	50	
	> 3 m	114(=)	115		54(-)	95		105(=)	99		85(=)	72	
SD	<5 tree/100 m <sup>2</sup>	52(-)	81	$p < 0.01$	16(-)	73	$p < 0.01$	50(=)	49	$p < 0.01$	84(=)	75	$p < 0.05$
	5-10 tree/100 m <sup>2</sup>	52(-)	85		37(-)	81		25(=)	62		18(=)	31	
	> 10 tree/100 m <sup>2</sup>	77(+)	15		93(+)	13		69(+)	27		29(=)	25	
SH	<1.3 m	134(-)	172	$p < 0.01$	111(-)	161	$p < 0.01$	120(=)	138	$p > 0.05$	123(=)	126	$p > 0.05$
	1.3-1.7 m	21(+)	8		20(+)	4		11(=)	0		4(=)	3	
	> 1.7 m	26(+)	1		15(+)	2		11(=)	0		4(=)	2	
DtS	<0.5 m	11(+)	5	$p < 0.01$	28(+)	5	$p < 0.01$	14(=)	5	$p < 0.01$	10(=)	7	$p < 0.01$
	0.5-1.5 m	89(-)	106		75(=)	81		66(=)	71		22(-)	50	
	> 1.5 m	81(=)	70		43(-)	81		64(=)	62		99(=)	74	

Continues

## Appendix 1. Continued.

Factors	Item	Spring			Summer			Autumn			Winter		
		Obs	Exp	$\chi^2(\text{Sig})$	Obs	Exp	$\chi^2(\text{Sig})$	Obs	Exp	$\chi^2(\text{Sig})$	Obs	Exp	$\chi^2(\text{Sig})$
HC	50%	48(-)	170	p < 0.01	16(-)	142	p < 0.01	9(-)	127	p < 0.01	33(-)	118	p < 0.01
	50~80%	73(+)	11		26(=)	19		16(=)	10		53(+)	11	
	> 80%	60(+)	0		104(+)	6		119(+)	1		45(+)	2	
SG	<10°	150(+)	16	p < 0.01	89(+)	10	p < 0.01	113(+)	2	p < 0.01	117(+)	27	p < 0.01
	10°~20°	24(-)	45		52(+)	29		31(=)	33		13(-)	45	
	> 20°	7(-)	120		5(-)	128		0(-)	103		1(-)	59	
SL	Upper slope	17(-)	53	p < 0.01	49(=)	65	p < 0.01	32(=)	45	p < 0.01	4(=)	7	p < 0.01
	Middle slope	25(-)	85		54(=)	75		76(=)	77		11(-)	68	
	Lower slope	139(+)	43		43(+)	27		36(+)	16		116(+)	56	
SA	Sunny slope	137(+)	55	p < 0.01	15(-)	118	p < 0.01	53(-)	93	p < 0.01	62(+)	39	p < 0.01
	Partial shade slope	35(-)	76		69(+)	34		75(+)	27		53(=)	49	
	Shady slope	9(-)	50		62(+)	15		16(=)	18		16(-)	43	
AL	< 1600 m	56(=)	52	p > 0.05	0(-)	44	p < 0.01	5(-)	27	p < 0.01	52(=)	48	p > 0.05
	1600~2000 m	52(=)	56		4(-)	29		6(-)	27		30(=)	34	
	2000~3000 m	62(=)	62		119(+)	74		94(+)	67		34(=)	31	
	> 3000 m	11(=)	11		23(=)	20		39(+)	17		15(=)	18	
DtW	< 500 m	101(=)	97	p > 0.05	42(-)	67	p < 0.01	44(=)	39	p > 0.05	54(=)	52	p > 0.05
	500~1 000 m	19(=)	22		19(=)	15		21(=)	15		19(=)	19	
	> 1 000 m	61(=)	62		85(=)	85		79(=)	84		58(=)	60	
DtH	< 500 m	34(=)	34	p > 0.05	2(=)	6	p > 0.05	0(=)	0	p > 0.05	8(=)	6	p > 0.05
	500~1 000 m	16(=)	16		4(=)	11		0(=)	5		18(=)	14	
	> 1 000 m	131(=)	131		140(=)	150		144(=)	133		105(=)	111	
DtR	< 50 m	80(-)	143	p < 0.01	14(-)	109	p < 0.01	7(-)	30	p < 0.01	87(-)	109	p < 0.01
	50~100 m	52(+)	18		44(+)	25		48(=)	53		30(+)	13	
	> 100 m	49(+)	20		88(+)	33		89(+)	55		14(=)	9	
HiC	> 25%	41(+)	2	p < 0.01	69(+)	0	p < 0.01	30(+)	0	p < 0.01	13(+)	0	p < 0.01
	25~50%	59(+)	7		35(+)	13		39(+)	4		17(+)	4	
	50~75%	46(=)	45		22(=)	21		33(+)	7		42(+)	12	
	> 75%	35(-)	127		20(-)	133		42(-)	127		59(-)	115	

The symbols (=), (+) and (-) located beside the observed values signify that those values were found to be (according to Bonferroni Intervals) in equal, greater, or lesser proportion than the respective expected values. (+) indicates that red deer preferred category i; (-) indicates that red deer avoided category i; (=) indicates that red deer showed no obvious selection according to category i.

Difference between used and comparison plots is statistically significant at p < 0.05 based on a chi-square goodness-of-fit test.

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