Comparative analysis of winter diets and habitat use by the sympatric blue sheep (Pseudois nayaur) and Alashan red deer (Cervus alashanicus) in the Helan Mountains, China

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Comparative analysis of winter diets and habitat use by the sympatric blue sheep (*Pseudois nayaur*) and Alashan red deer (*Cervus alashanicus*) in the Helan Mountains, China

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Abstract. Research that elucidates the differences in the habitat use and diet of sympatric species is essential and meaningful for protection strategies. The habitat use and diet composition of blue sheep (*Pseudois nayaur*) and Alashan red deer (*Cervus alashanicus*) in the Helan Mountains, China, were examined from November 2013 to February 2015. Despite the partial overlap in habitat, the habitat used by blue sheep and Alashan red deer were significantly different. Blue sheep preferred mountain woodland steppe with high degree of slope at farther distances from water resources and bare rock. Alashan red deer selected winter habitat in moutain grassland with flat slopes, closer water resources, further distances to human disturbances and bare rock. The diet of blue sheep was significantly different from that of Alashan red deer regarding the proportions of the forage categories. Blue sheep grazed primarily on shrubs (36.7 %) and grass (23.1 %), while the diet of Alashan red deer was dominated by shrubs (43.6 %) and trees (25.6 %). Contrary to Alashan red deer, blue sheep preferred to forage on herbaceous plants.

Key words: habitat utilization, diet composition, niche overlap, sympatric species

Introduction

Interspecific interactions among coexisting species, such as resource partitioning and food competition, are widely studied in theoretical ecology and practical wildlife management (Abrams 1998, Murray & Illius 2000, Bagchi et al. 2003, Ahrestani et al. 2012, Wu et al. 2016). The niche theory predicts that there should be at least some minimal amount of differences in ecological requirements among sympatric species to avoid competitive exclusion (Pianka 1974), but the mechanisms that lead to resource partitioning in ungulate communities still remain unclear. Understanding the overlap of resource utilization in terms of food and habitat could be a useful approach to explore such interactions (Mysterud 2000, Pokharel & Storch 2016, Tuboi & Hussain 2016). Normally, high similarities in diet and habitat indicate more intense interspecific competition (Wegge et al. 2006).

Blue sheep (*Pseudois nayaur*) are endemic to the Tibetan Plateau and the surrounding mountain regions (Shackleton 1997). The blue sheep reach their eastern range limits in the Helan Mountains between the Ningxia Hui Autonomous Region and the Inner Mongolia Autonomous Region, Northwestern China. The blue sheep is a medium size herbivore, with a weight of 35.5-70 kg and a body length of 1.15-1.65 m, prefers alpine meadow and high elevation mountains on the Tibetan Plateau (> 4000 m). While it inhabits various habitats including mountainous grasslands, mountainous savannas, montane conifer forests, and subalpine shrublands and meadows in the Helan Mountains (Liu et al. 2005a). The Alashan red deer (*Cervus alashanicus*) in the Helan Mountains are one of eight subspecies of red deer (*Cervus elaphus*) in China. This subspecies is currently distributed in only the Helan Mountains and is the only wild population surviving in China (Sheng 1992). In addition, Alashan red deer are also a geographically isolated subspecies with the smallest distribution range and population number among the eight Chinese subspecies (Chang

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et al. 2010). It is bigger than the blue sheep, weighs 154-245 kg, the body length is about 1.57-2.26 m.

The blue sheep and Alashan red deer are two wild ungulates living sympatrically in the Helan Mountains, and both are listed as Category II nationally protected animals (Luo et al. 2009). Since natural enemies such as the snow leopard (*Uncia uncia*), wolf (*Canis lupus*), and lynx (*Lynx lynx*) have basically disappeared in the 1980s, there are no large predators in the Helan Mountain area. Recently, the population of blue sheep rapidly increased and became the dominant species in the Helan Mountains (Liu et al. 2007a), while the Alashan red deer population has exhibited a relatively lower and stable growth rate in recent decades (Zhang et al. 2006). Blue sheep and Alashan red deer are mixed feeders that feed on different proportions of browses and grasses based on the seasonal changes in food quality throughout the year (Hofmann 1989, Schaller 1998, Mishra et al. 2004, Shrestha et al. 2005). Previous studies focused on the food habit or habitat use of one species (Liu et al. 2005a, 2007b), or just compared the differences of those two sympatric ungulates from only one aspect (Luo et al. 2009). In order to obtain a better understanding of their niche separation, we studied the diets and habitat use comparation of the coexistent blue sheep and Alashan red deer in winter, which could provide a solid evidence for the niche differentiation of the sympatric ungulate species. For ungulates on mountains, the severe conditions in the winter could have a pronounced effect on food and habitat use: low temperatures could increase the energy expenditure of the animals (Mason 1998, Bobek et al. 2016), and the reduced quality and biomass of forage may intensify the food competition between the two sympatric species (Shi et al. 2016), especially in the Helan mountains, where there is rainless and sparse vegetation. Studying the difference in diet and habitat use in winter may provide profound insight into the interspecific relationship between the two herbivores (Suryawanshi et al. 2010, Obidzinski et al. 2013).

Most previous studies have concentrated on the competition or coexistence between blue sheep and domestic livestock in the Trans Himalayan regions (Mishra et al. 2004, Shrestha et al. 2005, Shrestha & Wegge 2008a, b). However, little information is available on the niche separation of wild sympatric herbivores in China. Blue sheep, Alashan red deer and musk deer (*Moschus chrysogaster*) are mainly three kinds of ungulates distributed in the Helan Mountains, while the number of musk deer has dropped sharply since the 1880s, it is quite rare at present (Liu 2009). Therefore, blue sheep and Alashan red deer are the two dominant herbivores that may exist competition in the Helan Mountains. The main objectives of this study were to determine the winter forage and habitat of blue sheep and Alashan red deer in the Helan Mountains and provide basic information for assessing the interspecies relationships of the two coexisting species. In addition, understanding the pattern of resource partitioning between the two species is a crucial component required for the managers to develop effective conservation and management guidelines.

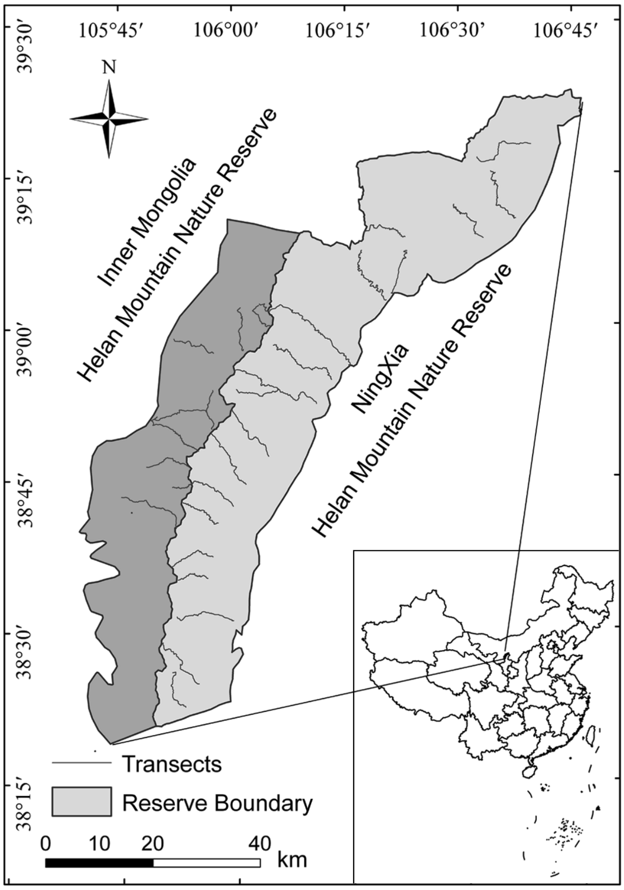

Fig. 1. Location and distribution of the study area. The gray shading represents the Helan Mountain Nature Reserve in the Inner Mongolia Autonomous Region, while the light area represents the reserve in the Ningxia Hui Autonomous Region, China.

Material and Methods

Study area

The study was conducted in the Helan Mountains (38°21′-39°22′ N, 105°44′-106°42′ E) between the eastern Yinchuan Plain in the Ningxia Hui Autonomous Region and the western Alashan Plateau in the Inner Mongolia Autonomous Region (Fig. 1). It covers an area of 2740 km^2. The mountain stretches more than 200 km from north to south and 20-40 km from east to west. It has a typical Asian monsoonal climate, and is the dividing line between desert and semi-desert grasslands. The whole year is dry, with a mean annual precipitation of 420 mm. The average annual and winter temperatures are –0.9 °C and –13.2 °C, respectively.

The vegetation is typical for temperate arid and semiarid upland vegetation with clear vertical distribution. The mountain grassland type distributed at 1400-1600 m, dominated by *Stipa breviflora*, *Ajania fruticulosa*, *Ptilagrostis pelliotii*, *Oxytropis aciphylla*, *Convolvulus gortschakovii* and *Salsola laricifolia*. The mountain woodland steppe type (1600-2000 m) is dominated by *Ulmus pumila*, *Prunus mongolica*, *Stipa grandis* and *S. bungenana*. The mountain conifer forest type (1900-3000 m) is dominated by *Picea crassifolia*, *Pinus tabulaeformis*, *Juniperus rigida* and *Dasiphora parvifolia*. The subalpine shrubland and meadow type (3000-3556 m) is dominated by *Salix cupularis*, *Caragana jubata* and *Kobresia* spp. (Di 1986).

Comparison of habitat use

The comparation of habitat use by blue sheep and Alashan red deer was sampled during two surveys (November 2013 to December 2014, November 2014 to February 2015) using 25 line transects. Transects were laid in a stratified random sampling manner (according to the broad topographic and vegetation classes) and established along the valleys. Transects ranged from 2.4 to 22.3 km, for a total of 469.2 km, the width of the transect was 15 m. The transects traversed the entire study area from east to west and covered all vegetation types.

A team of three observers conducted the survey. Data were collected by searching for the blue sheep and Alashan red deer or their fresh signs along the 25 line transects. When target animal were observed, we observed them with vantage points using 8 × 32 binoculars (ZEISS, Germany) and a 20-60 × variable spotting scope (FEIRSH, China). We recorded the species, group size, sex, age group, date and time, and noted the characteristics of the utilized habitats. Due to the high vigilance of animals, it is difficult to observe them closely. After the blue sheep or Alashan red deer departed the area, we conducted detailed sampling. When we found evidence of animal activity (e.g. fresh pellets, hoofprints, feeding sites, or bedding sites) along the selected transects, we determined that the sites were recently utilized (Zhang et al. 2013). Due to the difference between the body size of blue sheep and Alashan red deer, it was easy to differentiate the signs left by those two ungulates. According to our experience from long-term field investigation, we found that the size and shape of their feces and hoofprints are different, the feces of blue sheep is one end pointed and the other blunt round, while the shape of Alashan red deer's is bullet-shaped or oval pattern (Tian 2008), and the bullet-shaped tip is less sharp than those of blue sheep. Besides, compared to the Alashan red deer, the hoofprints of blue sheep are smaller and more tapered.

We used a 20 × 20 m plot to determine the variables of the trees, a 10 × 10 m quadrat for the shrub variables, and a 1 × 1 m plot for the grass variables. The habitat variables were recorded at the center of these quadrats and were related to vegetation structure, landform characteristics, composition of the tree layer (estimated on 20 × 20 m plot) and composition of the shrub layer (estimated on 10 × 10 m plot) (Table 1). We measured the distance to the nearest tree and shrub, distance to bare rock, snow depth, and weight of the ground vegetation. The distances to human disturbance and water resources were also determined from 1:50000 maps. Hiding cover (%) was estimated by placing a cover pole at the center of each plot (Kunkel & Pletscher 2001). The altitude was determined by a global positioning system (GPS) (UniStrong, China). We measured slope degree (°) with a compass (Kanpas, China).

Forage availability

A total of 94 plots (20 × 20 m) were randomly selected along the transects among the different vegetation types (Di 1986). The relative area of four types was 45.3 %, 42.2 %, 11.7 % and 0.8 % respectively. According to the proportion of each vegetation type, plot numbers in mountain grassland, mountain woodland steppe, mountain conifer forest and subalpine shrubland and meadow were 43, 40, 12, and 1 respectively. The availability of tree and shrub species was determined by the twig-count method (Elwood & Shafer 1963). The biomass of browse available was estimated by averaging the weight of the edible part in a single twig below two meters and multiplying that by the number of twigs available within each of the quadrats (Elwood & Shafer 1963). At the same places, the species and biomasses of grasses and forbs were counted and measured in five 1 × 1 m squares by clipping the above-ground herbaceous vegetation. The sampling was used to calculate the proportion of the available sample made up of the plant species.

Table 1. Characteristics of ecological factors used by blue sheep and Alashan red deer during winter in the Helan Mountains.

Variables	Categories	Description
Altitude (m)	Continuous	The altitude of the plot according to GPS
Slope degree (°)	Continuous	Slope degree of the hillside where the spot located measured with military compass
Slope aspect	Categorical	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 three main directions: sunny slope (135°~225°), partial shade slope (45°~135° and 225°~315°) or shady slope (315°~45°)
Slope location	Categorical	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)
Topography	Categorical	Categorized by the slope and fault of a hillside, divided into five levels: smooth undulating slope, moderately broken slope, distinctly broken slope, scree/landslide, cliff
Vegetation types	Categorical	Mountain steppe type, mountain open forest and steppe type, mountain coniferous forest type, Alpine bush and meadow type
Dominant tree	Categorical	The tree covers 70 % of the density in the 20 × 20 m plot
Tree height (m)	Continuous	The mean height of trees in the 20 × 20 m plot
Tree density (individuals/400 m^2)	Continuous	The total number of trees in the 20 × 20 m plot
Distance to the nearest tree (m)	Continuous	Distance from the center of the 20 × 20 m plot to the nearest tree
Shrub height (m)	Continuous	The mean height of shrubs in the 10 × 10 m plot
Shrub density (individuals/100 m^2)	Continuous	The number of shrubs in the 10 × 10 m plot
Distance to the nearest shrub (m)	Continuous	Distance from the center of the 10 × 10 m plot to the nearest shrub
Forage biomass (g)	Continuous	Weight of the ground vegetation. Cutting the current year's branches of trees and shrubs below 2 m, and the herbage grows above the ground in five 1 × 1 m squares, drying at 60 °C for 24 h, calculate the average weight
Distance to water resource (m)	Continuous	The distance from the spot to the nearest water resource
Distance to human disturbance (m)	Continuous	The distance from the spot to the nearest place of human activity such as highway, road and shelter forest station, etc.
Distance to bare rock (m)	Continuous	The distance from the spot to the nearest bare rock
Hiding cover (%)	Continuous	The coverage of the hiding conditions. Percent hiding cover was determined by visually estimating the percent of the target animal or a substitute (a 1 m stick) obscured at 30 m in the four cardinal directions
Snow depth (cm)	Continuous	The mean snow depth within five 1 × 1 m squares

Diet

We collected fresh fecal pellets of blue sheep and Alashan red deer monthly from November 2013 through February 2014. At the same time, we collected the branches, leaves and barks of all the plants in the active areas of those two animals as reference samples. Crews searched for fresh pellet groups along the 25 line transects across the entire study area. Two pellets from each pellet group were selected randomly to make composite samples. All pellet groups that were determined to be fresh (based on colour and consistency) were collected as they were encountered. The feces were identified by species from the shape of the pellets and the nearby hoofprints.

The plants and fecal samples were placed in plastic bags respectively, and cryopreserved at –20 °C. All the plant and fecal samples were prepared for microhistological analysis as described by Sparks & Malechek (1968). Dietary species can be recognized in fecal samples by microscopic analysis of the plant cuticle (Metcalfe 1960). Samples were oven-dried at 60 °C for 48 h and ground individually using a grinding mill and 1 mm screen. Approximately 0.5 g of the remaining plant and fecal materials were placed in a beaker that contained 10 ml of 10 % nitric acid. We examined 20 random fields on each slide at 100× magnification (Pradhan et al. 2008). To reduce the inconsistencies due to observer bias, all identifications were conducted by the same observer. The frequency of each plant species was recorded and converted to relative density (Johnson 1982). Plants were generally identified to the species or genus level.

$$F = 1 - e^{-d}$$

$$r^i = d^i / \sum_{i=1}^{m} d^i$$

F is relative frequency, e is the natural logarithm and d is the mean particle density, r^i is relative density, where $i = 1, \dots, m$ and d^i is the particle density for each species.

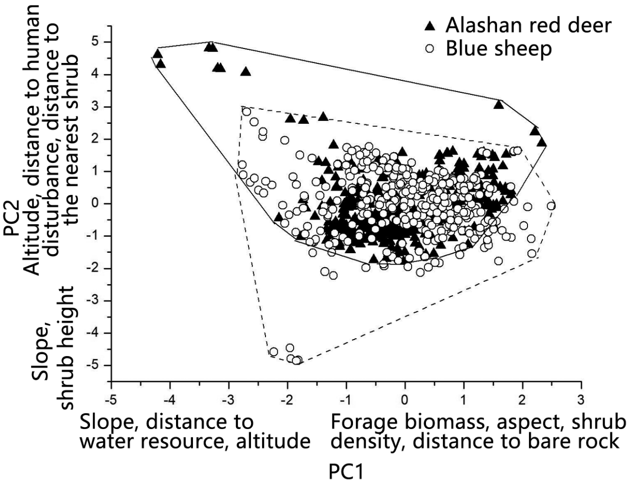

Fig. 2. Distribution of blue sheep and Alashan red deer locations along the first two principal component axes based on principal component analysis.

Data analysis

We assessed all data for normality with a Kolmogorov-Smirnov test. We used a Mann-Whitney U test to compare the differences in the 14 continuous habitat variables between blue sheep and Alashan red deer, then used the Chi-square test to analyze whether there are differences in the selection of five categorical variables. Principal component analysis was used to describe the vegetation characteristics of the habitat utilized by the sheep and deer (Liu et al. 2016). We did not rotate the variables and only extracted components that had eigenvalues ≥ 1. These components usually describe the variation within the variables sufficiently (Chatfield & Collins 1980, Johnson & Wichern 1992, McGarigal et al. 2000). We used discriminant function analysis to explain any differences in habitat between the species. We used a Chi-square transformation of the overall Wilks's lambda to test for differences in the group centroids. We used stepwise variable selection to identify the most discriminatory variable accounting for any variation between the sheep and deer (Malaney & Frey 2006).

We used Ivlev's selectivity index (ISI; Ivlev 1961) to describe the selectivity of each plant species, in relation to the abundance or availability of plant species in the environment (Brown et al. 2018).

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where r is the proportion of the diet made up of the plant species and p is the proportion of the available

Table 2. Descriptive statistics and tests for habitat variables that differed significantly between blue sheep and Alashan red deer in the Helan Mountains during the winter.

Variables	Alashan red deer		Blue sheep		Mann-Whitey U tests	P
	$\bar{X}$	SE	$\bar{X}$	SE		
Tree density (individuals/400 m^2)	6.21	0.33	2.88	0.14	–5.597	≤ 0.001**
Tree height (m)	6.19	0.31	4.01	0.14	–2.534	0.011*
Distance to the nearest tree (m)	8.08	0.91	23.82	4.31	–4.371	≤ 0.001**
Shrub density (individuals/100 m^2)	5.87	0.29	7.60	0.27	–3.286	≤ 0.001**
Shrub height (m)	1.57	0.04	1.50	0.02	–1.576	0.115
Distance to the nearest shrub (m)	1.69	0.11	0.93	0.06	–7.589	≤ 0.001**
Forage biomass (g)	616.46	25.32	59.89	2.56	–15.828	≤ 0.001**
Slope degree (°)	8.92	0.52	37.88	1.00	–15.452	≤ 0.001**
Altitude (m)	1738.21	22.51	1871.87	23.09	–3.753	≤ 0.001**
Distance to water resource (m)	452.79	36.04	941.96	41.24	–8.203	≤ 0.001**
Distance to human disturbance (m)	2474.48	109.92	1388.32	93.57	–8.783	≤ 0.001**
Distance to bare rock (m)	75.52	8.67	4.17	0.39	–15.368	≤ 0.001**
Hiding cover (%)	80.82	0.95	68.36	1.73	–1.464	0.143
Snow depth (cm)	2.54	0.27	0.31	0.05	–10.862	≤ 0.001**

A Significant P values: $^{*}P < 0.05$, $^{**}P < 0.001$

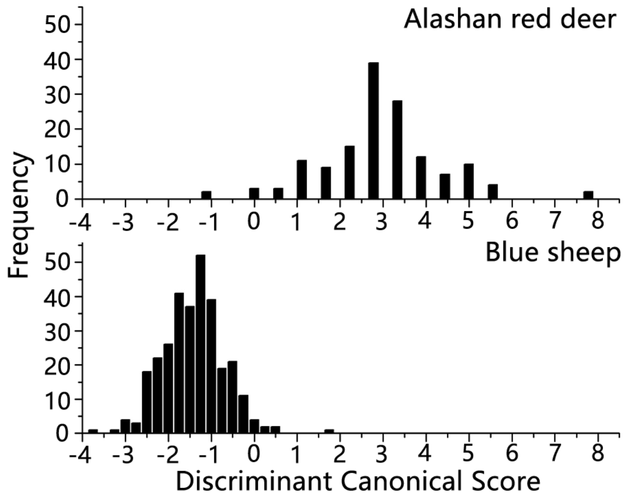

Fig. 3. Canonical scores of blue sheep and Alashan red deer habitats during the winter in the Helan Mountains, China.

sample made up of the plant species. This selectivity index ranges from –1 to +1. Thus, an E_i of 1 denotes maximum preference of one species, 0 denotes use exactly according to availability and a value of –1 denotes total avoidance.

A Chi-square test was performed to test if the proportions of trees, shrubs, grass, sedges and forbs were the same for blue sheep and Alashan red deer. A Chi-square test was used to test the null hypothesis that the two species had the same overall diets in terms of the quantities of individual food plant species and categories. SPSS 13.0 for Windows was used for all statistical procedures.

Results

Comparison of habitat use

From 2013 to 2015, we documented 145 Alashan red deer and 304 blue sheep localities. The hiding cover and shrub height did not differ between the sheep and deer habitats. However, the other 12 continuous habitat variables exhibited significant differences between

Table 3. Diet composition and Ivlev's selectivity index of blue sheep and Alashan red deer during winter in the Helan Mountains, China.

Category	Plant species	Percentage of diet		Ivlev's selectivity index	
		Blue sheep	Alashan red deer	Blue sheep	Alashan red deer
Tree	*Pinus tabulaeformis*	0	4.5 ± 0.6	–1	0.2
	Picea crassifolia	0	2.7 ± 0.3	–1	0.019
	Juniperus rigida	0.2	2.8 ± 0.2	–0.692	0.436
	Ulmus pumila	9.6 ± 0.6	4.5 ± 0.5	–0.147	–0.483
	Cotoneaster spp.	1.6 ± 0.3	1.8 ± 0.3	–0.467	–0.419
	Other tree	5.3 ± 0.5	9.3 ± 0.9	0.738	0.842
Shrubs	*Salsola* spp.	4 ± 0.4	1.4 ± 0.1	0.481	0
	Berberis spp.	0	1 ± 0.1	–1	–0.683
	Spiraea spp.	1.6 ± 0.2	2.5 ± 0.3	–0.636	–0.485
	Rosa spp.	1.6 ± 0.2	2.1 ± 0.2	–0.256	–0.125
	Dasiphora spp.	4.2 ± 0.5	5.8 ± 0.7	–0.192	–0.033
	Prunus monglica	2.4 ± 0.4	4.1 ± 0.5	–0.368	–0.118
	Caragana spp.	8.8 ± 0.7	9.2 ± 0.7	0.419	0.438
	Lespedeza spp.	2.6 ± 0.2	3.6 ± 0.3	0.405	0.532
	Leptodermis ordosica	0.8	1 ± 0.1	–0.2	–0.091
	Other shrubs	10.7 ± 0.8	12.9 ± 1	0.562	0.623
Grass	*Stipa* spp.	6.2 ± 0.7	5 ± 0.5	–0.398	–0.485
	Other grass	16.9 ± 1.1	10.7 ± 0.5	0.657	0.507
Sedges	*Carex* spp.	4 ± 0.5	1 ± 0.1	–0.08	–0.649
	Other sedges	16.9 ± 1.1	10.7 ± 0.5	0.84	0.636
Forbs	*Heteropappus altaicus*	1.3 ± 0.1	0.4	–0.212	–0.667
	Ajania fruticulosa	0.5	0.7	–0.762	–0.682
	Artemisia spp.	3.1 ± 0.3	3.5 ± 0.3	–0.34	–0.286
	Other forbs	10.5 ± 0.9	5.2 ± 0.5	0.511	0.209

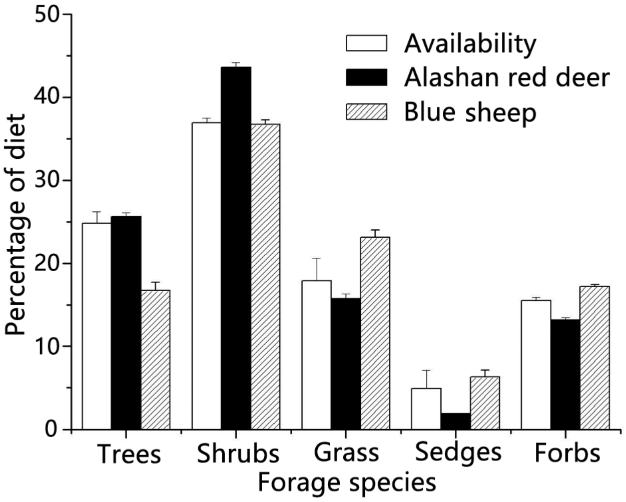

Fig. 4. Frequency of main food items found in the feces of Alashan red deer and blue sheep in the winter.

the two species (Table 2). Chi-square test showed that there were extremely significant differences in the choice of slope location ($\chi^2 = 116.839$, df = 2, $P < 0.001$), topography ($\chi^2 = 59.394$, df = 4, $P < 0.001$), vegetation types ($\chi^2 = 23.760$, df = 3, $P < 0.001$), and dominant tree ($\chi^2 = 94.655$, df = 6, $P < 0.001$) between the blue sheep and Alashan red deer, while in the choice of slop aspect ($\chi^2 = 0.942$, df = 2, $P > 0.05$) was not significant.

The principal component analysis extracted six principal components, which accounted for 65.37 % of the total variation in the blue sheep and Alashan red deer habitats. Based on the screen plot criterion, we retained two principal components (PC) for further explanation, which together accounted 33.46 % of the total variation in the two species habitats (Fig. 2). Forage biomass, aspect, shrub density, and distance to bare rock had high positive factor loadings in PC1 (19.97 % of the variation). Slope degree, distance to water resources, and altitude had high negative loadings in PC1. This component represents the sites used on the south-facing aspects with higher forage biomass and more shrubs. The south-facing aspect had increased sunlight, which facilitated the growth of herbaceous and woody plants. Principal component two accounted for 13.49 % of the total variation in habitats. The high positive loadings included altitude, distance to human disturbance, and distance to the nearest shrub. The high negative factor loadings were related to slope degree and shrub height.

The overlap in habitat that was not evident in the histogram of canonical scores, and the habitat use between blue sheep and Alashan red deer was significantly separated along the discriminant function (Wilks' $\lambda = 0.17$, $\chi^2 = 792.87$, df = 9, $P < 0.001$; Fig. 3). The discriminant analysis indicated an eigenvalue of five and a canonical correlation of 0.913, which accounted for 100 % of the variation. The high percentage (98 %) of the original groups that were correctly classified also agreed with this difference. Misclassification of Alashan red deer locations (5.52 %) occurred more frequently than misclassification of blue sheep locations (0.33 %). The stepwise discriminant analysis showed that forage biomass was the best discriminating variable based on its high standardized canonical coefficient (0.74). Other significant discriminating variables included tree height, snow depth, distance to human disturbance, and distance to bare rock (in order of importance).

Diet

We collected pellets from 144 sheep groups and 119 deer groups. The plant species found in the diets were classified as trees, shrubs or browse, grass (Gramineae), sedges (Cyperaceae), and forbs (other dicotyledonous herbs, and monocotyledonous plants such as Liliaceae). The fecal samples indicated that the Alashan red deer diet was dominated by shrubs (43.6 %) in the winter, among which, *Caragana* spp. alone accounted for 9.2 % of the diet (Fig. 4). Trees (25.6 %) were the second most common resource. Among the trees, *Pinus tabulaeformis* and *Ulmus pumila* were both dominant species with equal proportions (4.5 %) in the diets of the deer. Other resources were grass (15.7 %), forbs (13.2 %), and sedges (1.9 %).

The diet of blue sheep was significantly different from that of Alashan red deer regarding the proportions of forage categories ($\chi^2 = 154.1$, df = 4, $P < 0.001$). Shrubs (36.7 %) constituted the bulk of the sheep diet in the winter, while grass constituted 23.1 % of the diet. The proportion of *Caragana* spp. was 8.8 % and was less in the sheep feces than in the Alashan red deer feces. Grass constituted 23.1 % of the sheep diet, while *Stipa* spp. constituted 6.2 %. Trees constituted 16.7 % of the diet of blue sheep. In contrast to the fecal composition of Alashan red deer, the intake of *Pinus tabulaeformi* by blue sheep was < 0.1 %, while the proportion of *Ulmus pumila* (9.6 %) exceeded that of Alashan red deer. The proportion of forbs in the diet of blue sheep was 17.2 %. In addition, sedges were utilized by blue sheep significantly more than Alashan red deer, including *Kobresia* spp. (2.3 %) and *Carex* spp. (4.0 %) (Fig. 4).

Our data revealed that different proportions of forge categories were consumed by the two herbivores. 1) Tree species were more commonly consumed by the Alashan red deer than by the blue sheep (Table 3), and

Pinus tabulaeformis, *Picea crassifolia* and *Sabina* spp. were not found in the feces of blue sheep. *Ulmus pumila* was used by both blue sheep and Alashan red deer, but the proportions of intake by blue sheep and Alashan red deer were diverse (9.6 % and 4.5 %; respectively). 2) Alashan red deer preferred to graze on trees and shrubs (69.2 % in total), while blue sheep preferred shrubs and grass (59.8 % in total). The herbage (including grass, sedges, forbs) used by the two ungulates was significantly different. Herbage constituted 30.8 % of the Alashan red deer diet, while it constituted 46.6 % of the blue sheep diet.

Ulmus pumila was the constitution of mainly food of the two ungulates, but was not their preferred food in winter. *Caragana* spp. made up 9.2 % of the deer diet, and was a preferred food of Alashan red deer. Species of herbaceous plant (grass, sedges and forbs) preferred by Alashan red deer were less than by blue sheep. Contrary to blue sheep, Alashan red deer chose to avoid foraging most herbaceous plant (Table 3).

Discussion

Comparison of habitat use

Due to differences in visibility among habitats, there may be deviations in habitat use studies based on visual observation of animal locations. More animal locations can be observed in open habitats such as grasslands, while visibility is low in lush vegetation areas such as forests, and fewer animal locations are observed. In our investigation, the transect set along valleys and covered all vegetation types, a team of three observers searched 15 m wide transects for trace for blue sheep and Alashan red deer, ensure that almost all traces were collected in the transect to reduce deviations due to visibility.

The blue sheep and Alashan red deer in the Helan Mountains faced lower predation risks (or poaching), as there were few predators in this region. In ungulates, habitat use may be influenced by the need to maximize net-energy intake, minimize predation risk and thermal stress, or maintain social contacts with conspecifics (Fryxell & Lundberg 1997, Fortin et al. 2003, Singh et al. 2010). The features of the habitat used by ungulates are the result of trade-offs. From the results of the analysis of the plots selected by Alashan red deer and blue sheep, it was found that tree density, tree height, forage biomass and distance to the nearest tree were higher in the plots selected by Alashan red deer than those selected by blue sheep (Table 2). Those four variables of the plots could explain that the habitat use by the Alashan red deer could supply better shelter and sufficient food to the large-bodied ungulate. Contrary to the summer habitat (unpublished data), Alashan red deer and blue sheep preferred to utilize low elevation mountains (< 2000 m) with vegetation types such as mountain grassland and woodland steppe (Luo et al. 2009). These large variations can be attributed to the differences in seasons. First, differences in food availability. In winter, herbaceous plants at high elevations are withered and covered by snow, which makes them difficult to find (Liu et al. 2005b). Second, differences in temperature and wind strength. The wind at low elevations is weak. The advantages of temperature and wind strength in the low elevation regions can ensure that ungulates will use less energy to find sufficient food. Third, significant decrease in the number of people entering the mountain area compared with other seasons, and food availability and resource abundance is higher in the low altitude areas compared with high altitude where snow depth is greater (Liu et al. 2009). Besides, in spring, because of the end of snowmelt, the blue sheep and Alashan red deer begin to move from the relatively lower areas in the winter towards higher altitudes in the spring, and mountain conifer forests become their primary habitat (Luo et al. 2009).

Our results demonstrated that their habitat use differed, as the two species tended to occur in different areas. We found a significant difference in vegetation type, dominant tree, topography and slop location selection between them in this study, previous habitat use studies showed that blue sheep selected mountain woodland steppe and trees dominated by *Ulmus glaucescens*, selected the steep middle or upper slop (Liu et al. 2005b), while Alashan red deer selected winter habitat of mountain grassland dominated by *Stipa breviflora* and *Ajania fruticulosa*, preferred gentle (< 20°), lower slop or valley bottom (Luo et al. 2009). This is mainly due to the fact that blue sheep is good at climbing on steep cliffs to avoid human interference, while red deer does not have the ability to climb rock, and can only choose lower slopes with a gentle slope. In winter, Alashan red deer and blue sheep all selected sunny slope, mainly because in the sunny slope, animals could receive more sunlight and a higher temperature, which can reduce the loss of body energy, accelerate the snow melt and increase food availability. In the northern temperate regions, the quantity and quality of forage species exhibited dramatic changes among seasons. The availability and biomass of forage in the winter is the lowest of the entire year, making it difficult for ungulates to obtain enough energy (Mautz 1978, Parker & Robbins 1984, Chen et al. 1999). It is critical for ungulates to endure the terrible surroundings in winter (Moen 1976, Mautz 1978, Mysterud & Østbye 1995). Under this scenario, Alashan red deer revealed an association with the habitat variables that reflected the possibilities to maximize forage intake, while minimizing the habitat overlap with blue sheep to coexist in the same domain.

Diet

Different digestibility of particular plants could have an impact on the results of the analysis. Warren et al. (1984) considered that using fecal analysis to study herbivores food habits would generally overestimate grasses, trees and shrubs, and underestimate the content of forbs. Therefore, we believe that the proportion of grass, shrub and trees may be slightly higher than the actual value in this study, while the actual proportion of forbs in the food composition is lower than the result by microscopic analysis. Despite this, microhistological analysis of feces is widely used in herbivorous diet studies for its ease of sampling and the same or even higher accuracy as gastric analysis (Chang et al. 2010). The fecal samples indicated that Alashan red deer fed primarily on shrubs and trees. The diet composition of blue sheep was dominated by shrubs and grass. The diet of the ungulates is influenced by food availability and weather conditions (Cornelis et al. 1999, Gebert & Verheyden-Tixier 2001). In addition, the features of the feeding habitat and interspecies competition can also influence the food niche (Bertolino et al. 2009). In winter, Alashan red deer selected mountain grassland dominated by *Stipa breviflora* and *Ajania fruticulosa*. Blue sheep selected mountain woodland steppe dominated by *Ulmus glaucescens* trees (Luo et al. 2009). Different habitat use resulted in the higher shrub intake by both ungulates. However, although Alashan red deer had a greater opportunity to feed on grass, the grass intake level was higher in blue sheep than in Alashan red deer (Fig. 4), which indicated that the diet of red deer represents the group of animals classified as "browsers" while the diet of blue sheep is typical of so-called "grazers" (Hofmann & Stewart 1972). The difference in body size between blue sheep and Alashan red deer may be an important reason for the diet partitioning, compared with blue sheep, trees are more accessible to larger Alashan red deer.

Hofmann (1989) considers that the distinct characteristic between grass and browse, caused difference feeding styles among herbivores specializing on either grass or browse. Grass has a higher proportion of cell wall material and available for cellulolysis by rumen micro-organisms. While browse is rich in cell contents and has a lower proportion of cell-wall material. In addition, the chemical difference in properties leading to large structural differences between grass and browse. The grass material consumed by ruminants tends to be long and fibrous in structure whereas the leaves of browse plants break down into small polygonous particles during mastication (Spalinger et al. 1993). Moreover, plant secondary metabolites are largely absent from graminaceous species but are generally abundant in forbs and especially browse species (Harborne 1988). Therefore, we suspect that the large difference in physical and chemical characteristics of vegetation result the difference in the composition of blue sheep and red deer, and there may develop physiological adaptations for them to their different diet type. Hofmann (1989) laid the groundwork for the debate over the different digestive strategies between browsers and grazers from aspect of reticulo-rumen size, retention time and passage rate, mean particle size escaping rumen, and so on. Duncan & Poppi (2010) summarized the various levels at which food processing by browsers and grazers might be different, and proposed that much attention should be paid to differences in post-absorptive metabolism of plant secondary metabolites.

Influences of the availability of different forage types among seasons are obvious. Contrary to the summer when food availability is richest, the tree category constituted 89.6 % of the Alashan red deer diet. In addition, grass constituted approximately 70 % of the blue sheep diet (Chang et al. 2010). However, in winter, the percentages of trees in the Alashan red deer diet and grass in the blue sheep diet declined to 24.8 % and 23.1 %, respectively. Compared with the mountain conifer forest, where red deer mainly occur in summer, there were fewer trees in the mountain grassland, so the proportion of trees in the Alashan red deer diet declined. According to the niche theory in ecology (Lack 1971), when sympatric species utilize the same resource in a similar way, the other resources used by them will be significantly different. Our study on the diet of sympatric ungulates, Alashan red deer and blue sheep, is correlated with this theory. When Alashan red deer and blue sheep used high proportions of shrubs, the contributions of tree and grass were significantly different (Fig. 4, Table 3).

Pinus tabulaeformis, *Populus davidiana* and *Ulmus pumila* accounted for 13.3 % of the diet of Alashan red deer, but *Ulmus pumila* was not the preferred food of Alashan red deer (Table 3). *Ulmus pumila* constituted 9.6 % of the sheep diet, but the value of it was negative. The selectivity of foods may be the results of nutritional requirements, the need to maximize protein intake and decrease fiber intake to increase digestibility (Tixier & Duncan 1997, Klaus-Hügi et al. 1999). Different plant species differ in protein and fiber contents (Klaus-Hügi et al. 1999), which also influences the choice by an animal. Therefore, further studies need to analyze the crude protein and fiber contents of foods to deeply understand the foraging strategy of the two ungulates in the winter.

This study provides evidence of food segregation between blue sheep and Alashan red deer. In the Helan Mountains, the availability and biomass of forage are low, especially in the winter. Even so, because of the difference in diet, there is less competition between them in terms of food.

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