

Comparison of foraging strategies and effects of the Wapiti and Siberian roe deer on Japanese yew

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Abstract

The foraging strategies of sympatric ungulates with similar ecological niches are important for understanding ecological niche differentiation, resource utilization, competition, and coexistence and for understanding the ecological impacts on plant communities in the ecosystem. The behavior of the wapiti (*Cervus elaphus*) and Siberian roe deer (*Capreolus pygargus*) foraging on Japanese yew (*Taxus cuspidata*) has affected its succession and renewal in the northeastern forests of China, which has become an urgent problem for the relevant departments. This study analyzed the foraging strategies of the wapiti and Siberian roe deer on Japanese yew from July 2021 to January 2024 using field investigations and infrared camera monitoring in the Muling National Nature Reserve, Heilongjiang Province, China. It was found that the wapiti and Siberian roe deer have different foraging strategies in terms of time, space, and behavior. Temporally, they both preferred to forage for the saplings of the Japanese yew during the winter season, the degree of overlap in foraging rhythms was medium ($D_{hat1}=0.67$), and the diurnal foraging activity index (DRAI) of the wapiti was larger than that of the Siberian roe deer. Spatially, the suitable foraging habitat of the Siberian roe deer was twice that of the wapiti, and their overlap was low in the location and direction of saplings and the distance of the seed tree. Behaviorally, the foraging intensity of the wapiti was heavy, and Siberian roe deer was low. Foraging reduced the average primary branch height, number of new branches, and length of lateral branches of saplings, and the influence of the wapiti was significantly greater than that of the Siberian roe deer. This study provides a scientific basis for solving the conservation and management problems of the deer animals foraging on Japanese yew and contributes to further understanding of the competition-coexistence mechanism of sympatric species.

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Keywords: *Cervus elaphus* ; *Capreolus pygargus* ; *Taxus cuspidata* ; foraging strategy; Kernel Density Estimation; Maximum Entropy Model

INTRODUCTIONThe foraging strategy of ungulates is a key link between primary production and food webs (Elsayed and Din, 2019). It influences the structure and trends of changes in the biome (Shoener, 1987; Wang et al., 2001), species distribution, resource utilization, and population dynamics (Heleno et al., 2012; Tylianakis et al., 2010; Zanni et al., 2021), and plays a major role in maintaining structural integrity and balance (Ge et al., 2012; Kasiringua et al., 2020; Wang et al., 2019a). Studies have found that the foraging of ungulates affects the growth of plants, seriously leads to the failure of renewal, and has a negative effect on interspecific competition (Bödeker et al., 2021; Konôpka et al., 2021; Kamler et al., 2010; Klopčič et al., 2010; Vacek, 2017), and spruce (*Picea abies*) seedlings grow slowly when foraged by roe deer (*Capreolus capreolus*) (Bergquist et al., 2003). Faced with this situation, plants will develop defense mechanisms; for example, sheep (*Ovis aries*) reduce their intake when the flavonoid content of their food is too high (Sun, 2008). Interactions between sympatrically distributed animals and plants have been a classic proposition in evolutionary ecology, and the ecological impacts produced by animals on plants have been a popular topic of discussion in conservation biology and biodiversity conservation (Feng, 2022). In northeastern China, Japanese yew (*Taxus cuspidata*) is a tertiary relict plant (Liu, 2007), which is a wild and endangered class I national protected plant. The wapiti (*Cervus elaphus*) and Siberian roe deer (*Capreolus pygargus*) are both protected animals and are the main prey of the Amur tiger (*Panthera tigris*) and Amur leopard (*Panthera pardus orientalis*). The wapiti, Siberian roe deer, and Japanese yew are, therefore, all the main protection species that need to be focused on for the protection and management of national parks and nature reserves. Previous studies have found that both the wapiti and Siberian roe deer foraged on Japanese yew under environmental stresses such as low temperatures, snow cover, and lack of food resources in winter (Feng, 2022). The Japanese yew accounts for 13% of the winter food composition of the wapiti, which leads to significant damage to the saplings (Zhu et al., 2019). As a result, their number and distribution range has declined sharply (Diao et al., 2020; Yang, 2018). On the other hand, the number of ungulates, such as the wapiti, is also decreasing in reserves due to human activities such as long-term forest logging, illegal poaching, and road construction in the past (Dixon et al., 2021; Sarula et al., 2019). Protecting wildlife like the wapiti, without affecting the succession and renewal of the Japanese yew forests has become an urgent problem for the management department of nature reserves. This study, therefore, analyzed the impacts of these two ungulates on Japanese yew by comparing their temporal and spatial strategies, and behavioral characteristics, to provide a scientific basis for solving the problem of their protection and management. The results not only contribute to further understanding of the competition-coexistence mechanism of sympatric species but also enrich the study of animal and plant interaction and co-evolution.

MATERIALS AND METHODS
2.1 Study areaThe study area is located in the Muling National Nature Reserve, in the southern part of the Laoyeling, in the northern part of the Changbai Mountain (130°00'–130deg28'E, 43deg49'–44deg06'N). The south is bordered by the Tianqiaoling Forestry Bureau of Jilin Province, the east is bordered by the Suiyang Forestry Bureau of Heilongjiang Province, and the west, north, and northeast are connected with the Gonghe Management Office, Shuangning Forest Farm, and Yangmuqiao Forest Farm of Muling Forestry Bureau, with a total area of 356.48 km² (Feng, 2022). The

mountains in this area are low, with altitudes ranging from 500m to 900m, and the landforms are distributed in bands. The climate is the typical temperate continental climate with an average annual temperature of approximately -2. The rainy season is short, and precipitation is concentrated, with an average annual rainfall of 514 mm and an annual frost-free period of 130 d (Tian et al., 2022). The forests in the reserve are primarily coniferous, broad-leaved forests, mixed coniferous and broad-leaved forests, and thickets, with 839 plant species belonging to 113 families and 373 genera. The dominant species are red pine (*Pinus koraiensis*), purple linden (*Tilia amurensis*), and red-barked spruce (*Picea koraiensis*). There are 42 vertebrate species belonging to six orders and 14 families, represented by the Amur tiger, Amur leopard, wapiti, sika deer (*Cervus nippon*), Asian black bear (*Ursus thibetanus*), and wild boar (*Sus scrofa*).

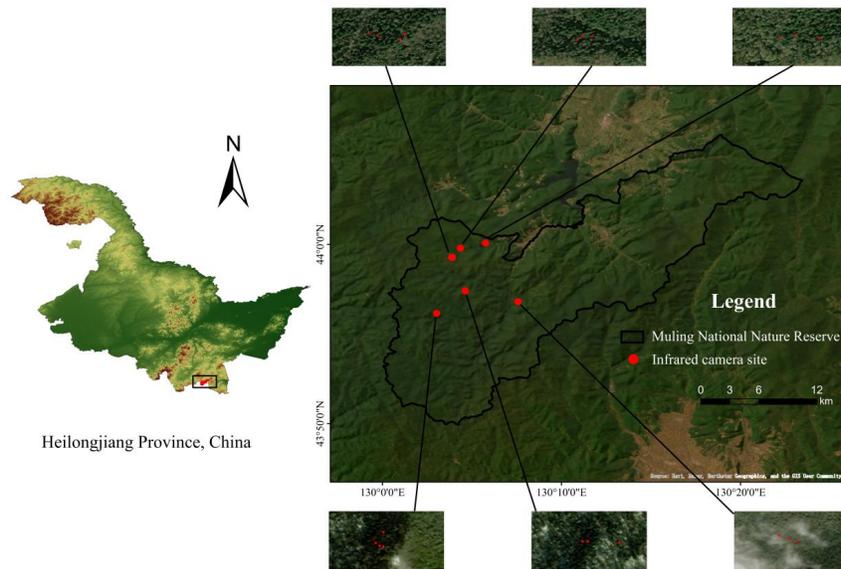
2.2 Methods

2.2.1 Field investigation

Areas with a relatively concentrated distribution of Japanese yew were selected for field investigations every winter from 2021 to 2024. The saplings were divided into foraging and control groups. During the survey, the saplings that were foraged on were labeled and their height, length of lateral branches, number of branches foraged, total number of branches, and information about the surrounding environment were recorded. Normal saplings were selected as controls in the corresponding areas, and the plant height and number of branches were recorded. The height of the primary branch growth, the number of new branches, and the length of lateral branch growth for each sapling were recorded every summer from 2021 to 2024.

The footprints and foraging traces were combined to distinguish saplings foraged by the wapiti or the Siberian roe deer. A total of 1947 foraging traces were observed. Among them, 1,235 were of the wapiti and 712 of the Siberian roe deer.

2.2.2 Infrared camera monitoring



Twenty infrared cameras were installed in the study area (Figure 1). The cameras were placed 30–90 cm above the ground. The height can not only capture the entire saplings but also obtain a full shot of the ungulates browsing them. Camera parameter settings were as follows: photo (three photos) + video (15s). After the camera was installed, the weeds in front of the shooting area were removed to prevent misshooting and blocking the lens (Zhao et al., 2020). The monitoring period lasted 2.5 years.

FIGURE 1 Location of the Muling National Nature Reserve in northeast China

2.2.3 Environment variable data

According to research needs, environmental variables are divided into four categories:

- (1) Land-use types: Scrub, evergreen coniferous forest, deciduous coniferous forest, mixed coniferous forest, deciduous broad-leaved forest, and farmland, were obtained using Landsat 8 remote sensing image interpretation.
- (2) Anthropogenic disturbance factors: Rural roads and forest trails were obtained by vectorization in ArcGIS 10.8 software using forest topographic maps.
- (3) Topographic factors: Elevation, aspect, and slope direction were obtained by mask extraction of a 30m resolution digital elevation model (DEM) using the spatial analysis module of the ArcGIS 10.8 software.
- (4) Water sources: Streams were obtained by vectorization in the ArcGIS 10.8 software using forested topographic maps.

2.2.4 Data analysis

2.2.4.1 Foraging rhythms of the wapiti and Siberian roe deer

Taking the average time of sunrise and sunset of the local year as the demarcation, the day was divided into day and night, with reference to the local climate. May to October was classified as the warm season, and November to April was classified as the cool season. The daily and annual foraging rhythms were analyzed in this study by using the kernel density estimation method (Chen et al., 2019) with the overlap package and activity package of R. Delta4 values were selected for calculations when both the sample sizes compared were ≥ 75 , and the Delta1 values were selected when the size was < 75 . In addition, the degree of temporal overlap between the activities of the two species was classified as high overlap when $\Delta > 0.75$, medium overlap when $0.50 < \Delta < 0.75$, and low overlap when $\Delta < 0.50$ (Monterroso et al., 2014).

The foraging patterns of the wapiti and Siberian roe deer on Japanese yew saplings were analyzed by calculating the relative abundance index for the day and night (D_{RAI}), month (M_{RAI}), and season (S_{RAI}) (Liu et al., 2022). The formulas were as follows: $D_{RAI} = (D_{ij}/N_i)100$, $M_{RAI} = (M_{ij}/N_i)100$, and $S_{RAI} = (S_{ij}/N_i)100$. D_{ij} denotes the number of independent foraging occurrences of species i in the time period j (both day and night), M_{ij} denotes species i in the time period j (annual), and S_{ij} denotes species i in the time period j (cold and warm seasons).

2.2.4.2 Foraging habitats suitability prediction

The systematic resampling method was used to analyze the points to avoid spatial autocorrelation caused by too close a distance between them, to standardize the data of the environmental variables, and to conduct Spearman correlation analysis with SPSS 19.0. The selected points and environmental variables were used to predict suitable foraging habitats; 75% of the points were used for the construction of the model, 25% were used for validation, and the model was run for 10 cycles. This was evaluated using the cutting method and its comprehensive contribution. The evaluation criteria used were as follows: AUC range from 0.5 to 0.6 was considered as failing, from 0.6 to 0.7 was poor, from 0.7 to 0.8 was fair, from 0.8 to 0.9 was good, and from 0.9 to 1.0 was excellent. All operations were performed using MaxEnt 3.3.

The suitable habitats for the Japanese yew and ungulates were reclassified using ArcGIS 10.8. The average value of the maximum training sensitivity and specificity after 10 modes of operation was used as the threshold for the distribution of suitable foraging habitats (Li, 2022). The habitats of Japanese yew were divided into two levels—0–0.153 were unsuitable habitats, and 0.153–1 were suitable. The foraging habitats of the ungulates were divided into three levels—0–0.55 were unsuitable foraging areas, 0.55–0.75 were generally suitable and 0.75–1 were suitable.

2.2.4.3 Foraging characteristics of the two ungulates and their effects on saplings

Taking Japanese yew as the center, the study area was extended in eight directions—east, west, south, north, northeast, southeast, northwest, and southwest. The sapling points were recorded along with the information on whether foraging occurred or not within 50m in each direction. A total of 71 points were collected and plotted using the `fmsb` package in R. The characteristics of ungulates foraging on saplings were summarized using infrared camera data. The t-test and Kolmogorov-Smirnov test were used to analyze the following: (1) whether the monthly relative abundance index of the two ungulates foraging for young trees was different; (2) whether there was a difference in the distance between the two ungulates foraging on the young tree and the mother tree; and (3) whether the growth height of the main branches, the number of new branches, and the growth amount of lateral branches after foraging by the two ungulates were different. All operations were performed using R 4.2.1.

RESULTS 3.1 Foraging time strategies of the two ungulates The diurnal foraging activity index of the wapiti was higher than that of the Siberian roe deer ($D_{RAI}=92.3\%$), and the nocturnal feeding activity index of the Siberian roe deer was also higher. There were two peaks in the diurnal activity rhythms of the wapiti foraging on saplings, which were from 7:00 to 8:00 and from 14:00 to 15:30, with the overall shape of an "M," and the size of the peaks varied. There were three peaks for the roe deer, from 6:30 to 9:30, 15:30 to 18:30, and 24:00 to 2:00, with the entire peak being wavy. In terms of the degree of overlap, the highest overlap indices were observed at 7:00 and 15:00, and temporally the degree of foraging was moderate ($D_{hat1}=0.67$) (Figure 2).

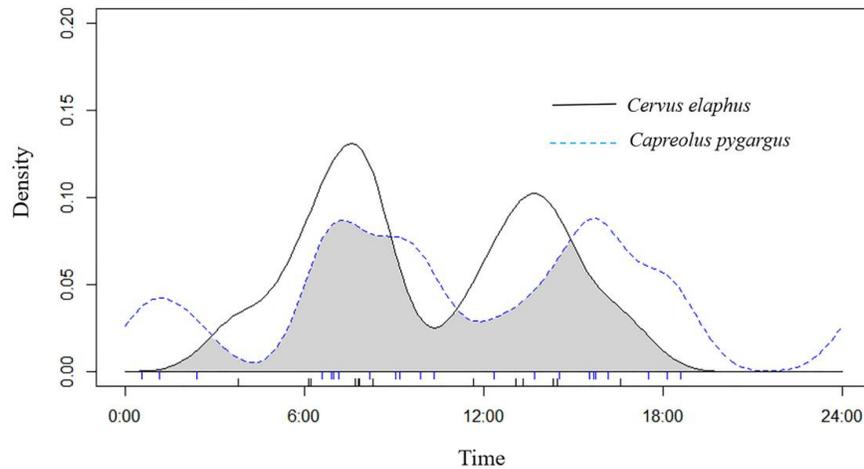


FIGURE 2 Diurnal foraging rhythm of two species of deer Japanese yew saplings

The monthly relative abundance index (M_{RAI}) of wapiti foraging demonstrated an unimodal trend of first increasing and then decreasing, reaching its peak in February (38.5%), which was approximately twice that of roe deer (22.8%), whereas there was no obvious pattern for the latter as a whole (Figure 3). This indicated that the two ungulates foraged on Japanese yew saplings seasonally. The results demonstrated that there was a difference in the relative multiplicity index (S_{RAI}) of foraging between them in the cold season ($p < 0.05$).

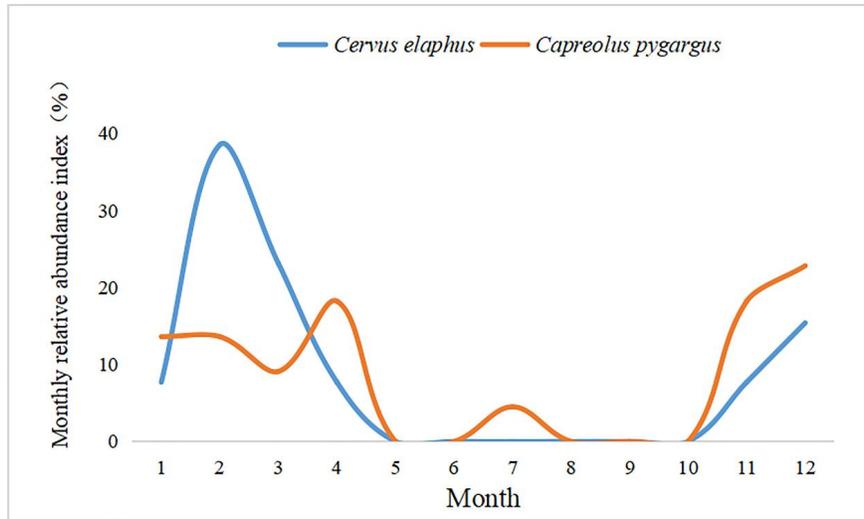


FIGURE 3 Monthly relative abundance index of two species of deer foraging on Japanese yew saplings

3.2 Spatial strategies of foraging in two deer species

3.2.1 Habitat suitability of the Japanese yew

The result of the receiver operating characteristic curve (ROC) demonstrated that the AUC was 0.921 ± 0.035 , and the prediction reached the "good" standard. The habitat suitability analysis showed that the area unsuitable for the study was 292.71 km², which is 82.11% of the total area, and the suitable area was 63.77 km² accounting for 17.89% of the total area (Figure 4).

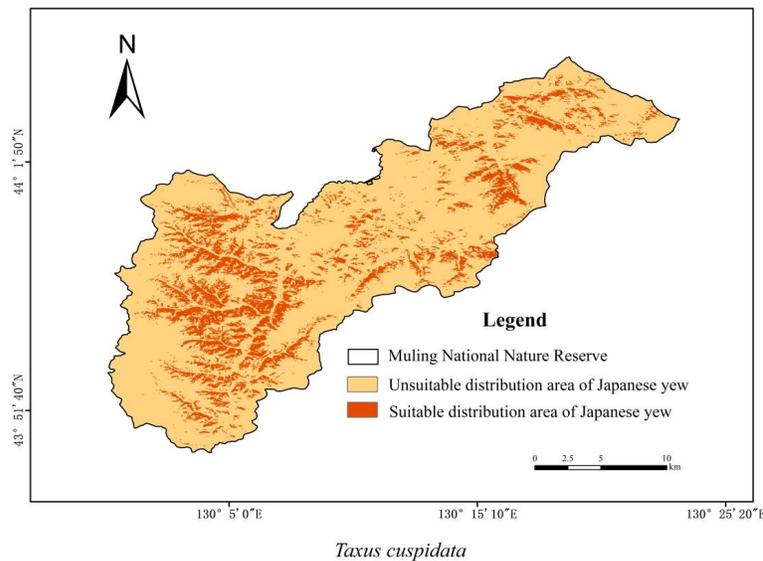


FIGURE 4 Distribution map of habitat suitability for Japanese yew

3.2.2 Suitable foraging habitats of the two ungulates

The results of ROC showed that the AUC was ≥ 0.8 , reaching the "good" standard (Table 1). This indicates that the MaxEnt model was able to predict the potential foraging distribution area.

TABLE 1 MaxEnt results of Red Deer and Siberian Deer Foraging on Northeast Taxus Habitat

Species	Feeding points	Spatial post-screening loci	AUC	Standard Deviation
Wapiti	69	17	0.894	0.035
Siberian roe deer	82	23	0.907	0.026

The model results demonstrated that vegetation type was the most beneficial environmental factor in predicting suitable foraging habitats for the two ungulates, and the contribution rate of the wapiti was 50%, whereas that of the Siberian roe deer was 40.4%. Among these, evergreen broadleaf and mixed conifer forests had the greatest impact, whereas deciduous broadleaf forests had the least. Slope direction (21.9%) and altitude (13.9%) were the key factors affecting the foraging habitat of the wapiti, followed by aspect (13.9%), distance from road (4.8%), and distance from water (3.6%). Slope direction (23%) and slope (21.5%) were also key factors for Siberian roe deer; altitude (9.4%), distance from roads (3.3%), and distance from water sources (2.4%) contributed the least (Table 2).

TABLE 2 The Importance of Environmental Variables

Environmental variables	Wapiti	Siberian roe deer
Vegetation types	0.500	0.404
Aspect	0.219	0.230
Slope	0.139	0.215
Altitude	0.058	0.094
Distance from road	0.048	0.033
Distance to water source	0.036	0.024

The prediction results demonstrated that the wapiti foraged on saplings at an altitude of 700 m, with slopes of 20–30 degrees, aspects to the north, and far away from the road (2000 m) and the water source (3500 m) in the reserve. The foraging habitat suitability gradually increased with increasing distance from the evergreen coniferous forest and mixed coniferous forest. However, the Siberian roe deer preferred an altitude of 650 m, with slopes of 15–20 degrees, and the other factors were similar to the wapiti (Figure 5).

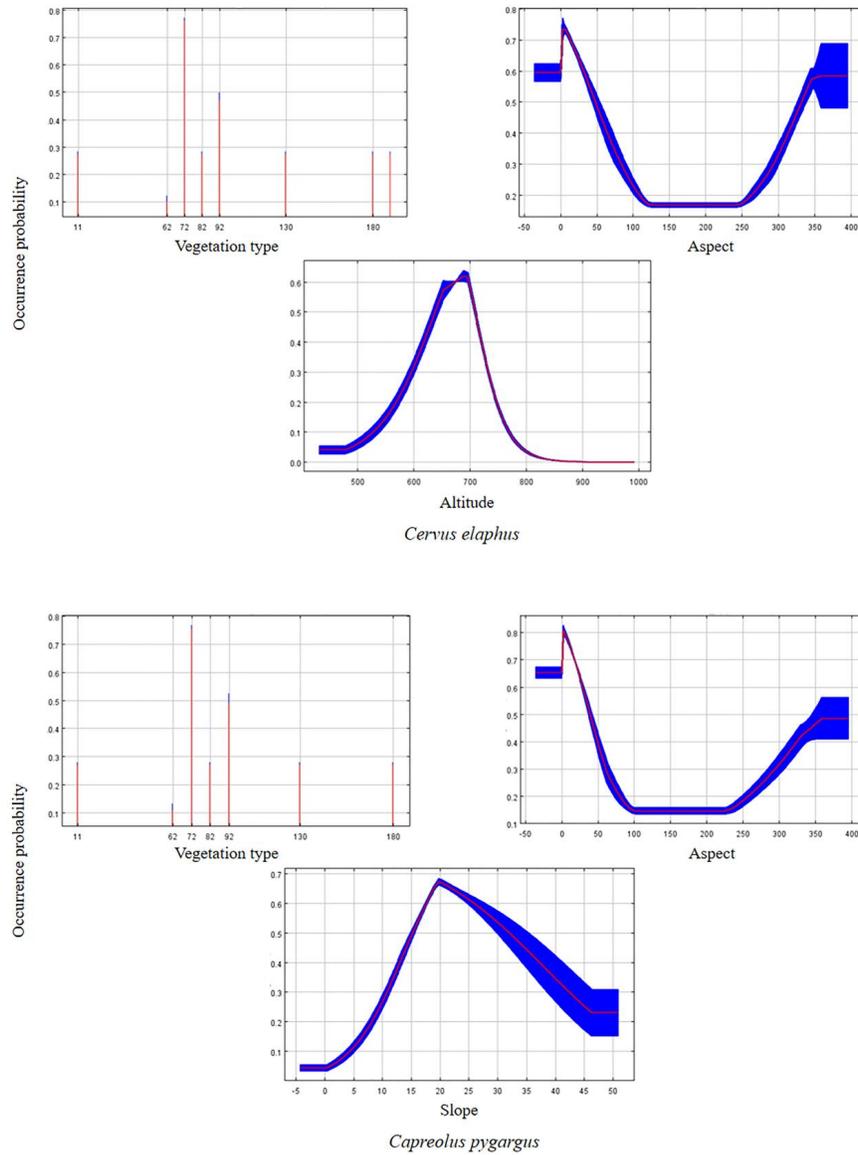


FIGURE 5 Response curves of major environmental variables

Note: Among the vegetation types, 11 are covered by herbaceous plants; 62 is a deciduous broad-leaved forest; 72 is an evergreen coniferous forest; 82 is a deciduous coniferous forest; 92 is a mixed coniferous and broad-leaved forest; 130 is grassland; 180 is a wetland

The suitability analysis of foraging habitat demonstrated that the area of suitable, average, and unsuitable habitats for the wapiti foraging in the study area was 0.98 km², 5.6 km², and 57.1 km², accounting for 1.53%, 8.78%, and 89.69% of the total area of the study area, respectively. The areas of suitable, average, and unsuitable habitats for Siberian roe deer foraging were 1.69 km², 6.5 km², and 55.67 km² in that order, accounting for 2.65%, 10.05% and 87.30% of the total area of the study area, respectively (Figure 6) (Table 3).

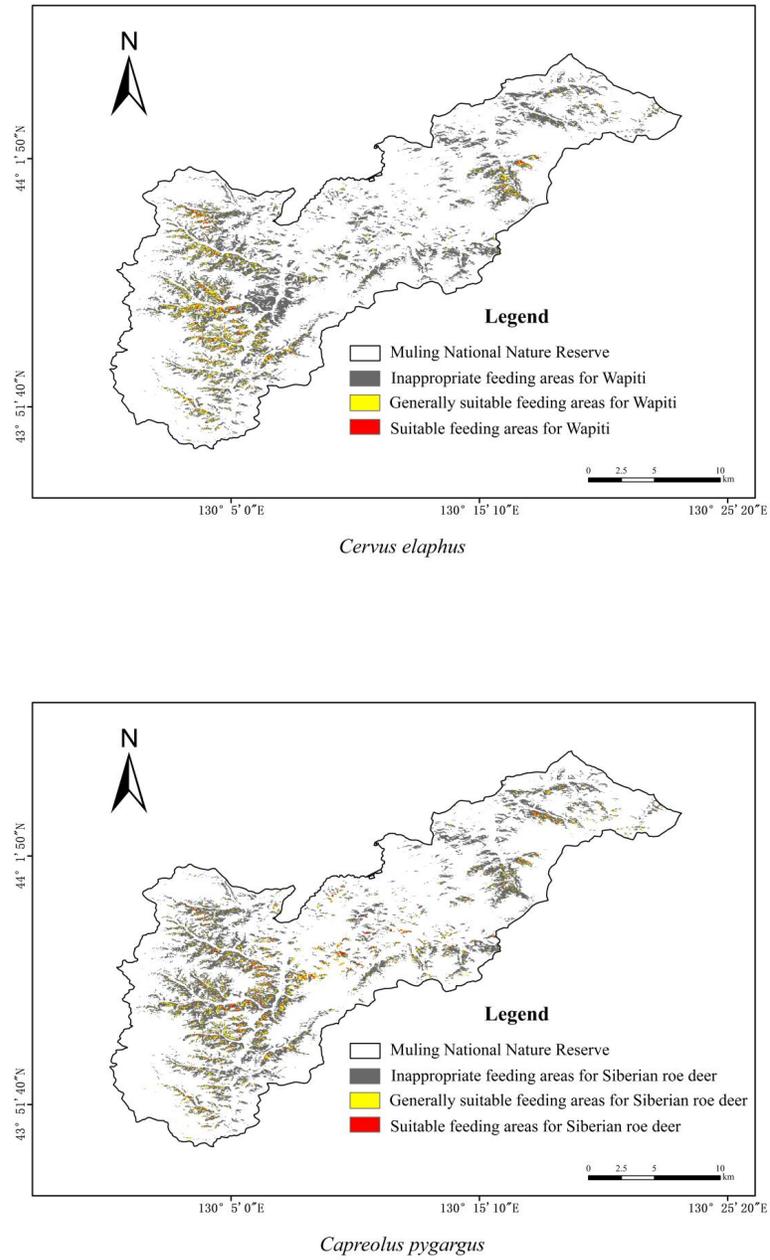


FIGURE 6 Suitable distribution map for foraging on saplings of Japanese yew

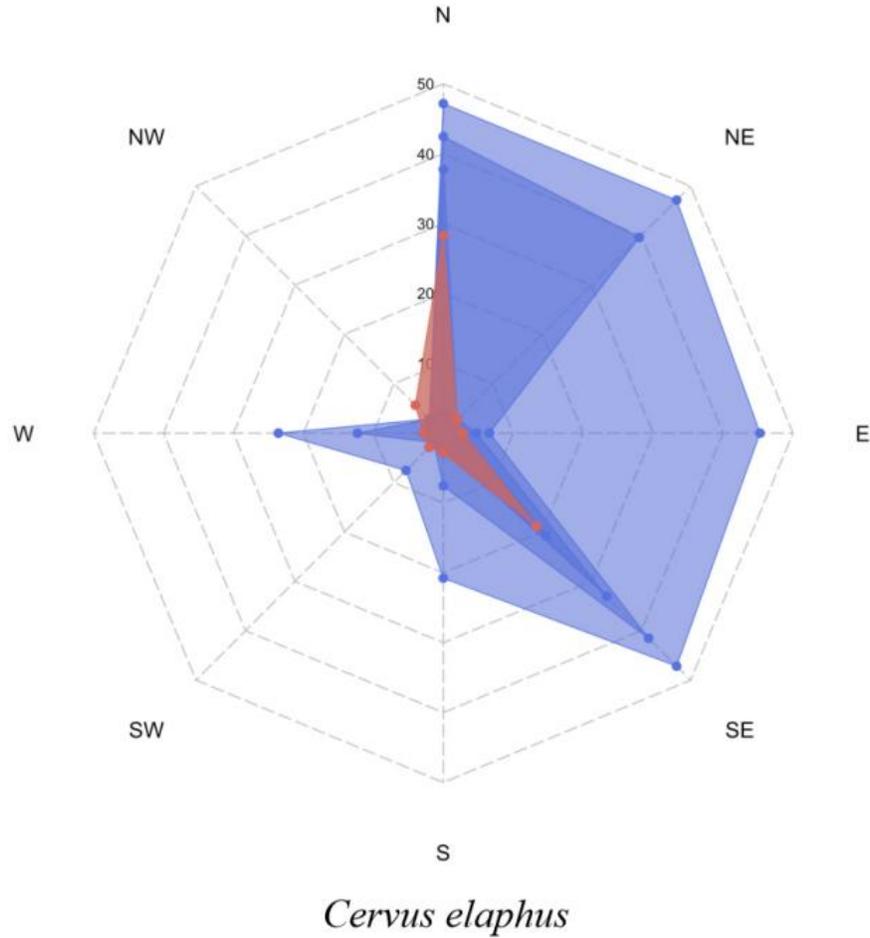
TABLE 3 Habitat suitability analysis of two species of deer foraging on Japanese yew

Species	Indisposition	General suitability	Suitable
Wapiti	57.1km ²	5.6 km ²	0.98 km ²
Siberian roe deer	55.67 km ²	6.5 km ²	1.69 km ²

3.3 Characteristics of foraging behavior of the two ungulates

3.3.1 Foraging distance

The wapiti preferred to forage on saplings located close to mature trees, ranging from 1.5 m to 30 m in the northwest and 295° to southeast 140°. The Siberian roe deer presented some variability ($p < 0.05$); their feeding distance was longer, ranging from 8 m to 50 m and its range was wider from 315° to south 180° (Figure 7).



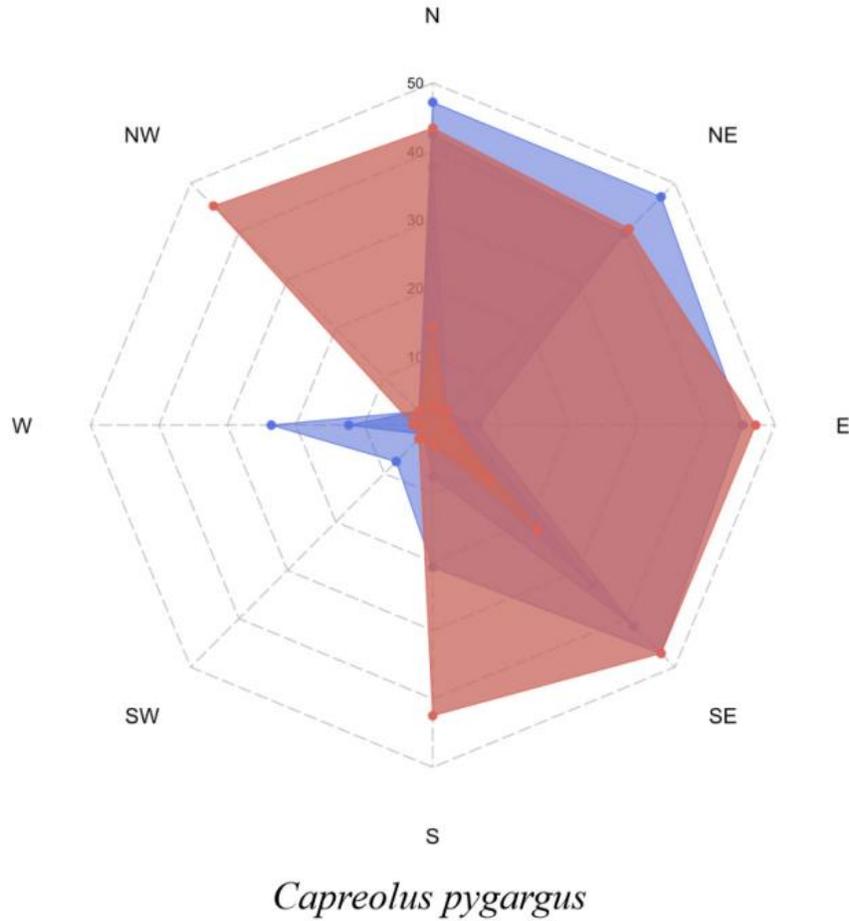


FIGURE 7 Relationship between the distance between foraging Japanese yew saplings and mother trees

Note: The red is the foraging area, and the blue is the area where Japanese yew grows

3.3.2 Foraging intensity

According to the infrared camera monitoring and field investigation results, the **Siberian roe deer browsed lightly (10%–20%) on the saplings**, foraging on ports 1–3 cm from the newborn lateral branch of the current year with inconspicuous traces and small foraging ports. **The forage intensity of wapiti was high (70%–100%)**, and most of the branches and leaves and the foraging ports were not neat (Figure 8).

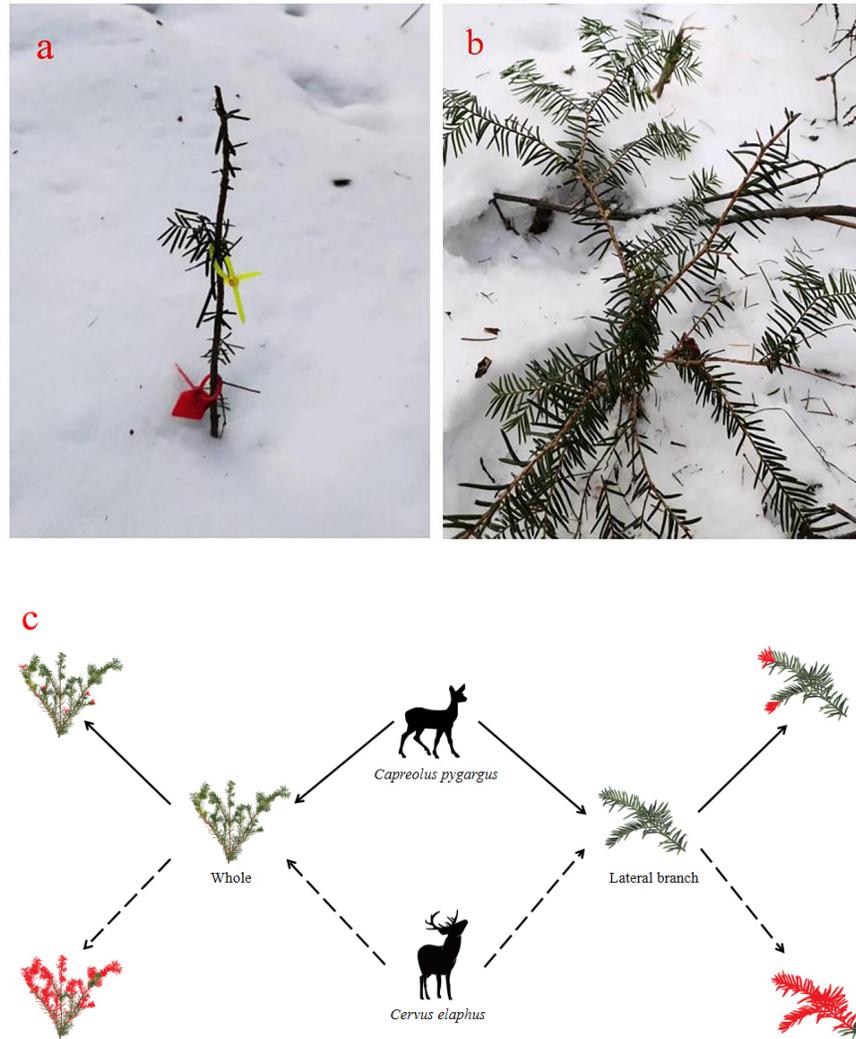


FIGURE 8 The degree to which two species of deer animals forage on Japanese yew saplings (a: wapiti; b: siberian roe deer ; c: red represents the foraging part)

3.4 Effects of foraging by two species of deer on Japanese yew saplings

There were some differences ($p < 0.05$) in the average growth height of the main branches, number of new branches, and length of lateral branches between the two ungulates after foraging on the saplings. All the above variables decreased after foraging. There were significant differences between the wapiti and control groups ($p < 0.05$), while the differences were not significant between the **Siberian roe deer** and control group ($p > 0.05$) (Figure 9). These results indicate that the influence of the wapiti foraging on Japanese yew saplings is much greater than that of the **Siberian roe deer**.

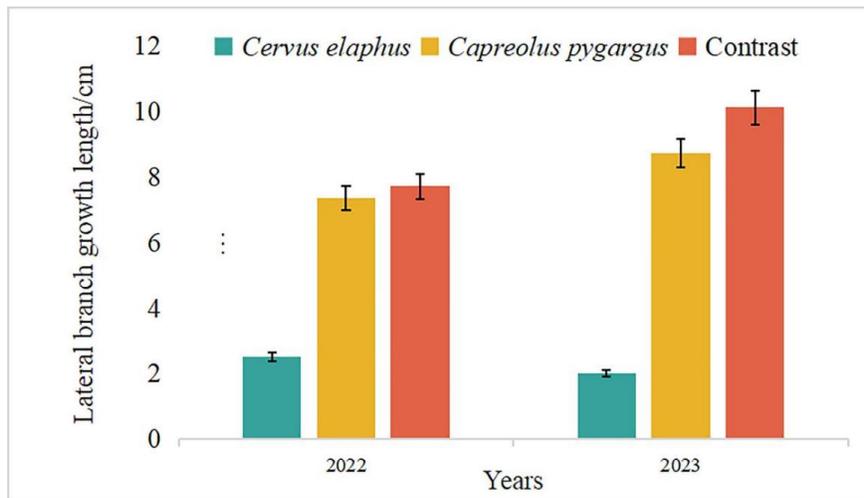
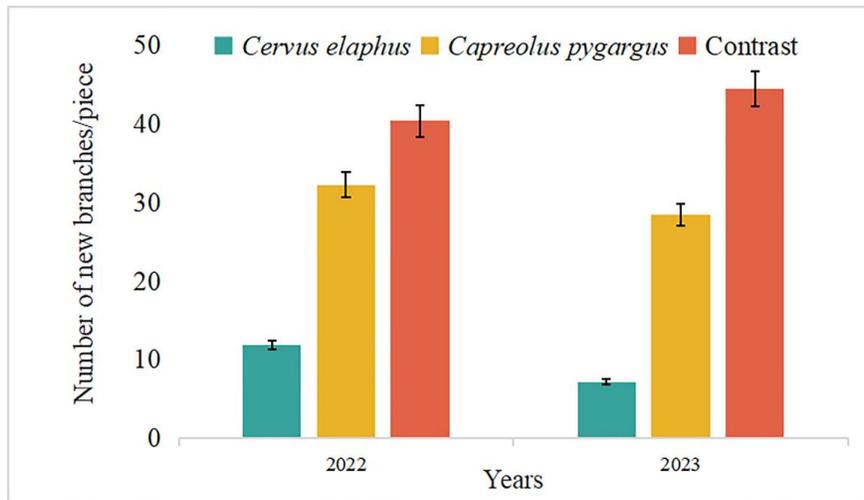
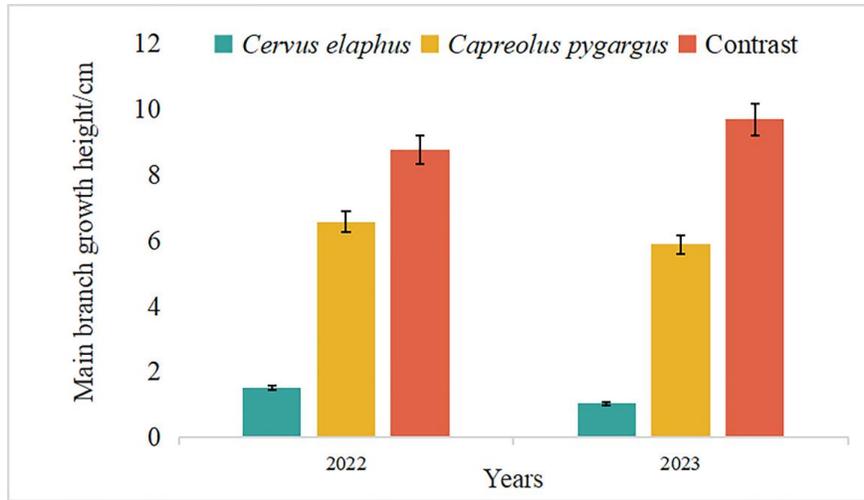


FIGURE 9 Effects of foraging on saplings of Japanese yew

DISCUSSION4.1 Temporal strategies for foraging on the Japanese yew in two deer species In the present study, infrared camera detection revealed differences in the temporal strategies of two ungulates foraging on Japanese yew saplings. The daily activity rhythms of the wapiti presented two peaks throughout the year. However, there were significant differences between them, with a short duration but high density of foraging activity in the early morning, and a lower density but longer duration in the afternoon. This is similar to the results of Kamler’s study (Kamler et al., 2007), which may be due to temperature extremes in winter; their peak daily activity usually occurs during the warmer period before sunset. The Siberian roe deer foraged both day and night, but there was a large nocturnal difference between the two ungulates, which may be a competitive strategy. The activity patterns of species change with the season, demonstrating some plasticity in achieving coexistence by reducing temporal overlap with competitors during foraging activities (Monterroso et al., 2014; Romero-Muñoz et al., 2010; Rheingantz et al., 2016). The foraging frequency during the warm season was significantly lower than that during the cold season. The possible reasons are as follows: (1) The temperature is suitable and food resources are abundant in the summer. They can replenish nutrition with other types of green plants, thereby reducing their foraging in Japanese yew. (2) In summer, the level of concealment in the forest is higher, which is conducive to avoiding the enemy and does not require a higher intensity of foraging activity other than reproductive needs. (3) Japanese yew is one of the few green plants grown in winter that has higher energy, protein, and carbohydrate contents than other plants (Huang, 2015).

4.2 Foraging spatial strategies of the two ungulates The population size and distribution of ungulates are inextricably linked to plant resources (Wang et al., 2019b), and they often face trade-offs between high-quality food and food abundance in winter, which is related to the spatial scale (van Beest et al., 2010). The wapiti and Siberian roe deer have similar ecological niches. They had different foraging strategies in space in the current study, which may be due to two reasons. (1) The population size of **Siberian roe deer is larger than that of the wapiti, and their reproductive capacity is better.** (2) The foraging range of **the Siberian roe deer** was large. The predicted results demonstrated that the vegetation type, which is one of the main sources of competition, was the main factor influencing the suitability of foraging habitats. Their occurrence probability was negatively correlated with distance from the coniferous forest distribution. This is similar to the results of Tian Xinmin et al. in their 2022 study on the distribution number and habitat suitability of the wapiti populations in the Muling forest area (Tian et al., 2022). The response curves of the environmental variables demonstrated that suitable foraging areas are weakly avoided roads and farmland and are insensitive to human activities. This is because the Japanese yew is distributed far from roads and residential areas, and the frequency of human activity is low. Different habitat selection and utilization strategies are, therefore, key factors that promote the distribution of sympatric species (Liu et al., 2020; Xia et al., 2019). Populations with similar ecological niches tend to select different habitats to reduce competition and ensure survival and reproduction. It may be concluded that the relevant departments should target the management of the habitat of the Japanese yew population and strengthen the in situ conservation of scattered distribution saplings to create favorable conditions for the recovery of the population in the Muling Forest area.

4.3 Foraging characteristics of two ungulates and the effects on saplings In the long term, vegetation system dynamics may depend on seedling replenishment. A study of alpine plant communities found that trampling and foraging by large and small herbivores negatively affected plant communities (Feng et al., 2022). Zhou found that a few individuals in the regeneration layer were not conducive to the development and recovery of the population when he studied the resource characteristics of the Japanese yew population (Zhou et al., 2004). One reason for this is animal foraging (Diao et al., 2020; van Beest et al., 2010; Yang, 2018). In a study on the diet of the wapiti, it was found that Japanese yew accounted for a relatively large portion of its food composition and that Siberian roe deer and sika deer also consumed a certain amount of Japanese yew (Feng, 2022; Huang, 2015; Zhong, 2020; Zhu et al., 2019). The extent to which wapiti forage for Japanese yew belongs to heavy foraging. In addition, the wapiti looks for fallen trees, forage for several branches and leaves, and forage on as many mature tree branches as possible, which were found to be 3 m from the ground. Bergquist 2003 found that the foraging of roe deer (*Capreolus capreolus*) has impacted the growth of saplings, which accumulate over time. Three consecutive years of foraging reduces growth height by one year (Bergquist et al., 2003; Olofsson et al., 2004). This current study

received similar results. The average growth height of the main branches, number of new branches, and length of the lateral branches of the saplings decreased after foraging by both ungulates. The damage degree of the wapiti was much greater than that of the Siberian roe deer. Saplings that were heavily foraged on by wapiti branched out from the root. This may be due to the strong selectivity of wapiti in winter, making it difficult for saplings to grow beyond their foraging height. It may be considered that foraging by large herbivores affected the growth and survival rate of the saplings, causing damage. Considering their special biological characteristics, such as slow growth, poor stress resistance, and low survival rates (Yang, 2018), foraging by ungulates aggravates this phenomenon, which is not conducive to normal growth and may affect the natural regeneration of populations. In the short term, there are obvious differences between the two ungulates in foraging and the impact on saplings, which have a certain negative impact on their growth; however, the impact on succession and renewal needs further study.

CONCLUSIONThe wapiti and Siberian roe deer reduce or avoid direct competition for their resources through different foraging strategies in the Muling National Nature Reserve to ensure their nutritional requirements in the harsh winter environment. Temporally, they also preferred to forage for Japanese yew saplings during the cool season, with a moderate degree of overlap. Spatially, suitable foraging habitats of the Siberian roe deer were approximately twice those of the wapiti, and their overlap was less in location, direction, and distance from mature trees. Behaviorally, they have different foraging intensities, and the influence of wapiti on the growth of saplings is much greater than that of the Siberian roe deer. It is, therefore, recommended that the local conservation management department take necessary measures to restrict the wapiti from foraging on the saplings of the Japanese yew to protect the saplings in the scattered distribution. It is further recommended to provide favorable conditions for the succession and renewal of the forests of Japanese yew without affecting the habitat activities of the wapiti and the normal recovery of the trees to maintain the stability of the forest ecosystems and biodiversity of the region.

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Conflict of interest statement

The authors declare no conflict of interest.

Data availability statement

The relevant data of this paper can be found in the supporting materials.