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DIFFERENCES IN FEEDING STRATEGY OF LARGE HERBIVORES AND THEIR IMPACT TO VEGETATION

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Summary: We studied the distribution, impact on vegetation and composition and quality of diets of red deer and roe deer. The aim of the study was to analyze the feeding strategies of the ungulate species in mountain habitats with limited food supply and to deduce implications for their management. (1) Botanic composition of the diets was influenced by the animals' foraging specialisation and by food availability. Red deer ate grasses on the ridges in the growing season while forbs and browse were present in substantial amount in their diet at lower altitudes. (2) The diet quality was higher in general in roe deer than in red deer but during late winter the roe deer consumed the diet based on spruce needles of very low quality. The quality of red deer diet was lower in the ridge site than at the valley where the food supply was more diverse. Browsing of ungulates strongly influenced the rowan.

Key words: deer, diet, diet quality

Introduction

One of those serious problems the forest management in Central Europe has to deal with is the browsing impact of free-living herbivores which often limits the regeneration of the forest [1, 2, 3]. The natural relations of herbivore populations are impaired and ruminants often inhabit sites of sub-optimal food supply where some of the important food sources may be limited or even absent; sometimes they share their habitat with one or more of the introduced species and the total population density of herbivores is then close to the carrying capacity of the environment. Feeding behaviour of herbivores therefore causes great direct losses in forestry revenues in the form of damaged trees, which is only partially compensated by the income from game management [4, 5, 6]. Elimination of some attractive woody species induce further indirect losses that are difficult to quantify, from increased costs used for stand regeneration, longer time needed to achieve established plantations as well as worse immunity of forest stands to biotic and abiotic factors [7, 8, 9, 10, 11]. In this context the overabundance of herbivores can be defined as a condition where herbivores are causing local extinction of native plant species [12]. Such situation has developed in the most localities in the Czech Republic where red deer (*Cervus elaphus*) is present. The objective of this paper is to summarize the feeding strategies of the red deer, roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) in two different environments: 1. in the area of subalpine meadows on mountain summits; 2. in the area of secondary spruce stands at the foot of the mountains; and to evaluate their position in mutual competition for food in the habitat with limited food resources. We have tested the following hypotheses: 1) the structure of diet of individual species is in accordance with their expected diet corresponding to the respective feeding type; 2) concentrate selectors (roe deer) will prefer the high-quality components of food supply than intermediate type (red deer, chamois); 3) species that are able to effectively utilize the food sources of lower quality (red deer, chamois) will be better in adapting to habitat with prevalence of grasses than roe deer.

Material and Method

Study site

The data were collected in the northeast of the Czech Republic (the Jeseníky Mts. and the Králický Sněžník Reserve). The altitude ranges from 800 to 1400 m a.s.l. and the climate is characterized by long and severe winters with high snow cover. The proportion of Norway spruce (*Picea abies* L.) is about 98%, European beech (*Fagus silvatica* L.) only 0.5% and rowan (*Sorbus aucuparia* L.) 0.2%.

Forest stands in the lower parts of the study area have been extensively changed during the past 400 years and Norway spruce now comprises about 95 % of trees. The dense canopy layer reduces understory biomass to minimum, so the suitable food supply for herbivores is limited only to clear-cuts (about 10% of the area, part of them is fenced). Stands in the highest locations are mostly open with abundant herb layer with grasses and blueberry (*Vaccinium myrtillus* L.). The food resources for herbivores are evenly distributed and more abundant than in lower parts of the study area.

Methods

The study was carried out during two years 2004 and 2005. During this time data about distribution, density and browsing impact were collected. Data from sampling plots were collected in both years in three main seasons: 1.

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spring – after snow melting; 2. mid-summer – maximum of herb biomass; 3. autumn - end of vegetation growing season. In spring it was necessary to visit ridge and top localities about three week later then foothill localities due to different time of snow melting.

Distribution and density of herbivores
We used the faecal standing crop method (counting of pellet groups with unknown accumulation period) which is cost effective with sufficient precision [13] and was successfully used in similar habitats [14]. Transects were 2 m wide and placed randomly through the monitoring plot in both types of stands (old forest, clear-cut), making sure that transects did not follow deer pathways. Transects were not marked (at next visit were randomly chosen again). The number of pellet groups was recorded each 10 m of transects. The total length of transects varied from 400 to 600 m per plot so they covered at least 12.5 % of the individual monitoring plot.
Density of species was estimated using the following formula: $D\ [ind./km^2] = n*106/(S*t*f)$, where n is the number of pellet groups found on the plot, S is the size of the plot in m^2, t is the time (in days) of plot exposure and f is the defecation rate of the respective species. We used defecation rates of 19 groups for red deer and 14 groups for roe deer per day respectively [13]. The age of individual pellet group we estimated from the appearance of pellets. We applied experiences with pellet group decomposition in similar conditions [14] and counted only groups with estimated age < 30 days.

Herbivore browsing
Intensity of shoot browsing was monitored at the same monitoring plots, which were used for density statement, at three tree species: spruce, beech and rowan in spring (winter browsing) and in autumn (summer browsing). These are the most abundant species in the studied environment and represent low palatable, occasionally used and highly preferred food items for herbivores, respectively. At each visit we randomly chose 15-50 saplings of each tree species present on the plot. Spruce is distributed over the whole study area in naturally regenerated shrub layer. Naturally regenerated beech saplings occur at several places where the remains of the original old stands have been preserved and it was present at 11 of the 27 monitoring plots in altitudes from 800 to 900 m a.s.l. Beech was also planted on fenced plots where no browse was detected and these plots we used as comparative ones. Rowan has regenerated naturally or has been planted at all monitoring plots. It is a species of high importance for forests at the ridges and is intensively browsed by herbivores. We monitored browsing only on naturally regenerated and not protected rowan saplings. For all studied tree species we have recorded their height (we analysed only individuals threatened by browsing, i.e. under 200 cm), number of freshly browsed and unbrowsed shoots and length of terminal shoot. For rowan we determined also density of saplings.

Food supply and dietary analysis
The vegetation cover was examined at the culmination of the vegetation season; at the valley locality on the clear-cut plots and in the old stands in June, on the subalpine meadows at the ridges locality in July. The cover of the individual plant species in the herb layer was recorded at partial plots of 40 m^2 (N=18 at ridges; N=19 at valley) and the vegetation composition were estimated to categories according to the main types (see Fig. 3).
Samples of vegetation and faeces were collected during four seasons (spring = May, summer = July, autumn = September and winter = November to January). From each season, were examined 15 samples of pellet groups from each herbivore species on botanic composition of diets and 5 samples of vegetation (simulation of browsing) of the plant species whose proportion in the diet of ungulates was over 1% of volume (1 percentage cover).

Evaluation of quality of the diet

The samples of vegetation and faeces were dried in a ventilated drying chamber at 60°C and were assessed for the content of crude protein (CP), fat, crude fibre, nitrogen-free-extract and ash [5]. To compare the nutritional quality of the individual diet component the metabolizable energy was calculated (ME) [6]. Five samples of vegetation were used to assess the nutritional value of individual diet component.

The diet composition of ungulates was investigated by microscopic analyses of plant remains in their faeces. From each of the faecal samples collected, one pellet was removed and used to prepare a microscopic slide. The representation of various diet components was estimated on the basis of their relative coverage in the microscopic field. In evaluating the overall character of the diet, the components were pooled to form primary forage classes: grasses, *Rubus* spp., browse (leaves and shoots of broadleaved trees), needles, forbs and ferns. Preferences of the individual plant species in the diet were expressed by Ivlev's electivity index: $E_i = (r_i - n_i) / (r_i + n_i)$, where r_i = percentage of i species in the diet; n_i = percentage of i species in the environment. In general, the diet item with E_i= -0.3 and 0.3 we considered as non selectived, items of E_i <-0.3 as avoided and items of E_i >0.3 as preferred. The level of the quantitative similarity of diets between two species or between one species in two areas was expressed

by means of the similarity index $SI = y_i$ where y_i is the lower value of an item i jointly consumed by both species under study. The similarity index can be in an interval from 0% (completely different diet) to 100% (identical diet).

Data analyses

Two-tailed parametric tests were used where possible for statistical evaluation (ANOVA, t-test). When necessary, data was modified by the logarithmic transformation to improve a normality of their distribution. In cases where preconditions of parametric evaluation were not fulfilled, Mann-Whitney U-test and Spearman correlate coefficient was applied. The Chi square goodness of fit test or contingency table was used for evaluation of deer faeces distribution.

Results and Discussion

Distribution of herbivores

Herbivores stay in upper parts until the onset of winter and then migrate to lower located areas. At the beginning of winter, the density of herbivore tracks was 5 – 9 times higher in the lowest locations than in the highest one. Density of red deer could not be monitored in summer on the foothill localities because of very dense vegetation and rapid decomposition rate of pellets. In autumn the density of red deer at the ridge localities was also similar to top localities ($p>0.05$; $n=64$) and was higher than at the foothill localities ($F_{2,172}=11{,}885$; $p<0.001$ and $F_{2,217}=18.598$; $p<0.001$, respectively). Density at the foothill localities was substantially lower compared to higher parts. The mean density of red deer from spring to autumn was 56, 30 and 15 ind./km² at the top, ridge and foothill localities, respectively.

Pellet distribution showed that red deer used the habitats at the foothill, the ridges as well as the top parts in both years of the research with the same intensity (t-test, $p>0.05$ for all cases). However, distribution of pellets in the environment was not random. Red deer repeatedly used the same plots with similar intensity. There was significant correlation between pellet density at individual localities in October 2004 and October 2005 ($r_s= 0.606$; $p=0.006$; $n=19$).

Impact of herbivores on trees

The impact of herbivores on natural regeneration of spruce was marginal in winter as well as during vegetation growing season of both studied years. We examined the total of 817 spruces (34751 shoots); marks of herbivore browsing were found at approximately 1% of individuals. Spring controls revealed higher browsing (10% of shoots on average) in comparison with vegetation growing season (3% of shoots on average). In spring, browsing occurred more in foothill localities than in ridge and top localities $P=0.026$). In vegetation growing season the difference was not significant ($P>0.05$).

Beech saplings were present only at several plots at the foothill and ridge localities. During both studied years we examined total of 1338 individuals/15345 shoots. Beech was browsed during summer as well as during winter. During summer browsing damage were caused mainly by ungulates (in the autumn we found 6.2% of freshly browsed shoots in total). Beech browsing in winter varied from 6 to 67% browsed shoots and was caused mainly by hare (over 95% of the damaged shoots). The average increment of the monitored individuals was only 12 cm per one year. Intensive browsing during vegetation influences the growth of beech; however, it does not cause a direct threat to its regeneration. The critical season is winter when hare eat sprouts; the natural regeneration of beech is disrupted and the trees changes to the typical bonsai-like shape at the snow cover height.

Rowan is a natural component of forest stands in the studied area. Mature individuals are distributed over the whole area and young saplings appear in the shrub layer. Density of rowan saplings at our sampling plots was from 13 to 1880 individuals per ha. We examined total of 2451 individuals and 5427 shoots. The small number of shoots per saplings indicates higher exposure of this species by browsing as well as can be caused by higher herbivore impact. The highest density of rowan saplings was at the top and foothill localities ($\overline{X} \pm s_d = 425 \pm 1000$ and 450 ± 760 ind./ha, respectively). At the ridge localities, its density was lower (287 ± 620 ind./ha, $\chi^2 = 10.49$; $df=2$; $p<0.01$).

Rowan was considerably browsed by herbivores during summer at all plots. The overall intensity of rowan browsing in summer in the whole study area was similar in both study years (29.5% in 2004 and 23.6% in 2005). Intensity of summer browsing was 32.2%, 17.5% and 16.2% at the foothill, top and ridge localities respectively in both years. Intensity of browsing in winter was 47.6%, 9.3% and 39.7%. Growth of rowan saplings was limited at the ridge and top localities and retarded at foothill localities by herbivore browsing. Browsing of herbivores prevent growth of rowan over the ground vegetation. The length of terminal shoots was 3cm, 3cm, and 15cm at the foothill, top and ridge localities respectively in both years. We did not find any young rowan higher than 150 cm in the whole area. The average height of rowan differed between localities (ANOVA; $F=710$; $df=2$; $P<0.001$) and was 21.7 ± 13.6 cm at the top, 27.8 ± 16.7 cm at the ridge and 71.6 ± 41.6 cm at the foothill localities. Such differences between localities are caused by height of other vegetation.

We did not find any significant relationship between the intensity of rowan shoot browsing and height of rowan, density of rowan and density of red deer. The distribution of red deer pellet groups was not influenced by the density

of rowan. Browsing of herbivores is nevertheless the main cause of elimination of rowan from shrub layer. We have investigated several fenced plots at the top and ridge locality and found higher density of rowan in the fenced in comparison to unfenced plots (1732±1343 and 2479±2194 ind./ha in fenced and 287±619 and 450±762 ind./ha in the unfenced plots; χ^2_1= 19.04 and 30.88; p<0.001). Height of older rowans in the fenced plots was over 5 m.

Selection of food by the studied species

We have compared the cover of the main vegetation types at the two studied localities and the relative volume of these components in the diet of red deer, chamois and roe deer in summer. The studied localities differed in the average cover of the individual main vegetation types. The differences were significant (df =34; p<0.005 in all cases) except for the cover of ferns (p=0.389).

At the ridges locality, red deer and chamois consumed grasses non-selectively. Grasses dominated in diets of both species and in vegetation cover respectively (Ei=0.17 and 0.18). Blueberry was avoided (Ei= -0.91 and 0.94 respectively) analogous to forbs (Ei= -0.91 and -0.52 resp.).

At the valley, both red and roe deer preferred leaves of raspberry (Ei=0.71-0.74), which formed the main component of their summer diet. All of the remaining diet components which were less nutritious were avoided by both deer species (Ei from -0.49 to -0.98).

Nutritional value of diet

The simulated diet varied in nutritional values in herbivore species and in seasons. In the growing season, the content of energy in the consumed plants ranged 8.9 -10.9 MJ/kg of dry matter and the content of crude protein from 117 to 250 g/kg of dry matter. The most valuable were leaves of woody species, while the least valuable were grasses. In winter the content of energy ranged 7.8 - 10.8 MJ/kg of dry matter and content of crude protein from 69 to 123 g/kg of dry matter. In this period, the highest-quality component was Bramble (*Rubus fruticosus*), while the component of the lowest quality was spruce.

Conclusion

In the study area, red deer concentrate on the ridges during vegetation growing season, while in winter they migrate away. The vertical seasonal migration leads to high concentration of red deer on the top localities and one of the results of intensive pasture in that area is an elimination of rowan from the shrub layer, despite the fact that rowan is not an important component of red deer diet. Attractiveness of the top areas is due to the supply of grasses and possibly to the quiet environment and it is not realistic to encourage the growth of rowan at the tops through reduction of red deer density within the study area.

Impact of red deer on other tree species is weak. Norway spruce is not affected by herbivore browsing and beech is browsed by red deer in vegetation growing season and brown hare in winter. The only long-term solution is therefore to increase the abundance of deciduous trees in older stands and thus secure sufficiency of natural regeneration that would withstand the impact of herbivores.

In the studied environment, red and roe deer utilized the food sources in accordance with their feeding strategies. The characteristics of the environment caused insignificant differences in the quality of diet between red and roe deer at the valley locality in summer (prevalence of raspberry). In spring and autumn, roe deer was able to consume food of higher nutritional value than red deer. The strictly limited food supply at the ridges locality excluded survival of roe deer, while red deer and chamois concentrated on the open areas. For all of the studied species, winter is a season of critical lack of food. In this period the food supply is limited and the diet of all species tends to be very similar. Nevertheless, the feeding strategies and food selection of each of the species are different. From the food supply available in this season red deer consume grasses in the first place (diet is composed of wavy hair grass and spruce in the ratio of 1:1). Roe deer consumes mostly needles when there is lack of broadleaved species.

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