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Original article

Feeding patterns of red deer *Cervus elaphus* along an altitudinal gradient in the Bohemian Forest: effect of habitat and season

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We studied diet composition of red deer *Cervus elaphus* in the Bohemian Forest by micro-histological analysis of 207 samples of red deer faeces obtained on the Czech and the Bavarian side of the border. We carried out the research from October 2006 to February 2008, and collected samples every two months at nine monitoring plots that were situated at different altitudes (i.e. from 600 to 1,250 m a.s.l.). Our results confirmed the classification of red deer among intermediate feeders with a mixed diet of graminoids (29.4%) and concentrate food items (60.6%). Concentrate food items were dominant in their diet all year round; however, the diet composition during the winter season differed from the diet composition during the vegetation season. This change was mainly represented by the strong increase in consumption of coniferous trees (from 5.7 to 26.4%) during winter. The amount of graminoids in the diet was higher during the vegetation season, which was caused by the intensive consumption of graminoids at two top-hill plots (up to 90% per sample). Likewise bilberry, *Vaccinium myrtillus*, with ripe berries was identified as an important food source only at the mountain ridge (up to 33% per sample). In agreement with our prediction, the diet composition of red deer at windthrow gaps (Blatný vrch Hill and Schachtenau) differed from the diet composition at undisturbed forest sites. At the gaps, ferns were an intensively consumed food source (up to 80% per sample). Contrary to other mountain areas, ferns made up a much larger share of the diet not only during autumn and winter but also during spring and summer. At Schachtenau, red deer also fed extensively on bramble *Rubus* sp., which intensively proliferates at the gaps. Diet composition of red deer in the Bohemian Forest differed between seasons, between plots at the mountain ridge and plots situated at lower altitudes as well as between windthrow gaps and undisturbed forest sites. However, further research of diet selectivity is necessary to explain in detail the observed feeding patterns.

Key words: Bavarian Forest National Park, Cervus elaphus, PCA, seasonal and spatial variation, Šumava National Park

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Ungulates play a key role in European forest ecosystems by affecting vegetation structure and composition (Putman 1994, Hobbs 1996, Gill 2000, Gill & Beardall 2001). Deer*browse interactions usually cause numerous conflicts between forestry management, deer management and natural conservation; therefore, the knowledge of deer feeding ecology is essential for development of rational management plans, especially in conservation areas.

Red deer *Cervus elaphus*, classified as an intermediate feeder, feed opportunistically on mixed diet of grasses and concentrate food items as browse, forbs and fruits (Hoffmann 1989). The general patterns of diet selection focus on maximising the energy intake rate and minimising the intake of anti-nutritional or toxic compounds (Hanley 1997). Basically, red deer can use two different foraging strategies: as a concentrate selector, i.e. consuming faster fermenting but less digestible diet with certain amount of tannins, or as a grazer, i.e. consuming slowly fermenting but better digestible fibre diet with a smaller volume of anti-nutritional or toxic compounds (Demment & Van Soest 1985, Verheyden-Tixier et al. 2008). It is predicted that red deer select concentrate food items when the overall browse quality and availability are high (during the vegetation season) and switch to a grass-based diet as a response to the decline of concentrate food availability which usually occurs during winter (Dumont et al. 2005, Verheyden-Tixier et al. 2008).

In temperate forests, the quantity and quality of available food sources vary spatially with habitat structure and temporally with season/year (Dzięciołowski et al. 1975, Demment & Van Soest 1985, Gebert & Verheyden-Tixier 2001, Hamel et al. 2009). Natural disturbances such as windstorms as well as human activity (harvesting and planting of trees in managed forests) modify forest habitat structure considerably and thereby also the food availability (Degen et al. 2005, Storms et al. 2006, Moser et al. 2008). Deer are usually attracted to natural or artificial clearings where food and shelter sources develop rapidly (Widmer et al. 2004, Degen et al. 2005). Consequently, according to the optimal foraging theory applied to diet composition, if the availability of a preferred food item is higher, the specialisation on this item also increases (Storms et al. 2006).

Habitat structure and deer food availability of the Bohemian Forest are substantially influenced by periodically occurring windstorms and subsequent bark-beetle outbreaks (Jonášová & Prach 2004, Svoboda & Pouska 2008). Furthermore, a portion of the red deer population migrates vertically from a low-elevation winter range to a high-elevation summer range (Šustr & Jirsa 2006). This movement is assumed to prolong the period with access to young plants of high nutritional quality (Demment & Van Soest 1985, Mysterud et al. 2001). Thus, changes in habitat structure, as a consequence of windstorms and seasonal migration, may substantially influence local feeding habits of red deer in the Bohemian Forest.

Our study deals with seasonal and spatial variation of red deer diet composition. We used data on diet composition to test the following predictions. With regards to the optimal foraging theory and previous observations (e.g. Dumont et al. 2005, Verheyden-Tixier et al. 2008), we predicted that red deer will ingest more fibre diet during winter (grazer period) and less fibre diet during the vegetation season (browser period). Furthermore, we predicted that the diet composition of red deer will differ between windthrow, bark-beetle gaps and undisturbed forest due to the changes in food availability. Proliferation of some food sources at the gaps (e.g. bramble; Widmer et al. 2004, Degen et al. 2005, Storms et al. 2006) could influence their proportion in the red deer diet. Finally, we predicted differences in the diet composition between plots at the mountain ridge and plots at lower altitudes. The availability and quality of food sources can vary at different altitudes and could partially influence the vertical migration of deer to upper altitudes during the vegetation season (Mysterud et al. 2001).

Material and methods

Study area

We carried out our research from October 2006 to February 2008 in the Bohemian Forest within an area belonging to two national parks: the Šumava National Park (NP) on the Czech side of the border and the Bavarian Forest NP on the German side. The Šumava NP is the largest national park in the Czech Republic and covers an area of 69,030 ha. Together with the 24,250 ha of the neighbouring Bavarian Forest NP, these two parks form the largest forest complex in Central Europe known as 'The Green Roof of Europe'.

The average daily temperature and the annual precipitation are highly dependent on altitude and slope orientation; e.g. northeast-facing slopes of the Czech side of the border are situated in the rain shadow. The average daily temperature varies from 6°C (at 750 m a.s.l.) to 3°C (at 1,300 m a.s.l.). Compact snow cover is usually present at lower altitudes for approximately 100 days and at higher altitudes for up to 200 days per year (Heurich & Neurfanger 2005). The amount of snow fall in both winters of our research (2006/07 and 2007/08) was below average. In the areas at lower altitudes ($<$ 900 m a.s.l.), the snow cover was only present for brief periods.

Because of their different histories, the Czech and the Bavarian sides of the border differ in forestry management. The natural character of vegetation of the Šumava NP has been greatly altered by long-term silvicultural practices, and non-indigenous Norway spruce *Picea abies* monocultures have been recently planted at many locations. As a consequence of periodically occurring windstorms and subsequent bark-beetle outbreaks, large deforested areas have been formed, mainly along the mountain ridge (Jonášová & Prach 2004, Svoboda & Pouska 2008). The Bavarian Forest NP is plagued by similar problems, however, natural forests are preserved better and larger areas are covered with natural beech-fir forest, with only a small proportion of spruce.

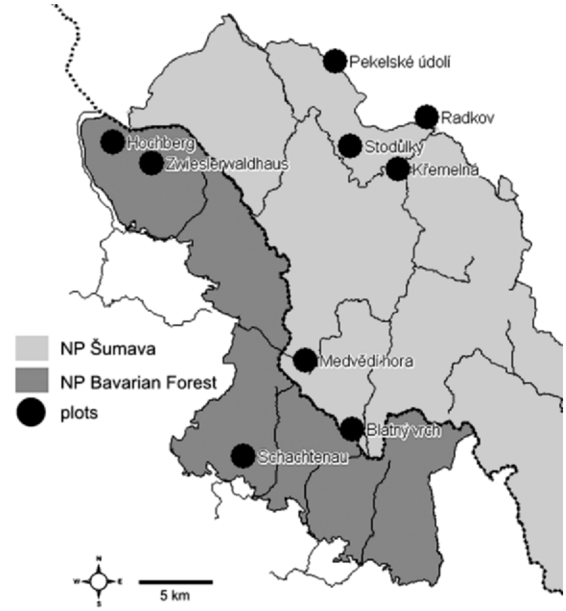

Figure 1. Locations of the nine monitoring plots on the German and the Czech sides of the Bohemian Forest.

Methods

In the Bohemian Forest, we randomly chose nine monitoring plots for red deer faeces collection, each covering 0.785 km^2 (i.e. a circle with a diameter of 1 km; Fig. 1). These plots represented different habitat types and were situated at different altitudes in order to account for the seasonal vertical migration of red deer (Table 1). Six monitoring plots were situated on the Czech side of the border, and two of these plots were established on the mountain ridge (Blatný vrch Hill and Medvědí hora Mountain; top-hill plots), with red deer present only during the vegetation season. Two other plots, Stodůlky and Křemelná, were situated in the intermediate range of the Šumava NP, where the animals are present throughout the year (northeastern intermediate plots), and the last two plots, Radkov and Pekelské údolí Valley, were located at lower altitudes of the Šumava Protected Landscape Area close to the border of the Šumava NP, where red deer occur only during winter (foot-hill plots). The remaining plots, Schachtenau, Hochberg and Zwieslerwaldhaus, were situated on the Bavarian side of the Bohemian Forest (southwestern intermediate plots). Hochberg and Zwieslerwaldhaus represent the same habitat type. Hence, the samples were pooled together and were further referred to as

Table 1. Monitoring plots based on dominant habitat type, elevation category and altitude (in m a.s.l.) and time of sampling.

Monitoring plots	Dominant habitat type	Elevation category	Sampling
Radkov	Meadows (45%) surrounded by pine-spruce forest (55%)	Foot-hill plots 600 - 700 m	Winter
Pekelské údolí Valley	Meadows (15%) surrounded by spruce monoculture (85%)		
Stodůlky	Open deciduous woodland with meadows (60%) surrounded by spruce monoculture (40%)	Northeastern intermediate plots 800 - 950 m	Annually
Křemelná	Pine-spruce forest (70%) with adjacent meadows (30%)		
Blatný vrch Hill	Regenerating forest after windstorm and bark-beetle outbreak (100%)	Top-hill plots 1,150 - 1,250 m	Vegetation season
Medvědí hora Mountain	Open subalpine spruce forest partially infected by bark-beetle (100%)		
Schachtenau	Regenerating mixed forest after windstorm and bark-beetle outbreak (100%)	Southwestern intermediate plots 800 m	Vegetation season
Hochberg	Beech-fir-spruce forest with well-developed shrub layer (100%)	Southwestern intermediate plots 700 - 850 m	Annually
Zwieslerwaldhaus	Beech-fir-spruce forest with well-developed shrub layer (100%)		

Hochberg only, primarily because we found many more samples at Hochberg (30 faecal samples) than we found at Zwieslerwaldhaus (four faecal samples).

Faecal samples of red deer were collected every two months from October 2006 to February 2008. Due to the seasonal vertical migration of red deer, we were not able to collect samples at all locations throughout the year. During the two winters (February 2007, December 2007 and February 2008) we collected the samples at the northeastern intermediate and foot-hill plots, and at Hochberg. During the vegetation season (all the remaining periods) the samples were collected at top-hill and all intermediate plots (see Table 1).

Micro-histological analysis of faeces

In total, 207 pellets were processed by microscopic analysis (at 50-100x magnification) to establish the botanical composition of the diet. The inside of one pellet was taken from each faecal sample and was homogenised in water. A part of this material was then randomly taken out and was placed on a glycerine slide (Homolka & Heroldová 1992). The surface of the cover slide (18 × 18 mm) represented 100%; thus one visual field at 50x magnification represented approximately 2% of the sample. During the analysis, the surface area covered by each plant fragment in each visual field was estimated by eye (Prokešová 2004). This made it possible to establish the quantitative composition of the diet (percentage of volume, %v). The total number of fragments per slide was 110 on average. The fragments were classified at family, genus or species level if possible (at 100x magnification). If this was not possible, the fragments were referred to one of the main groups: deciduous trees, coniferous trees, graminoids (grasses and sedges), forbs, bramble (including blackberry *Rubus fruticosus* and raspberry *R. idaeus*), bilberry (including *Vaccinium myrtillus* and *V. vitis-idaea*), fruits, ferns, mosses and unidentified fragments. Of the total 21,986 fragments, we were not able to classify 263, which represented 1.2% of all analysed fragments. In addition to %v, the proportion of samples, in which each food item was found, is given as a percentage of occurrence (%oc) in Appendix I.

Micro-histological analysis of faeces may overestimate some items (e.g. woody plants and grasses) and underestimate others (e.g. fruits and forbs) due to different digestibility (Dzięciołowski 1970, Anthony & Smith 1974). However, according to more recent studies, the results obtained using microscopic analyses of faeces are comparable to those obtained by rumen or stomach content analyses (Homolka 1986, Homolka & Heroldová 1992).

Statistical analysis of data

The proportions describing diet composition, known as compositional data, are non-independent with a large degree of co-linearity between volumes of food items within each sample (Aebischer et al. 1993, de Crespin de Billy et al. 2000). Thus, we performed Principal Component Analysis (PCA) using Canoco 4.5 for Windows (ter Braak & Šmilauer 2002) and analysed diet composition by examining the first two principal components *sensu* de Crespin de Billy et al. (2000) and Storms et al. (2008). Our data set was in the form of an n x p 'resource matrix' with n (samples) as rows and p (food categories) as columns. Supplemental environmental variables, i.e. collecting periods and study sites, were added as dummy variables. Input data were square-root transformed and centered. The biplot projection helped us to show the total variance of red deer diet composition data in a two-dimensional space. In the biplot, each food category is characterised by an arrow whose length is proportional to its overall relative abundance and also depends on the variation of use of the corresponding food category, among individual faecal samples. Consequently, dominant food categories are dispersed on the first factorial plane whereas the rare categories are concentrated around the origin. All faecal samples were displayed in the biplot at the centroids of the food categories, with each food category being given a weight equal to its proportion in the faeces. The higher the proportion of the category in the faecal sample, the closer the centroid of sample is to the head arrow of appropriate food category (de Crespin de Billy et al. 2000, Storms et al. 2008). We performed the PCA with all faecal samples to explain seasonal variation of red deer diet, and two separate PCAs with winter samples and samples from the vegetation season to explain the spatial variation in diet composition. The environmental variables were projected onto the PCA axes, *a posteriori* to assess the amount of variation in the PCA data that could be attributed to the environmental variables (Grover & Chrzanowski 2000). We used multivariate General Linear Model (GLM) in SPPS 11.5 to test the effect of locality, season and their interaction (response variables) on the diet composition data which were represented by sample scores of the first two principal components (dependent variables). All effect sizes, reported as η^2, were calculated by hand according to Cohen (1973), due to mislabeling in SPSS (Levine & Hullett 2002). We performed additional t-tests to detect the significance of differences between the vegetation season and winter, gaps and undisturbed forest sites, and mountain ridge and lower altitudes (Sokal & Rohlf 1981).

Results

Seasonal variation in red deer diet composition

We performed PCA on annual diet data to detect seasonal variation in red deer diet composition (Fig. 2). All one-month periods were included as dummy variables. Together, the first two principal components explained 48.5% of the total variance within the diet composition data. Based on factor loadings of particular food categories, the PC1 represents the gradient between samples with a higher volume of graminoids, bramble and/or ferns, and samples with a higher volume of coniferous trees. The PC2 represents the gradient between samples with a higher volume of graminoids and/or deciduous trees and samples with a higher volume of bramble and/or ferns. The changes in the proportion of these food items mostly described the variability in the seasonal feeding habits of red deer. Based on the results of multivariate GLM (Table 2), the highest proportion of the variance of PC1 was explained by season ($\eta^2 = 0.348$ for PC1). The effect of locality and the interaction locality*season was also significant but lower and explained much better the variance of PC2. The additional t-test performed on sample scores of PC1 and PC2 confirmed the difference between samples from the vegetation season and winter (PC1: $t = -10.343$, $df = 205$, $P < 0.001$; PC2: $t = -2.431$, $df = 205$, $P < 0.016$).

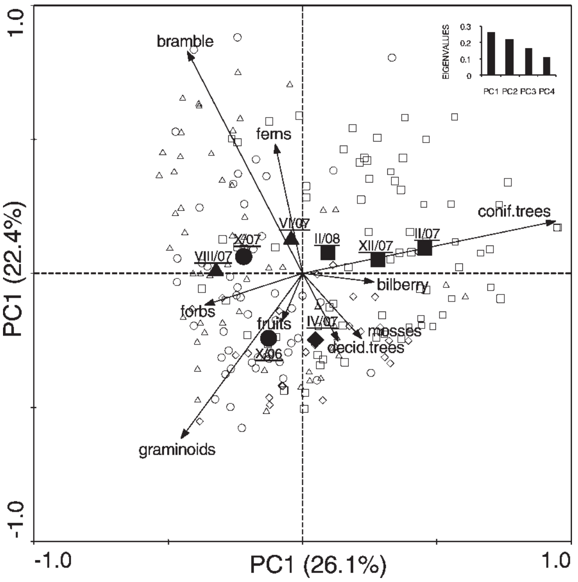

Figure 2. Species-centered PCA biplot on all red deer faecal samples (empty symbols: diamond, up-triangle, circle, square) with main food categories (arrows) and period's centroids (filled symbols: spring period-IV/07 = diamond; summer periods-VI/07 and VIII/07 = up-triangle; autumn periods-X/06 and X/07 = circle; winter periods-II/07, XII/07, II/08 = square). Screeplot of eigenvalues and percentage of total variance explained by PC1 and PC2 are given.

The volume of coniferous trees contributes positively and most strongly to the variability of PC1. This food item frequently occurred in samples during the whole year, but was mostly consumed during winter (periods II/2007, XII/2007 and II/2008; see Appendix I). Their consumption predominantly affected the difference between the winter samples and the samples from the vegetation sea-

Table 2. Results of the multivariate GLMs showing the effect of locality, season and the interaction locality*season on the diet composition data, represented by sample scores of PC1 and PC2, and performed on all samples, samples from the vegetation season and samples from the winter, separately.

	Locality				Season				Locality*Season			
GLM	F	df	P	η^2	F	df	P	η^2	F	df	P	η^2
All data												
PC1	7.865	7	< 0.001	0.077	35.780	7	< 0.001	0.348	3.924	27	< 0.001	0.147
PC2	19.067	7	< 0.001	0.232	12.787	7	< 0.001	0.156	5.373	27	< 0.001	0.252
Vegetation season												
PC1	33.996	5	< 0.001	0.345	29.018	4	< 0.001	0.236	6.696	16	< 0.001	0.217
PC2	40.608	5	< 0.001	0.450	14.937	4	< 0.001	0.132	4.301	16	< 0.001	0.153
Winter												
PC1	19.019	4	< 0.001	0.321	34.669	2	< 0.001	0.293	9.098	6	0.001	0.231
PC2	8.426	4	< 0.001	0.280	0.659	2	NS	0.011	1.913	6	NS	0.095

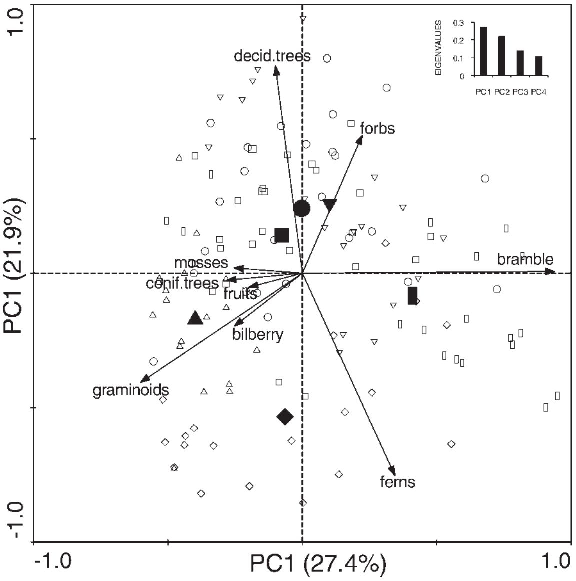

Figure 3. Species-centered PCA biplot of faecal samples from vegetation season (empty symbols: diamond, up-triangle, circle, square, down-triangle, box) with main food categories (arrows) and study site's centroids (filled symbols: Blatný vrch Hill = diamond; Medvědí hora Mt. = up-triangle; Stodůlky = circle; Křemelná = square; Schachtenau = box; Hochberg = down-triangle). Screeplot of eigenvalues and percentage of total variance explained by PC1 and PC2 are given.

son. Furthermore, the relationship between the centroid of the period IV/2007 (spring) and the deciduous trees arrow indicates that this food source was consumed the most during this period (on the average 31.1%). In October 2006 we detected a much higher volume of fruits in the red deer diet (9%) than in October of the following year (4%, including maize *Zea mays* grains). This primarily influenced the different positions of their centroid projections (see Fig. 2). Thus, the consumption of fruits seems to vary between years.

Habitat variation in red deer diet composition

The previous PCA has confirmed a strong difference between winter samples and samples collected during the vegetation season. Moreover, faecal samples were collected at different locations during these two periods (see Table 1). Thus, we performed separate PCAs for both periods to detect spatial variation in red deer diet composition.

Vegetation season

The first two principal components of PCA on samples from the vegetation season explained 49.3% of the total variance in the red deer diet data (Fig. 3). According to factor loadings, the PC1 represents the gradient between samples with a higher volume of graminoids and samples with a higher volume of bramble. The PC2 represents the gradient between samples with a higher volume of deciduous trees and samples with a higher volume of ferns. Multivariate GLM, which was performed on the first two principal component analysis sample scores, confirmed a significant effect of location, season and their interaction (see Table 2) on the diet composition of red deer during the vegetation season. The highest proportion of the variance of PC1 and PC2 was explained by locality ($\eta^2 = 0.345$ and $\eta^2 = 0.450$ for PC1 and PC2, respectively). The separation of the centroids of particular study sites within the 1st factorial plane illustrates differences detected in the red deer diet composition between the study sites. Additional t-tests confirmed the differences in diet composition between gaps and undisturbed forest sites (PC1: $t = -3.601$, $df = 123$, $P < 0.001$; PC2: $t = 6.836$, $df = 123$, $P < 0.001$) and between mountain ridge and plots at lower altitudes (PC1: $t = 4.335$, $df = 123$, $P < 0.001$; PC2: $t = 8.182$, $df = 123$, $P < 0.001$).

The diet composition of red deer at Stodůlky, Křemelná and Hochberg seems to be mostly similar to a higher volume of deciduous trees and/or forbs (Fig. 4). The diet composition of red deer at Blatný vrch Hill, Medvědí hora Mountain and Schachtenau differed markedly from the other sites as well as among each other. The highest volume of graminoids in the red deer diet was detected at both top-hill plots (up to 90% of the diet per sample; see Fig. 4). Furthermore, in the samples from Medvědí hora Mountain we found an exceptionally high volume of bilberry. This food item was eaten by red deer

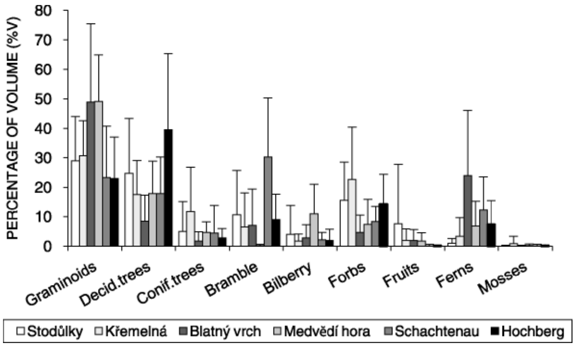

Figure 4. Proportions of the different food categories in the red deer diet during the vegetation season at the specific study sites, with mean and sd indicated.

mostly during August 2007, when berries were ripe, and its volume highly exceeded the average consumption at all other plots (see Fig. 4). At Blatný vrch Hill as well as at Schachtenau, both representing regenerating forest stands after windstorm and bark-beetle outbreak, ferns represented an intensively consumed food source mainly at the beginning of the summer (up to 80% per sample; see Fig. 4). At Schachtenau, bramble, especially raspberry, was a substantial component of the red deer diet (up to 65% per sample; see Fig. 4).

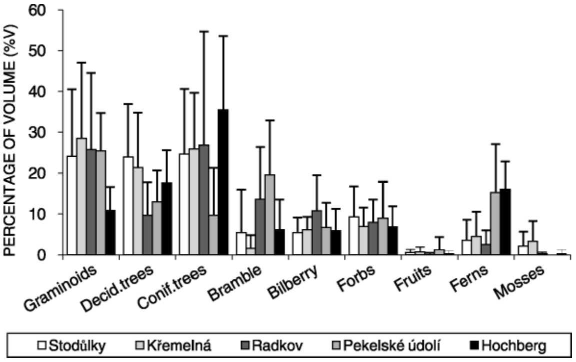

Figure 6. Proportions of the different food categories in the red deer diet during winter at the specific study sites, with mean and sd indicated.

Winter

The first two principal components of the PCA on winter samples explained together 60% of total variance within winter diet composition data (Fig. 5). Based on factor loadings the PC1 represents the gradient between samples with a higher volume of graminoids and those with a higher volume of coniferous trees. The PC2 represents the gradient between samples with a higher volume of deciduous trees and/or mosses and samples with a higher volume of bramble and/or ferns. Multivariate GLM, which was performed on the first two principal component analysis sample scores, confirmed a significant effect of location, season and their interaction (see Table 2) on the diet composition during winter (mainly based on the variance of PC1). Once again, the highest proportion of variance of PC1 and PC2 was explained by locality ($\eta^2 = 0.321$ and $\eta^2 = 0.280$ for PC1 and PC2, respectively).

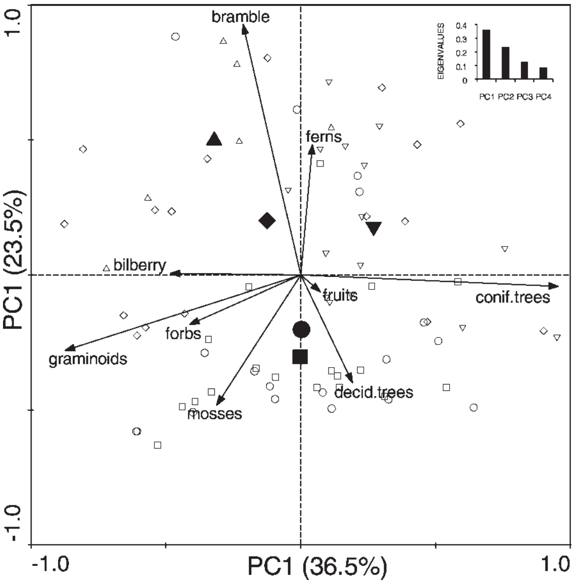

Figure 5. Species-centered PCA biplot of winter faecal samples (empty symbols: diamond, up-triangle, circle, square, down-triangle) with main food categories (arrows) and study site's centroids (filled symbols: Pekelské údolí = diamond; Radkov = up-triangle; Stodůlky = circle; Křemelná = square; Hochberg = down-triangle). Screeplot of eigenvalues and percentage of total variance explained by PC1 and PC2 are given.

Similarly, as during the vegetation season, the position of the centroids of particular study sites within 1st factorial plane demonstrated considerable spatial differences in red deer diet composition mainly represented by the values of PC2. The samples from the northeastern intermediate plots differed from the other sites in a higher volume of deciduous trees and/or mosses (Fig. 6), whereas the samples from the foot-hill plots contained a higher volume of bramble (see Fig. 6). At Hochberg, the samples contained the highest amount of coniferous trees (see Fig. 6).

Discussion

Our results confirmed the classification of red deer as an intermediate feeder (Hofmann 1989) with a mixed diet consisting of graminoids (29.4%) and concentrate food items (60.6%). According to the optimal foraging theory the shift to a grazer strategy is supposed to occur only when the availability of nutrients (soluble sugars and proteins) shifts markedly towards grasses (Hofmann 1989, Verheyden-Tixier et al. 2008). The results presented by Verheyden-Tixier et al. (2008) suggest that this shift occurs only during winter, when grasses contain more soluble sugars and proteins than deciduous browse. However, in the Bohemian Forest the red deer consumed predominantly concentrate food all year round and did not switch to grass-based diet during winter. Conversely, the amount of graminoids in the diet was higher during the vegetation season than it was in winter and was primarily influenced by the intensive consumption of graminoids at both top-hill plots.

The consumption of grasses during the vegetation season varies between central European mountain habitats. In Beskydy Mountains, the proportion of grasses in the red deer diet only represented 23% (Homolka & Heroldová 2003). In contrast, grasses were dominant in other mountain areas representing 92-95% in Jeseníky Mountains (Homolka 1995, 1996), 80% in Krušné Hory Mountains (Heroldová 1993), 70% in Krkonoše Mountains (Fišer & Lochman 1969) and 50-60% in the Swiss Alps (Suter et al. 2004). According to the optimal foraging strategy, the consumption of more nutritive and palatable concentrate food should be preferred to grass consumption during the vegetation season. Nevertheless, the grass consumption seems to be affected also by the species composition of alpine meadows. In areas with wavy hair grass *Avenella flexuosa* the grasses were intensively consumed (Heroldová 1993, Homolka 1995), whereas in areas with *Calamagrostis* sp. grasses were substituted by other food sources (Homolka 1995, 1996). In the Bohemian Forest, red deer can feed on both *Avenella* and *Calamagrostis* patches at both top-hill plots (J. Krojerová, unpubl. data). Thus, only further monitoring of food availability and diet selection patterns could help to clarify whether the extensive consumption of grasses results from the shortage of concentrate food items at these plots.

Red deer consumed a higher amount of bilberry (up to 33% and on average 23%) at the Medvědí hora Mountain than at other sites situated at lower altitudes. Bilberry is usually intensively consumed during winter in northern Europe (Cederlund et al. 1980, Mysterud et al. 1997), but in central European mountain forests it forms only a small part of the red deer diet (up to 10%; Homolka & Heroldová 2001, 2003). According to Albon & Langvatn (1992) the protein content of bilberry with ripe berries should be higher than that of graminoids and herbs and, furthermore, the content increases with the altitude. This could explain the higher consumption of bilberry just at the mountain ridge, where it could represent an important food resource for building up winter fat reserves (Van Soest 1982). Similarly, as in the case of grasses, the extensive consumption of bilberry could indicate also the scarce availability of other concentrate food items. This could be supported by a low proportion of other browsed species (deciduous, coniferous and/or bramble) in the red deer diet at the Medvědí hora Mountain.

Our results confirmed the second prediction, that differences exist in the diet composition between gaps and undisturbed forest sites. At Schachtenau, we detected the highest proportion of bramble, a plant species regularly proliferating at the clearings mainly at lower altitudes (Degen et al. 2005). Furthermore, a common feature of both our gap sites (Blatný vrch Hill and Schachtenau) was an unexpectedly high proportion of ferns in the red deer diet. Contrary to other mountain areas, ferns formed a much higher share of the diet not only during autumn and winter, but also during spring and summer (De Jong et al. 1995, Homolka 1996, Storms et al. 2006). Ferns are usually scarcely eaten by red deer (Gebert & Verheyden-Tixier 2001, Dumont et al. 2005) due to their high tannin and lignin contents, even though they may contain high concentrations of soluble sugars (Verheyden-Tixier et al. 2008). However, our results suggest that further chemical analyses are necessary to assess whether young fern leaves growing at sunny clearings differ in palatability and nutritive value from those growing in undisturbed forest, and whether the chemical composition varies between fern species. Red deer usually avoid ferns in the areas with prevalence of bracken *Pteris aquiline* (Dumont et al. 2005, Verheyden-Tixier et al. 2008) while in the areas with dominant lady fern *Athyrium filix-femina*, ferns can form a larger part of the diet (Storms et al. 2006). In the Bohemian Forest, red deer intensively browsed the related species alpine lady fern *A. distentifolium* which is dominant at the gaps.

The observed feeding patterns of red deer differed between winter and the rest of the year. This change was mostly represented by a higher consumption of coniferous trees during the winter. The intensive consumption of coniferous trees is often thought to indicate food limitation as a consequence of snow cover during winter (Helle 1980, Ammer 1996, Crête & Courtois 1997). However, in the Bohemian Forest, conifers represent a substantial part of the red deer winter diet, despite the low and briefly present snow cover which should not dramatically decrease the availability of other food items (J. Krojerová, unpubl. data). According to Verheyden et al. (2008), conifers contain a higher amount of soluble sugars in winter than they do in summer, and yet they still have a high concentration of tannins. The consumption of conifers by deer is also negatively influenced by a high monoterpene concentration (Duncan et al. 1994). However, the monoterpene concentration level can vary between various species (Ludley et al. 2009) and was detected to be lowest during the winter (Schoęnwitz et al. 1990). Thus, the palatability of conifers should be species as well as seasonally dependent. Contrary to spruce silver fir *Abies alba* belongs to the regularly browsed coniferous tree species in the European mountain forests (Motta 1996, Senn & Suter 2003, Heuzé et al. 2005). Even though the spruce-fir ratio in red deer diet could not be assessed using micro-histological analysis, some larger fragments, classified to species level, belonged to silver fir (see Appendix I). Likewise, based on our field observation, the silver fir was much more browsed at all study sites compared to the usually avoided spruce (J. Krojerová, unpubl. data). Consequently, we do not consider the observed high proportion of conifers in the red deer diet to be a sign of food limitation. The nutritive value of fir needles in comparison to spruce needles is questionable and should be resolved.

In the Bohemian Forest, red deer generally used food sources according to the strategy of a mixed feeder, but with a much higher consumption of concentrate food items throughout the year. However, the red deer diet composition varied seasonally as well as spatially. Further research of food availability as well as the assessment of nutritional value of particular food sources seems to be necessary, to explain the observed feeding patterns and all outlined hypotheses.

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Appendix I. Food items identified in red deer diet in the Bohemian Forest (%v=percentage of volume, %oc=percentage of occurrence). The total number of samples for each study period is given at the bottom of the table.

	2006		2007												2008			
Periods	October		February		April		June		August		October		December		February		Total	
Items	%v	%oc	%v	%oc	%v	%oc	%v	%oc	%v	%oc	%v	%oc	%v	%oc	%v	%oc	%v	%oc
Graminoids	39.2	100.0	15.6	100.0	33.3	100.0	23.1	100.0	32.7	100.0	37.8	100.0	20.9	100.0	29.6	100.0	29.3	100.0
Juncus sp.	-	-	-	-	-	-	-	-	+	3.3	+	3.3	+	8.7	0.1	10.0	+	3.4
Zea mays (leaves)	-	-	-	-	0.1	12.0	-	-	-	-	-	-	-	-	-	-	+	1.4
Coniferous trees	4.2	75.0	33.6	100.0	11.1	88.0	8.1	89.3	1.2	43.3	3.7	83.3	26.1	95.7	15.5	96.7	12.1	83.1
Abies alba	-	-	-	-	-	-	-	-	-	-	-	-	0.4	4.3	+	3.3	+	1.0
Pinus sylvestris (bark)	-	-	7.6	66.7	0.6	12.0	0.4	7.1	-	-	-	-	0.5	21.7	0.1	6.7	1.0	12.6
Deciduous trees	12.8	100.0	13.9	100.0	16.4	100.0	19.1	100.0	17.5	100.0	11.3	100.0	23.1	100.0	13.3	96.7	15.9	99.5
Betula sp.	-	-	-	-	0.1	8.0	-	-	-	-	0.2	10.0	-	-	-	-	+	2.4
Fagus sylvatica	1.3	25.0	-	-	13.7	52.0	5.0	39.3	0.9	40.0	0.4	40.0	1.4	52.2	0.2	16.7	2.8	33.8
Rosa canina	0.4	15.0	+	9.5	+	4.0	-	-	-	-	+	10.0	-	-	-	-	+	4.3
Salix caprea	-	-	0.4	23.8	-	-	-	-	0.1	3.3	+	10.0	0.2	21.7	0.6	13.3	0.2	8.7
Sambucus nigra	-	-	-	-	0.7	16.0	-	-	+	3.3	-	-	-	-	-	-	0.1	2.4
Sorbus aucuparia	5.8	60.0	1.2	19.0	0.3	44.0	-	-	-	-	0.3	20.0	0.1	8.7	-	-	0.8	16.9
Rubus fruticosus	0.6	30.0	6.9	66.7	1.0	36.0	2.4	32.1	1.0	50.0	3.5	60.0	6.3	73.9	9.3	86.7	3.9	55.1
Rubus idaeus	2.4	55.0	0.1	4.8	1.2	32.0	11.8	46.4	15.6	76.7	10.4	73.3	+	4.3	-	-	5.8	38.2
Vaccinium sp.	3.9	75.0	5.7	100.0	4.7	72.0	3.3	71.4	4.3	53.3	2.9	73.3	5.7	91.3	9.0	93.3	5.0	77.8
Forbs	14.7	90.0	8.3	95.2	12.3	100.0	6.1	92.9	16.0	96.7	11.1	96.7	5.9	95.7	7.6	100.0	10.2	96.1
Asteraceae	-	-	0.1	9.5	0.4	20.0	0.1	7.1	0.1	3.3	0.1	16.7	+	4.3	+	6.7	0.1	8.7
Brassicaceae	+	5.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	0.5
Daucaceae	-	-	-	-	-	-	-	-	+	3.3	+	6.7	-	-	-	-	+	1.4
Fabaceae	0.3	15.0	+	14.3	0.2	32.0	0.3	28.6	1.4	33.3	0.3	36.7	+	17.4	+	16.7	0.3	25.1
Lamiaceae	+	10.0	+	19.0	0.1	24.0	+	3.6	0.3	53.3	+	13.3	0.1	30.4	+	3.3	0.1	19.8
Ranunculaceae	+	10.0	+	4.8	+	4.0	+	28.6	+	26.7	0.1	33.3	+	8.7	-	-	+	15.5
Cirsium sp.	-	-	-	-	+	4.0	-	-	+	3.3	+	10.0	-	-	-	-	+	2.4
Galium sp.	-	-	-	-	-	-	+	3.6	+	6.7	+	3.3	-	-	-	-	+	1.9
Origanum vulgare	-	-	-	-	-	-	-	-	0.8	13.3	-	-	-	-	-	-	0.1	1.9
Polygonum sp.	-	-	-	-	-	-	-	-	-	-	-	-	0.3	4.3	-	-	+	0.5
Solidago sp.	-	-	-	-	-	-	-	-	+	10.0	0.2	20.0	-	-	-	-	+	4.3
Urtica dioica	-	-	-	-	-	-	+	7.1	+	10.0	+	13.3	+	4.3	-	-	+	4.8
Verbascum sp.	-	-	+	4.8	-	-	-	-	+	6.7	+	3.3	-	-	-	-	+	1.9
Viscum album	-	-	-	-	0.1	4.0	-	-	-	-	-	-	-	-	-	-	+	0.5
Seeds of forbs	0.1	5.0	0.3	42.9	-	-	+	3.6	1.2	53.3	0.2	13.3	1.3	26.1	0.1	6.7	0.4	18.8
Fruits	9.0	95.0	0.6	52.4	-	-	0.1	3.6	0.3	6.7	0.7	60.0	0.4	21.7	0.6	30.0	1.2	31.4
Zea mays (grains)	-	-	-	-	-	-	-	-	-	-	3.3	6.7	-	-	-	-	0.4	1.0
Ferns	4.0	60.0	2.1	66.7	0.8	48.0	16.6	89.3	5.8	80.0	12.0	90.0	6.8	91.3	10.8	96.7	7.8	79.2
Mosses	+	5.0	0.6	33.3	0.8	28.0	0.3	28.6	0.1	10.0	0.2	26.7	0.3	30.4	2.9	50.0	0.7	27.1
Unidentified fragments	1.3	65.0	3.0	81.0	2.3	84.0	3.3	57.1	0.3	20.0	1.3	43.3	0.2	21.7	0.2	16.7	1.4	46.4
Number of samples	20		21		25		28		30		30		23		30		207	