

Importance of alternative food resources for browsing by roe deer on deciduous trees: The role of food availability and species quality

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Abstract

Ungulate browsing on young trees is widely regarded as a problem for forest regeneration. It has been suggested that browsing on trees is less intense when there is abundant alternative forage such as herbs or shrubs, although present studies reported controversial results. We suggest that in case of selective browsers such as roe deer *Capreolus capreolus* the role of alternative forage does not only depend on plant species abundance but also on plant quality and the food resource units among which selection takes place. Thus, we tested whether roe deer use forage patches with higher quality food more intensively than other patches and whether they select high quality species within forage patches. Furthermore, we compared the amount of browsing on deciduous trees with the availability of alternative, higher quality forage. The study was conducted in a deciduous forest in the northern lowlands of Switzerland. Roe deer selected both high quality forage patches as well as high quality plant species groups within patches. Selection of individual plant species groups depended on their seasonal availability and nutritional quality. *Rubus* spp. had the highest relative quality of all species groups and was used more than in proportion to cover in all seasons. In contrast, deciduous trees were only selected during the peak of their nutritional quality in summer and used according to availability in winter and spring. We conclude that availability and relative quality of alternative food resources are key factors for browsing by roe deer on deciduous trees. Since availability and nutritional quality are seasonally variable, the importance of alternative food resources changes between seasons.

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1. Introduction

Increasing deer densities in European forests over the last century have led to conflicting interests of deer and forest management (Cederlund et al., 1998). Browsing by ungulates on tree seedlings and saplings has been regarded as a problem for forest regeneration across Europe as well as in northern America (Andrén and Angelstam, 1993; Motta, 1996; Reimoser and Gossow, 1996; Chouinard and Fillion, 2001). Ruminant ungulates are classified according to their contrasting foraging strategies: ‘grazers’ are bulk roughage feeders eating mainly grasses, ‘browsers’ are concentrate selectors which selectively ingest forbs and parts of woody plants such as leaves, buds and twigs (Hofmann, 1973). In the lowlands of Central Europe roe deer *Capreolus capreolus* L. is the only pure

browser, although intermediate or mixed feeders such as red deer *Cervus elaphus* L. and chamois *Rupicapra rupicapra* L. seasonally feed on woody plants. Browsers can affect tree regeneration in various ways (see reviews in Gill, 1992a; Côté et al., 2004): browsing may change tree growth and timber quality (Bergqvist and Örlander, 1998; Chouinard and Fillion, 2001; Vila et al., 2003), and selective feeding may alter species composition of the understory and the tree layer (Stromayer and Warren, 1997; Edenius et al., 2002). Currently, damage to forest regeneration is mostly addressed by reducing deer numbers and protecting tree saplings (Cederlund et al., 1998). While the effects of culling are controversial (e.g. roe deer: Welch et al., 1991; Bergqvist and Örlander, 1998; or moose *Alces alces* L.: Andrén and Angelstam, 1993; Hornberg, 2001), sapling protection is costly (Bergqvist and Örlander, 1998; Verheyden-Tixier et al., 1998). Alternatively, the problem of deer browsing on tree saplings may be approached by appropriate forest management (Gill, 1992b; Reimoser and Gossow, 1996). However, accurate models predicting occurrence and intensity

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of browsing are still lacking (Cederlund et al., 1998). It has been widely suggested that alternative food resources are a key factor for the incidence of browsing by ungulates on trees (Welch et al., 1991; Gill, 1992b; Vila et al., 2003). This argument especially goes for selective browsers such as roe deer whose foraging behaviour is mainly steered by food quality. It does probably not hold for less-selective intermediate feeders and grazers which are more flexible in tolerating large quantities of grass and browse at the same time (Iason and Van Wieren, 1999). Although there are studies indicating a decrease of browsing on saplings in the presence of abundant alternative food resources such as herbs or shrubs, results have not been conclusive, yet (Gill, 1992b; Verheyden-Tixier et al., 1998). So far, studies have essentially focused on the availability of alternative forage in respect to the availability of tree browse. However, diet selection by ungulates does not only depend on plant availability but also on plant quality. Diet selection by roe deer is known to be positively related to the protein content of the available plants and negatively related to their content of lignin and cellulose (Maizeret et al., 1991; Tixier et al., 1997).

According to optimal foraging theory ungulates must make decisions at different spatial scales: on the one hand, they have to decide which patches they will visit to forage, on the other hand they have to decide which food items to select within a patch and how long to stay within the selected patch (Charnov, 1976). These decisions strongly depend on the overall availability and quality of food in a habitat. When selecting among forage patches, roe deer should spend more time in high quality patches (inter-patch selection). Within a patch they should feed on the most profitable plant species until availability drops below a critical threshold (intra-patch selection). Furthermore, diet selection by roe deer seems to depend on patch and forage size, involving a trade-off between forage quality and quantity (Illius et al., 2002). In order to assess the importance of alternative forage for browsing on trees, availability of plant species has thus to be considered in conjunction with their nutritional quality and the spatial scale at which resource selection by herbivores takes place.

In a lowland forest of northern Switzerland we therefore tested: (1) whether roe deer use forage patches with higher quality food more intensively than other patches (inter-patch selection), (2) whether roe deer select high quality species within forage patches (intra-patch selection), and (3) whether selection differs among seasons. The importance of alternative forage for browsing by roe deer on trees was further assessed by comparing the amount of tree browsing to the availability of alternative species that are of higher quality than trees.

2. Methods

2.1. Study site

The study was carried out near Habsburg in the Canton of Aargau, Switzerland (47°28'N, 8°12'E; 400 m above sea level). The studied forest area (1.8 km²) is a mosaic of forest

stands of different vegetation type including several clearings. The tree layer is dominated by *Fagus sylvatica* L., which is accompanied by *Picea abies* (L.) Karsten, *Acer pseudoplatanus* L., *Fraxinus excelsior* L., and some *Abies alba* Miller. The understory vegetation is attributed for the most part to the vegetation association 'woodruff beech forest' (*Galio odorati-Fagetum typicum*; Keller et al., 1998), and can be divided into several vegetation types with differing vegetation compositions (Burnand et al., 1982). The study was restricted to the three most widespread vegetation types: (i) woodruff-beech forest, (ii) woodruff-beech forest with >50% estival cover of *Carex brizoides* Juslenius, and (iii) woodruff-beech forest with >30% estival cover of *Rubus* spp. Altogether these vegetation types cover an area of 1.1 km². We did not consider clearings but restricted the study to closed forest with >60% canopy cover because we wanted to study the role of vegetation composition for resource selection by roe deer independent of factors such as visibility or vertical forest structure (e.g. Mysterud and Ostbye, 1999; Moser, 2005). Roe deer are the only large herbivores in the studied area, their density being estimated at 14–17 individuals/km² forested area in 2000 (spotlight counts; pers. comm. hunting administration Canton Aargau).

2.2. Forage availability and browsing intensity

Since our goal was to study forage patches containing more than one plant species, we chose sampling plots of 1 m × 20 m. A total of 27 sampling plots was established at 8–10 random locations in each of the three vegetation types (stratified random sampling; see Moser, 2005; Fig. 1). Availability and use of food resources were measured in each sampling plot in three consecutive seasons: summer (July/August 2001), winter (February 2002), and spring (April 2002). Forage availability was estimated in terms of percent cover of all plant species present including herbs, shrubs, and trees. In order to measure food resources actually available to roe deer, all measurements were restricted to heights from 0 to 150 cm above soil level (Maizeret et al., 1991; Duncan et al., 1998). Diet selection was measured through abundance of browsing marks on individual plant species: in each sampling plot, the number of eaten plant parts (herbs: leaves, inflorescence; graminoids: tillers, inflorescence; woody species: leaves, twigs, buds) was recorded for each species present (Wallmo et al., 1973; Mysterud et al., 1999).

2.3. Forage quality

Following two studies on diet selection by roe deer in an oak-beech forest in western France (Maizeret et al., 1991; Tixier et al., 1997), we assessed the nutritional quality of plant species groups based on crude protein and the fibre components lignin and cellulose. We used data on the nutritional quality of plant species groups from Zweifel-Schielly (2005), who assessed these parameters in the understory of mixed-deciduous forests in the Canton of Glarus, Switzerland, in May/June, July/August, and October/November 2001 (Table 1). The study distinguished

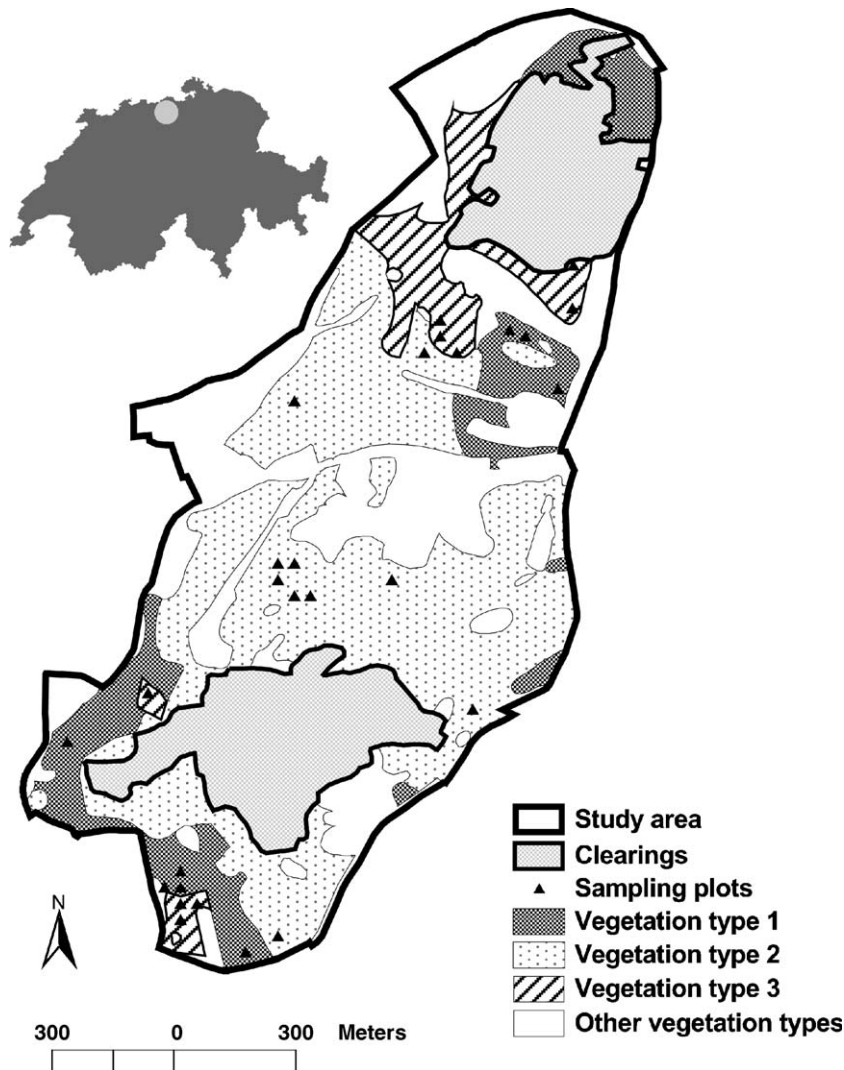


Fig. 1. Location of the 27 sampling plots in the study site near Habsburg, northern Switzerland. The whole area is forested with the exception of two clearings in the north and south, respectively.

between the following plant species groups: herbs, graminoids, *Rubus* spp., deciduous trees, and coniferous trees. It is known that environmental factors such as temperature, light, moisture, or soil affect the nutritional quality of plants (Van Soest, 1994). However, the effect of temperature, the most important factor affecting nutritional quality of a plant, seems to be uniform in all species. As far as we know it has not been tested whether the relative quality among plant species changes with other environmental conditions. Since seasonal average temperatures are similar in both sites (Habsburg: January -0.3°C , April 8.5°C , August 17.7°C ; Glarus: January -1.2°C , April 7.7°C , August 16.2°C), the relative nutritional quality of the species groups measured in Glarus should be comparable to that in Habsburg.

Based on the data of Zweifel-Schielly (2005), we calculated forage quality of a sampling plot as a combination of cover and nutrient content of the present plant species groups. As we know little about how animals perceive absolute nutrient contents of plants, and the scaling used for measuring nutrient

content may not be relevant for deer, we used ranked rather than absolute nutrient values for the calculation of patch quality. Nutrient components were ranked in such a way that high ranks denote high quality: crude protein was ranked in order of increasing content, whereas the fibre components cellulose and lignin were ranked in order of decreasing content (Tixier et al., 1997). Average ranks were attributed to species groups with overlapping intervals of mean \pm S.E. Forage quality of each sampling plot was then calculated as follows:

$$Q_j = \frac{1}{I} \sum_{i=1}^I c_{ij} \times r_i^{\text{quality}},$$

where c_{ij} is the cover of species group i ($i = 1, \dots, I$) in sampling plot j ($j = 1, \dots, N$), and r_i^{quality} is:

$$r_i^{\text{quality}} = (r_i^{\text{protein}} + (r_i^{\text{lignin}} + r_i^{\text{cellulose}})/2)/2.$$

Our definition of r_i^{quality} assumes that lignin and cellulose, and fibre and protein, respectively, have the same weight in defining

Table 1
Nutritional quality of different plant species groups according to season: nutrient content (mean \pm S.E.) and rank of mean nutrient content

Season	Species group	Nutrient content (g/100 g dry matter)			Rank		
		Crude protein	Cellulose	Lignin	CP ^a	Fibre ^b	Mean ^c
Spring	<i>Rubus</i> spp.	22.86 \pm 1.31	17.13 \pm 0.57	5.91 \pm 0.39	4.5	4.3	4.4
	Herbs	21.39 \pm 0.41	20.38 \pm 0.56	9.81 \pm 0.99	4.5	2.5	3.5
	Graminoids	17.37 \pm 0.75	28.76 \pm 0.65	4.81 \pm 0.28	2.5	3	2.8
	Deciduous trees	18.58 \pm 0.47	21.02 \pm 0.89	17.12 \pm 1.49	2.5	1.8	2.1
	Coniferous trees	14.87 \pm 0.94	15.50 \pm 2.50	11.45 \pm 2.12	1	3.5	2.3
Summer	<i>Rubus</i> spp.	15.69 \pm 0.62	20.30 \pm 0.56	6.27 \pm 0.32	4	4.8	4.4
	Herbs	16.37 \pm 0.43	25.94 \pm 0.69	9.62 \pm 0.92	4	2.8	3.4
	Graminoids	13.03 \pm 0.42	32.38 \pm 0.59	6.21 \pm 0.24	2	2.8	2.4
	Deciduous trees	15.18 \pm 0.36	22.92 \pm 0.87	16.59 \pm 0.93	4	3	3.5
	Coniferous trees	7.58 \pm 0.19	27.04 \pm 0.81	21.22 \pm 0.59	1	1.8	1.4
Winter	<i>Rubus</i> spp.	13.45 \pm 0.61	19.31 \pm 0.60	6.74 \pm 0.34	4.5	5	4.8
	Herbs	12.97 \pm 0.55	25.47 \pm 1.43	8.89 \pm 0.78	4.5	3.5	4
	Graminoids	9.10 \pm 0.33	32.73 \pm 1.11	7.97 \pm 0.72	2.5	2.3	2.4
	Deciduous trees	9.39 \pm 0.67	28.06 \pm 0.77	28.02 \pm 0.89	2.5	1.5	2
	Coniferous trees	7.21 \pm 0.26	23.61 \pm 0.71	20.71 \pm 0.44	1	2.8	1.9

Data on nutrient content from Zweifel-Schielly (2005).

^a Crude protein.

^b Average of the ranks for cellulose and lignin.

^c Average of the ranks for crude protein and fibre.

quality. This is an arbitrary assumption based on the fact that it is only known that these factors are important, but not how much each contributes to the nutritional quality of a food item (Maizeret et al., 1991; Tixier et al., 1997).

2.4. Data analysis

Data analysis was done on plant species groups because data on food quality were not available for individual species. Generalised linear models (GLM) were used to investigate the relationships between browsing by roe deer, forage quality and season. The response variable being discrete (number of browsing marks) we fitted a GLM with poisson distribution and log link. In the winter season, however, a GLM with normal distribution and identity link (which is equivalent to normal regression) provided better fit than poisson regression. Selection of species groups was defined and calculated according to Johnson (1980), i.e. the use of a species group was considered selective if the species group was used more than in proportion to its availability. The rank of availability of species group i within I ($i = 1, \dots, I$) and the

rank of usage of species group i within I were calculated for each sampling plot. The difference between the rank of availability and the rank of use of a species group was then tested by Wilcoxon signed rank test. Additionally, nonparametric confidence intervals (confidence level 0.95) were calculated. Statistical analyses were done using the statistical computing system R Version 1.7.1 (R Development Core Team, 2005).

3. Results

3.1. Nutritional quality of plant species groups

Rubus spp. and herbs were the species groups with the highest mean rank of nutritional quality, independent of season (Table 1). They were rich in crude protein but contained relatively low fibre. Graminoids were characterised by a high proportion of cellulose, while woody species contained major quantities of lignin. In contrast to the other plant species groups, the mean rank of nutritional quality of deciduous trees varied considerably between seasons. In autumn and spring, deciduous trees were

Table 2
Results of analysis of deviance on the effects of forage quality and season on the number of browsing marks per sampling plot

	df	R df	Poisson regression with log link				Normal regression ^a			
			Deviance	R Dev	F	P	Deviance	R Dev	F	P
Null model	80			11958				2303973		
Forage quality	1	79	1063	10895	1062.8	<0.001	198763	2105210	9.5	0.003
Season	2	77	1803	9092	901.7	<0.001	352872	1752338	8.4	<0.001
Forage quality \times season	2	75	592	8501	295.8	<0.001	178254	1574084	4.2	0.018

df: degrees of freedom; R df: residual degrees of freedom; R Dev: residual deviance.

^a Forage quality was square-root transformed.

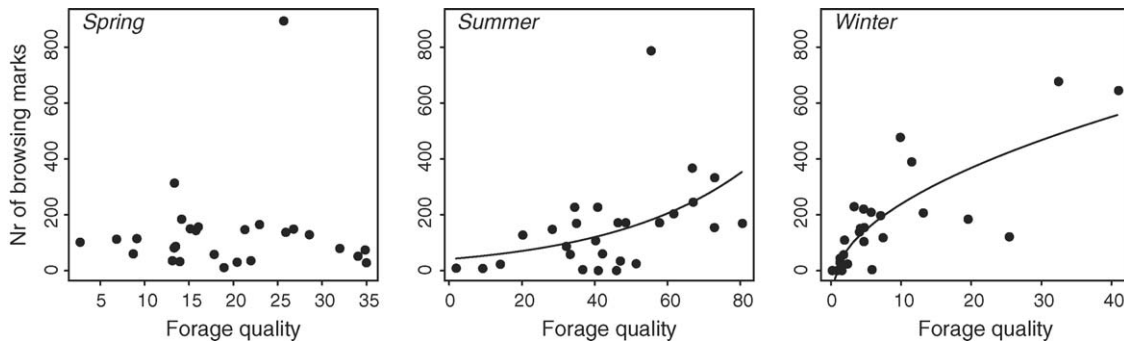


Fig. 2. Total number of browsing marks per sampling plot (20 m²) in relation to forage quality of the sampling plot in different seasons. The solid lines represent fitted glm-models: summer, $y = \exp(3.725 + 0.027x)$; winter, $y = -73.08 + 98.64x^{0.5}$. Note that x-axis scale differs between plots.

of relatively poor quality. However, moderate proportions of crude protein and relatively low fibre led to an increase in the nutritional quality relative to the other plant species groups in summer.

3.2. Inter-patch selection

Forage quality varied among sampling plots in all seasons, but variability was larger in winter than in summer and spring (coefficients of variation 1.262, 0.447, and 0.454, respectively). Both forage quality and season positively affected inter-patch selection (Table 2). However, there was a significant interaction between forage quality and season: the total number of browsing marks per sampling plot correlated with forage quality of a sampling plot in summer and winter, but not in spring (Fig. 2). Thus our study only partly supports the hypothesis of roe deer using patches with higher quality forage more intensively than other patches.

3.3. Intra-patch selection

Within patches, selection of high quality plant species groups was not consistent: while *Rubus* spp., the species group

with the highest mean rank of nutritional quality, was used more than in proportion to its cover in all seasons (Fig. 3), herbs were avoided despite their high relative quality (Table 1). Deciduous trees were used according to the seasonal variation in their nutritional quality: they were selected during the peak of relative quality in summer, whereas the number of browsing marks per sampling plot was proportional to availability in spring and winter. Concordant with their moderate to low nutritional quality, graminoids were avoided or used in proportion to their availability, respectively, in all seasons. In contrast, coniferous trees were selected in summer even though their nutritional quality was much lower than that of the other species groups. The number of browsing marks on deciduous trees in a sampling plot was not correlated with the cover of the higher quality species groups *Rubus* spp. and herbs (Fig. 4).

4. Discussion

Diet selection is a consequence of complex interactions of various factors and decisions made at different spatial and temporal scales, thus the application of optimal foraging theory to free ranging animals is difficult (Bailey et al., 1996; Litvaitis, 2000). Illius et al. (2002) previously investigated functional

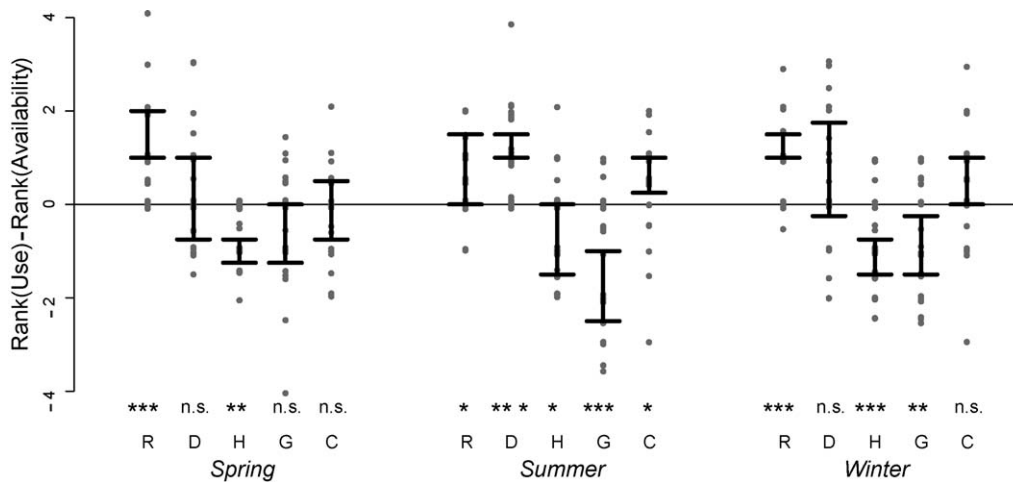


Fig. 3. Selection of different plant species groups by roe deer in spring, summer, and winter: difference between the rank of use of a species group and the rank of cover of the same species group in 27 sampling plots. Bars represent nonparametric, 95% confidence intervals. Dots represent sampling plots, they have been staggered on the y-axis for clarity. Significant departure from use in proportion to availability (horizontal line) is marked as: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (Wilcoxon signed rank test). R: *Rubus* spp.; D: deciduous trees; H: herbs; G: graminoids; C: coniferous trees.

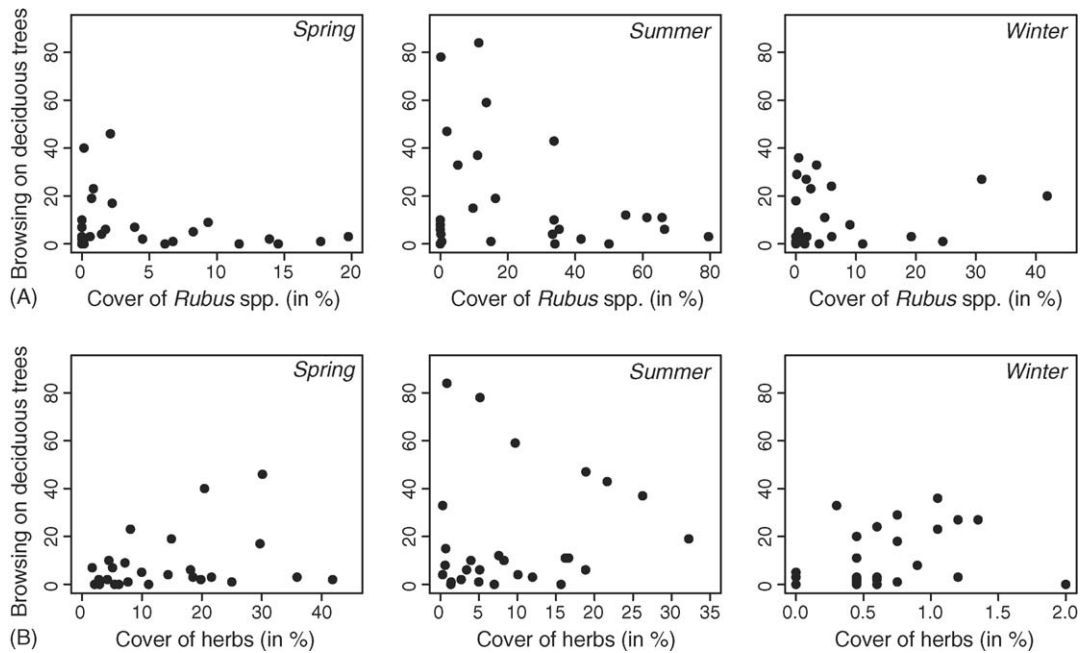


Fig. 4. Number of browsing marks on deciduous trees in a sampling plot (20 m²) in relation to the cover (%) of: (A) *Rubus* spp. and (B) herbs, respectively, in spring, summer, and winter. Note that *x*-axis scale differs between plots.

response mechanisms (use as a function of resource availability) in roe deer. However, this study involved selection of food patches at a much smaller scale than our study, namely at the scale of individual tree branches. They found that branch exploitation by roe deer is not governed by optimal patch use, but involves a trade-off between diet quality and quantity. In contrast, we found strong evidence for foraging behaviour of roe deer being governed by optimal foraging at the level of forage patches containing more than one plant species. On the one hand, roe deer selected forage patches with abundant high quality food (summer and winter), and on the other hand they adjusted their selectivity to the temporal variation in the quality of the different plant species groups. Thus, mechanisms of foraging behaviour can differ between scales at which foraging decisions take place. Consequently, the scale of measurements of a study has to conform to the scale of an organisms' response (Wiens, 1989).

Although foraging behaviour of roe deer seems to be concordant with optimal foraging theory in summer and winter, the lack of correlation between sampling plot quality and total number of browsing marks in spring indicates that the choices of roe deer at certain or all spatial scales may be restricted by other factors than forage availability and quality such as the spatial arrangement of plant species (Bergman et al., 2005), cover and visibility (Myerud and Ostbye, 1999; Moser, 2005), but also intraspecific and interspecific competition among individual animals, or social organisation of roe deer (Begon et al., 1990). For example, anti-predator behaviour may be an important constraint for does at the time of birthing in spring, resulting in a trade-off between selection of patches with high quality food and selection of cover (Myerud and Ims, 1999). Alternatively, the independence of browsing from sampling plot quality in spring might be explained by the high cover of

herbs in this season and the fact that herbs were avoided by roe deer despite their high relative quality. The avoidance of herbs may be the consequence of several factors: on the one hand, the significance of selection indices, like the one by Johnson (1980) used in this study, is limited for abundant, intensively used species such as herbs in spring, since the rank of use cannot exceed the rank of availability. Consequently, use can at most be proportional to availability. In the case of simultaneous selective feeding on other species, as, e.g. on *Rubus* spp. in our study, the rank of use may drop below that of availability despite intensive use. On the other hand, analysing nutritional quality at the level of plant species groups may obscure possible relationships between quality and usage of single herbaceous species, especially as herbs include a large number of species, which can differ considerably in nutrient content. Moreover, quality of roe deer forage may be affected by further chemical components, e.g. by defensive compounds such as tannins. However, roe deer are known to secrete tannin-binding proteins with their saliva (Hofmann, 1989; Robbins et al., 1995), thus the impact of defensive compounds on diet selection by roe deer is controversial (Verheyden-Tixier and Duncan, 2000; Clauss et al., 2003). Consequently, we need better knowledge of the factors that actually determine forage quality for roe deer, and we need to know more about the seasonal quality of individual plant species. This is not only necessary for herbs but also for deciduous trees, since it is known that selection among tree species occurs (Bergman et al., 2005).

Browsing on deciduous trees was not related to the availability of the higher quality species groups *Rubus* spp. and herbs. Thus, we conclude that availability of high quality forage does not directly affect the amount of browsing by roe deer on deciduous trees. In contrast, browsing on deciduous trees rather depends on their relative seasonal quality. In winter

and spring, when the relative quality of deciduous trees is rather poor, browsing on this species group seems to be a random process, since browsing intensity is only related to the cover of deciduous trees. Nevertheless, alternative food resources may be important insofar as the relative quality of tree browse depends on the quality of all the species present. Consequently, we expect deciduous trees to be selected by roe deer independent of their seasonal quality in sites with sparse high quality food.

5. Conclusions

Forest managers should take into account that availability and quality of food resources vary seasonally, thus the importance of alternative food resources may also differ between seasons. In order to avoid selective browsing by roe deer on deciduous trees in seasons where quality of deciduous trees is poor, appropriate forest management should provide abundant understory vegetation with high quality species such as *Rubus* spp. The establishment of such high quality alternative food resources requires good light conditions, e.g. by forest management measures that allow for higher canopy openness. *Rubus* spp. may not only protect tree saplings from heavy browsing by roe deer by providing better quality forage, it can, on the other hand, also reduce accessibility to saplings when occurring at high densities (Duncan et al., 1998). On the other hand, sapling protection restricted to the season when their nutritional quality is highest, could prevent selective browsing by roe deer on specifically sensible tree species especially in sites with sparse high quality forage.

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