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Resource selection by roe deer: Are windthrow gaps attractive feeding places?

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Abstract

Windthrow gaps are often regarded as attractive feeding places for roe deer *Capreolus capreolus* L. because they are considered to provide more forage than undisturbed forest stands. However, for temperate lowland forests in Central Europe, differences in the quantity of forage in gaps and undisturbed forest stands have not yet been quantified. In two deciduous forests in northern Switzerland, we studied seasonal forage availability in undisturbed forest stands compared to windthrow gaps, with the timber either cleared or uncleared, created by the storm Lothar in 1999. To assess the attractiveness of windthrow gaps for foraging roe deer, we measured seasonal browse consumption by roe deer in these three forest structure types. The amount of available forage mainly varied between seasons and, to a lesser extent, between forest structure types. Windthrow gaps did not generally provide larger quantities of food resources than adjacent undisturbed forest stands. Browse consumption was not directly related to forest structure type, but seems to be dependent on the vertical structure of the understory vegetation (herb/shrub layer). Within forest structure types, browse consumption was constant over seasons, but browsing on individual plant species varied according to season and study site.

Keywords: Diet selection; Food availability; Foraging; Forest structure; Gap; Roe deer

1. Introduction

Windthrow gaps have a major effect on both the fauna and flora of ecosystems (Wermelinger et al., 1995; Wohlgemuth et al., 2002). The numerous clearings created by the winter windstorm Lothar in the European forests in December 1999 drastically altered important habitat structures for deer, such as forage patches, resting areas, and connecting corridors. Generally, food resources and structural qualities, such as concealment cover, are important factors for habitat selection by roe deer *Capreolus capreolus* L., a widespread ungulate in European forests (Tufto et al., 1996; Andersen et al., 1998; Mysterud et al., 1999). Widmer et al. (2004) found that the size of the home ranges of roe deer in northeastern France declined after the windstorm Lothar and the home ranges shifted towards the windthrown areas. Similarly, the size of roe deer home ranges in western France was negatively correlated with edge density (contacts between different vegetation patches) after the windstorm (Said and Servanty, 2005). Various authors have suggested that windthrow gaps provide larger quantities of food than undisturbed forests and are therefore attractive feeding places for roe deer (Gaillard et al., 2003b; Widmer et al., 2004). However, only a few studies have actually quantified the impact of clearings on the availability of food resources and on browse consumption by ungulates. Stewart et al. (2000) showed that white-tailed deer *Odocoileus virginianus* visited clearings with intermediate forage biomass more intensively than clearings with low forage biomass or forest patches with high forage biomass.

Although roe deer are generalist herbivores that feed on a variety of plant species (Klötzli, 1965; Kossak, 1983; Duncan et al., 1998), they are dependent on high quality food due to their small body size (Illius and Gordon, 1992; Van Soest, 1994). The composition of available plant species (and thus food quality for roe deer) may vary between windthrow gaps and the adjacent undisturbed forest due to differences in light conditions (Wohlgemuth et al., 2002). Moreover, the quantity

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and composition of food resources do not only vary spatially with forest structure but also temporally with season (Morellet and Guibert, 1998; Brokaw and Lent, 1999).

The aim of this study was to quantify the seasonal availability of food resources in windthrow gaps and in undisturbed forest stands, and to assess seasonal browse consumption by roe deer in these forest structure types. In two lowland forests of northern Switzerland we tested: (1) whether windthrow gaps provide more forage for roe deer than adjacent undisturbed forest stands, (2) whether roe deer consume more browse in windthrow gaps than in undisturbed forest stands, (3) whether the quantity and composition of consumed browse differs between cleared and uncleared gaps, and (4) whether results vary according to season.

2. Materials and methods

2.1. Study sites

The study was carried out in two deciduous forests in the Central Plateau of Northern Switzerland at 400–450 m above sea level. The forest in Habsburg (Canton Aargau; 47°28′N, 8°12′E) covers 1.8 km^2, and that in Muentschemier (Canton Bern; 47°01′N, 7°10′E) 0.45 km^2. Both forests contain two substantial gaps (0.04–0.2 km^2) caused by the storm Lothar in December, 1999. One gap in each study site was timber cleared in 2000, and the other was left uncleared. In both sites, the tree layer is dominated by *Fagus sylvatica*, accompanied by *Picea abies*, *Acer pseudoplatanus* (only Habsburg), *Fraxinus excelsior*, and a few *Abies alba*. The understory vegetation in both forests is similar to the vegetation association woodruff beech forest *Galio odorati–Fagetum typicum* (Keller et al., 1998), which is very common in Central Europe (Ellenberg, 1988). In Habsburg, several vegetation types can be distinguished within this vegetation association (Burnand et al., 1982). The study was restricted to the three most widespread vegetation types, which covered altogether approximately 1.1 km^2: (i) woodruff-beech forest, (ii) woodruff-beech forest with >50% estival cover of *Carex brizoides*, and (iii) woodruff-beech forest with >30% estival cover of *Rubus* spp. Roe deer are the only large herbivore in the studied areas. Assessing roe deer density directly would have been beyond the scope of this study, but in Habsburg the local hunting authorities estimated roe deer density at 14–17 individuals/km^2 forested area in 2000 (spotlight counts, Mayle et al., 1999). These estimates have to be interpreted with caution, since spotlight counts are not a very reliable monitoring tool (Gaillard et al., 2003a).

2.2. Sampling design and assessed parameters

The study sites were stratified according to the following forest structure types: ‘undisturbed forest’ (>60% canopy cover), ‘timber cleared windthrow gap’, and ‘uncleared windthrow gap’. In Habsburg, each forest structure type was additionally stratified according to vegetation type. In each stratum, 6–10 sampling plots were established at random locations, resulting in a total of 55 sampling plots in Habsburg and 26 sampling plots in Muentschemier (stratified random sampling; details in Moser, 2005). As vegetation cover in the windthrow gaps was expected to be unevenly distributed, long narrow plots (1 m × 20 m) were chosen (Dale, 1999).

The amount and composition of available food resources were estimated in terms of percent cover of all plant species present. Plants included herbs, shrubs, and trees (estimated to the nearest 5%). Cover estimates are a rough index of biomass (Humphrey, 1985; Hermy, 1988), although not all of the measured biomass might actually be available to roe deer. However, very few species are not browsed by roe deer because they have chemical, structural or morphological defences (Klötzli, 1965; Kossak, 1983; Tixier et al., 1997). All measurements were restricted to heights from 0 to 150 cm above soil level, which corresponds approximately to the range of browsing roe deer (Maizeret et al., 1991; Duncan et al., 1998). The abundance of browsing marks on individual plant species was used as an index for browse consumption by roe deer (for further details, see Moser et al., 2006; cf. also Wallmo et al., 1973; Mysterud et al., 1999). Unlike grazers, concentrate selecting roe deer remove only small parts of individual plants, so that complete removal of above-ground biomass is unlikely (Klötzli, 1965; Hofmann, 1989). The nomenclature of plant species is according to Binz and Heitz (1990).

The vertical structure of the understory vegetation (herb/shrub layer) was characterised by the mean vegetation height of a sampling plot and the distribution of vegetation heights within a sampling plot (similar to the distribution of tree heights used by Kuuluvainen et al., 1998). Vegetation height was measured at 20 points along each sampling plot by dropping a cardboard square (25 cm × 25 cm) with a centre hole from the top of a measuring rod (150 cm) onto the vegetation. The number of browsing marks per sampling plot dropped significantly when the mean vegetation height exceeded 40 cm (Fig. 1). Thus, the distribution of vegetation height was calculated as the proportion of measurements >40 cm in each sampling plot. Data were sampled in three consecutive seasons: summer (July/August 2001), winter (February 2002), and spring (April 2002).

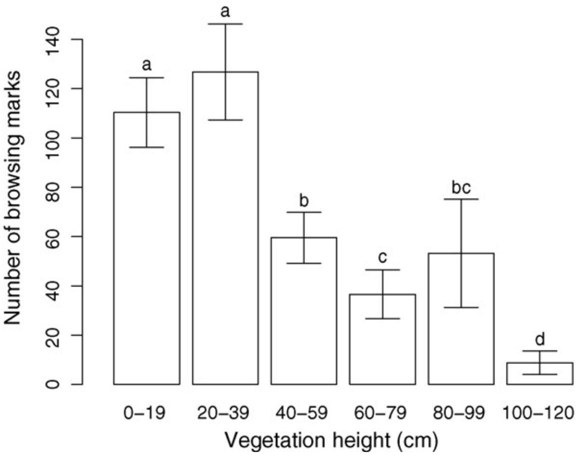

Fig. 1. Number of browsing marks in relation to vegetation height (mean ± S.E.). Different letters indicate significant differences between mean values based on pairwise two-sided Wilcoxon rank sum tests.

In the timber-cleared gap in Muentschemier, data sampling was restricted to the summer season because the herb layer was removed by the local forest management team in autumn 2001.

2.3. Data analysis

Differences in the total number of browsing marks and the total vegetation cover between forest structure types were tested using a pairwise two-sided Wilcoxon rank sum test (differences between forest structure types within season) and a pairwise two-sided Wilcoxon signed rank test (differences between seasons within forest structure type), respectively. Differences in the total number of browsing marks between classes of vegetation height were also tested using a pairwise two-sided Wilcoxon rank sum test. Non-parametric statistics were used because variances were very heterogeneous and sample sizes differed considerably. *p*-Values were corrected for multiple comparisons (Benjamini and Hochberg, 1995). Linear regression was used to investigate the effect of study site, season, forest structure type, and vertical structure of the understory vegetation on the number of browsing marks. A logarithmic transformation of the response variable was required to meet assumptions of normality and homogeneity of variances. Multivariate patterns of browse consumption were displayed by means of Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980). Species, which were browsed in less than two sampling plots were excluded from the analysis in order to minimise the effect of erroneously, identified browsing marks. In some sampling plots no browsing was found at all, but DCA cannot process all-zero samples (Legendre and Legendre, 1998). Since these samples contain important information and should not be omitted from the analysis, zero values were replaced by an arbitrary value of 0.0001, which is common practice in other multivariate techniques (e.g. compositional analysis, Aebischer et al., 1993). To test for differences in the composition of browsed plant species between seasons and forest structure types, two-sided *t*-tests were done on the corresponding DCA scores to obtain pairwise comparisons. *p*-Values were corrected for multiple comparisons (Benjamini and Hochberg, 1995). The statistical computing system R version 1.7.1 (R Development Core Team, 2005) was used for all statistical analyses and the package 'vegan' by J. Oksanen (version 1.6-0; www.R-project.org) for the DCA.

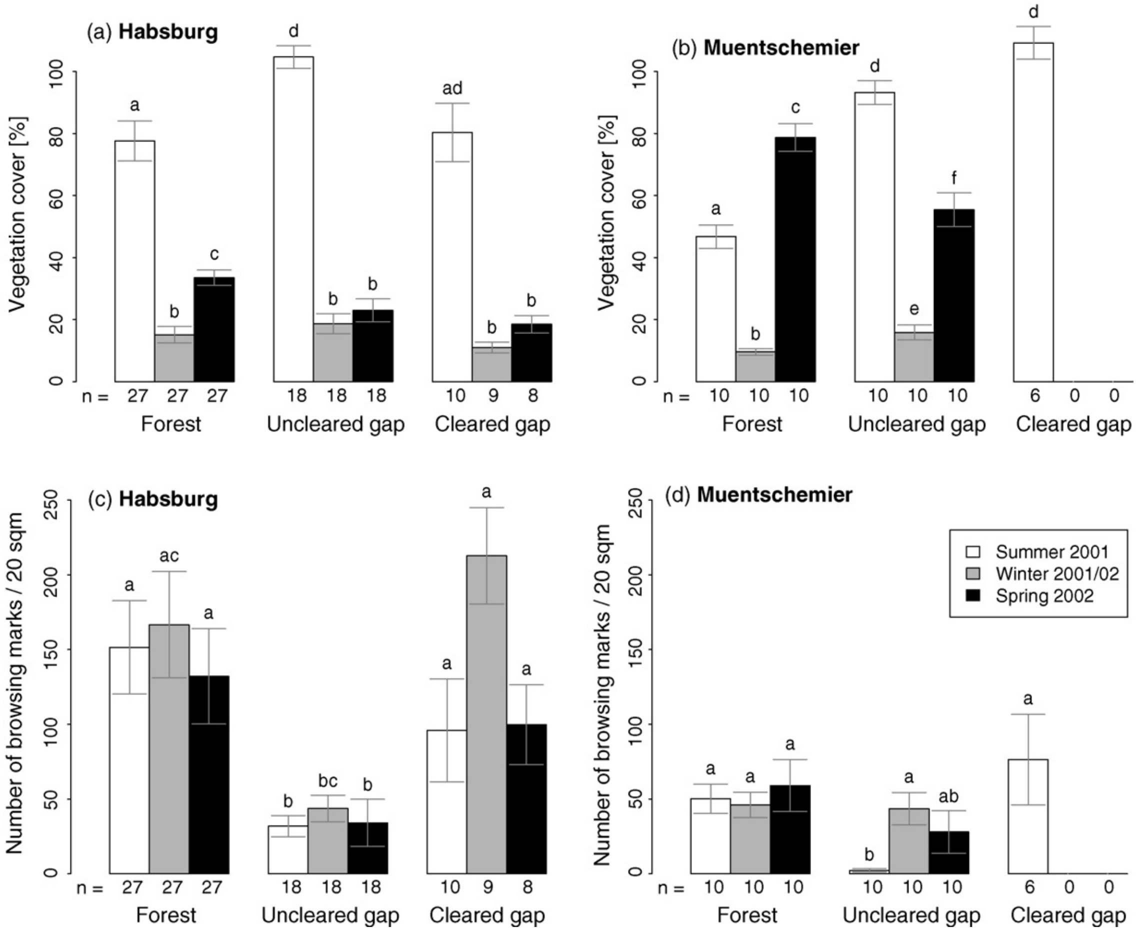

Fig. 2. (a, b) Vegetation cover (sum of percent cover of all plant species; may exceed 100% as species can overlap), and (c, d) number of browsing marks in different forest structure types and seasons (mean ± S.E.). Different letters indicate significant differences between mean values based on pairwise two-sided rank tests. Only differences between forest structure types within the same season (Wilcoxon rank sum test) and between seasons within the same forest structure type (Wilcoxon sign rank test) were tested.

3. Results

3.1. Forage availability

The seasonal pattern of overall forage availability was similar in undisturbed forest stands and windthrow gaps (Fig. 2a and b). In summer, vegetation cover was high in both the undisturbed forest stands and the windthrow gaps, and the overall cover was five to seven times greater than in winter. In spring, vegetation was sparse in Habsburg, but more abundant in the forest stands than in the timber cleared and uncleared windthrow gaps. This difference was mainly due to the geophyte *Anemone nemorosa*, which was absent in the windthrow gaps. In contrast, spring vegetation in Muentschemier was dense. In undisturbed forest stands, it covered an even larger area than the summer vegetation did. As in the forest in Habsburg, spring vegetation in Muentschemier mainly consisted of *A. nemorosa*, which was abundant not only in the undisturbed forest, but also in the uncleared windthrow gap.

3.2. Browse consumption in windthrow gaps versus undisturbed forest

The vegetation cover varied considerably with seasons, but the number of browsing marks within the forest structure types was very constant (Fig. 2c and d). There was no difference between seasons except in the uncleared gap in Muentschemier. In contrast, browsing intensity differed in the different forest structure types, and the number of browsing marks was substantially lower in the uncleared gap than in the forest or timber-cleared gap, especially in summer. However, there was no difference in the total number of browsing marks in the undisturbed forest and in the timber-cleared gaps. Browse consumption in the three forest structure types seems to be related to both the study site and the vertical structure of the understory vegetation (Table 1). While the vertical structure explains 20.9% of the variance in the number of browsing marks, the study site explains only 4.6%. Forest structure type per se, however, does not seem to adequately predict the amount of browse consumed by roe deer.

Table 1
Results of multiple linear regression on the effects of study site, season, forest structure type, and vertical structure of the understory vegetation (proportion of vegetation height measurements >40 cm) on the number of browsing marks per sampling plot (log-transformed)

Explanatory variables	Coefficient	*t*	*p*
Study site	−0.79	−3.88	0.0001
Season	−0.06	−0.50	0.6161
Forest structure	0.24	1.67	0.0962
Proportion of vegetation >40 cm	−2.53	−7.91	<0.0001

F-statistic: 20.93 on 4 and 223 degrees of freedom; R^2: 0.273.

3.3. Plant species browsed in the different forest structure types

In summer and winter, the plant species browsed in the gaps differed considerably from those browsed in the undisturbed forest (Fig. 3; $p < 0.01$, pairwise, two-sided *t*-tests on DCA Axis 1 scores or DCA Axis 2 scores, respectively). Leaves from deciduous trees constituted a large part of the deer's diet in the undisturbed forest in both summer and winter. In the timber cleared and uncleared gaps, the composition of the browsed species was similar in summer ($p > 0.05$, pairwise, two-sided *t*-tests on the DCA Axis 1 scores and the DCA Axis 2 scores, respectively), and roe deer mainly fed on *Rubus* spp. However, marked differences in the browsing in the different windthrow gaps were found in winter and spring: while *Rubus* spp. was again the main food in the uncleared windthrow gaps in both seasons, graminoids such as *Luzula luzuloides* or *Carex* spp. were intensively browsed in the timber cleared gaps (only data from Habsburg available; $p < 0.001$, pairwise, two-sided *t*-tests on DCA Axis 1 scores). In Habsburg, the composition of species browsed by roe deer was different in the undisturbed forest and windthrow gaps in spring, whereas no difference was found in Muentschemier (Habsburg: $p < 0.001$; Muentschemier: $p > 0.05$, pairwise, two-sided *t*-tests on DCA Axis 1 scores). This difference between sites is due to *Anemone nemorosa*, which was intensively browsed in both sites in spring, but was not available in the windthrow gaps in Habsburg.

4. Discussion

The differences in food availability found in the undisturbed forest stands and the windthrow gaps in our study sites depended both on season and study site. Contrary to our expectations, food availability was not generally higher in the windthrow gaps than in the adjacent undisturbed forest stands. Differences between the gaps and the undisturbed forest stands depended heavily on local vegetation characteristics, such as the presence or absence of geophytes in spring. Gaillard et al. (2003b) and Widmer et al. (2004) argued that fallen trees increase food availability in the short term by making accessible tree crowns and *Hedera helix* L. One year after the storm, no browsing marks were observed on fallen trees in our study sites, even though some of the trees had resprouted (B. Moser, pers. obs.). Thus, the importance of fallen trees as a food resource for roe deer may be both limited in time and depend on the availability of alternative food resources in the understory vegetation (Moser et al., 2006).

Food availability in spring and summer are regarded as critical for the nutrition of both fawns and female roe deer (Pettorelli et al., 2005). Consequently, the use of windthrow gaps for foraging should vary seasonally according to forage availability. However, browse consumption within forest structure types was constant over the year (except in the uncleared gap in Muentschemier) and the amount of removed browse mainly depended on the vertical structure of the understory vegetation. Various authors have suggested that resource selection of roe deer is connected to the availability of concealment cover, which reduces the risk of predation (Aulak and Babinska-Werka, 1990; Tufto et al., 1996). The low number of browsing marks in plots with a large proportion of high vegetation indicates, on the other

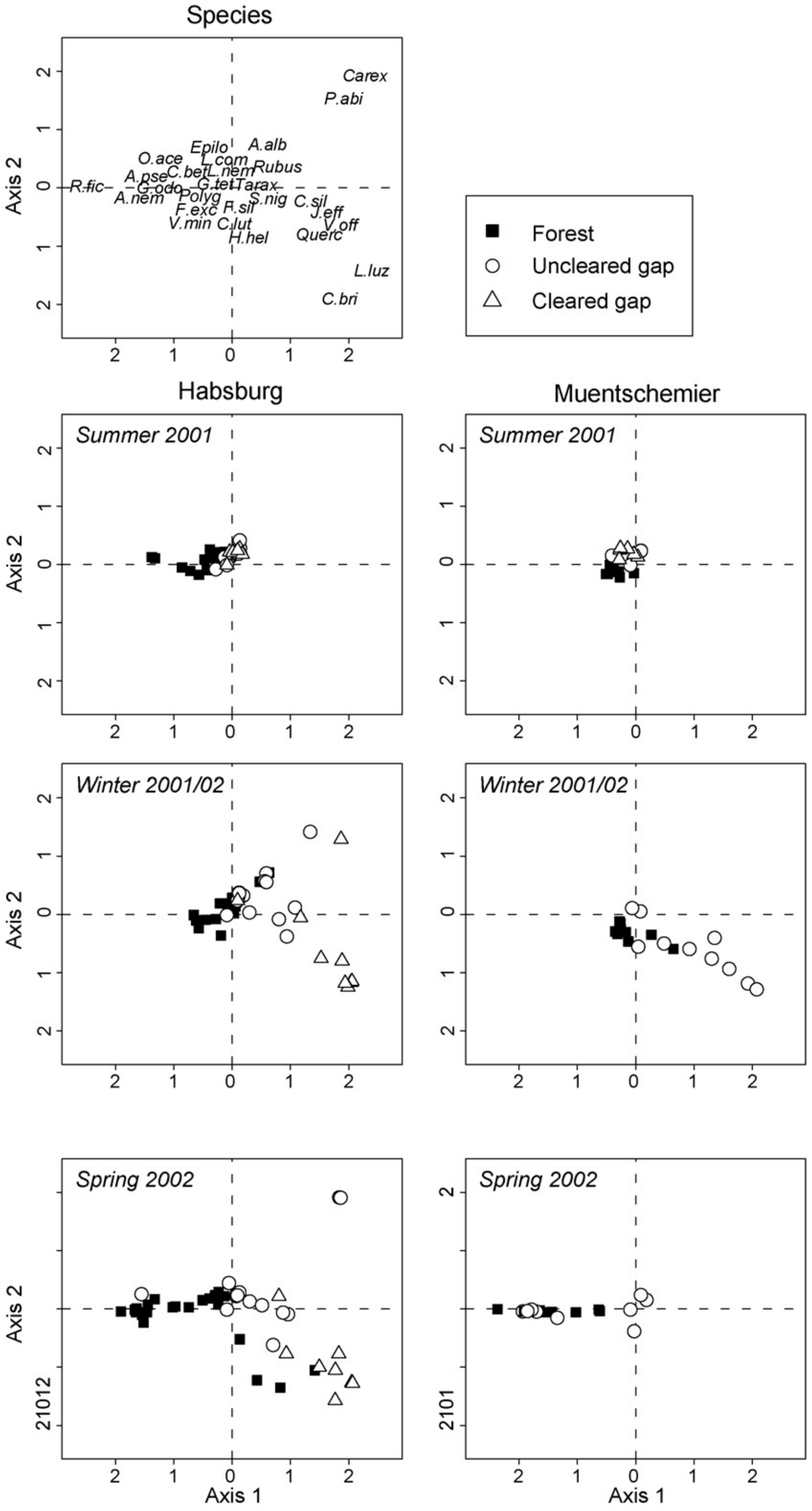

Fig. 3. Composition of species browsed by roe deer in different forest structure types in the two study sites, Habsburg and Muentschemier, in summer 2001, winter 2001/02, and spring 2002: Detrended Correspondence Analysis (DCA) of number of browsing marks. Points are labelled according to forest structure type. For legibility reasons, only species browsed in at least 20% of the sampling plots are displayed in the species plot. Species: A.alb, *Abies alba*; A.nem, *Anemone nemorosa*; A.pse, *Acer pseudoplatanus*; C.bet, *Carpinus betulus*; C.bri, *Carex brizoides*; C.lut, *Circaea lutetiana*; C.sil, *Carex sylvatica*; Carex, *Carex* spp.; Epilo, *Epilobium* spp.; F.exc, *Fraxinus excelsior*; F.sil, *Fagus sylvatica*; G.odo, *Galium odoratum*; G.tet, *Galeopsis tetrahit*; H.hel, *Hedera helix*; J.eff, *Juncus effusus*; L.com, *Lapsana communis*; L.luz, *Luzula luzuloides*; L.nem, *Lysimachia nemorum*; O.ace, *Oxalis acetosella*; P.abi, *Picea abies*; Polyg, *Polygonatum* spp.; Querc, *Quercus* spp.; R.fic, *Ranunculus ficaria*; Rubus, *Rubus* spp.; S.nig, *Sambucus nigra*; Tarax, *Taraxacum* spp.; V.min, *Vinca minor*; V.off, *Veronica officinalis*. Eigenvalue axis 1 = 0.800; eigenvalue axis 2 = 0.645; length of gradient along axis 1 = 4.443.

hand, that vegetation may also be too dense and have visual obstructive effects. Low visibility requires animals to be more vigilant, which reduces the amount of time available for foraging (Mrlik, 1998; Mysterud and Ostbye, 1999).

In North America, the nutritional quality of woody species has been shown to be lower in gaps than in undisturbed forests because the nitrogen concentration is lower and the tannin content is higher (Bunnell and Jones, 1984; Van Horne et al., 1988; Happe et al., 1990). Experimental studies indicate that this also applies to graminoids and herbs in the Swiss Central Plateau (Moser and Schütz, 2006). Roe deer are concentrate selectors and thus depend on high quality food (Hofmann, 1989). If windthrow gaps have lower forage quality, this may reduce their attractiveness as feeding places for roe deer even though they may have ample forage available at certain times, as e.g. in our study sites in summer.

We conclude that food quantity per se is an unreliable indicator of whether a feeding place is attractive or not. Our study indicates that the structural components of forest stands are important, since they are likely to affect essential parameters such as the availability of concealment cover, the level of visibility and the quality of food. It remains to be seen how widely this finding can be applied, since this study was restricted to just two sites and the gaps were rather small in comparison to the overall forest area. Further studies would greatly benefit from using larger sampling areas in combination with direct monitoring of roe deer.

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