Natural forage composition decreases deer browsing on Picea abies around supplemental feeding sites

Pablo Garrido[a], Sara Lindqvist[b] & Petter Kjellander[c]

[a] Faculty of Forest Sciences, School of Forest Management, Swedish University of Agricultural Sciences, PO Box 43, Skinnskatteberg 730 91, Sweden

[b] Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, Uppsala 750 07, Sweden

[c] Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan 73091, Sweden
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RESEARCH ARTICLE

Natural forage composition decreases deer browsing on *Picea abies* around supplemental feeding sites

Pablo Garrido[a*], Sara Lindqvist[b] and Petter Kjellander[c]

[a]Faculty of Forest Sciences, School of Forest Management, Swedish University of Agricultural Sciences, PO Box 43, Skinnskatteberg 730 91, Sweden; [b]Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, Uppsala 750 07, Sweden; [c]Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan 73091, Sweden

In southern Sweden, maintaining high cervid densities through supplemental feeding has become a common management practice. We aim at investigating deer browsing pressure on young Norway spruce in relation to distance from supplemental feeding sites. Because available forage is considered important in understanding browsing patterns, we modeled several factors affecting food availability, and their interaction effect with distance. We confirmed earlier studies about a locally high browsing pressure on natural vegetation adjacent to supplemental feeding sites where browsing pressure declined with distance and alternative forage abundance. Novel is that browsing on spruce occurred in 27.6% of the investigated plots. The browsing pressure of those plots averaged 9%. Distance was the most important factor in relation to browsing. The interactive effect of occurring field layer (FL), and deciduous trees was also highlighted as these significantly affected the relationship between browsing pressure on spruce and distance. In the studied conditions, browsing pressure ceased at ca. 205 m, whereas in scenarios of an abundant FL, browsing levels were negligible already at 0 m from supplemental feeding sites. We suspect that most of the browsing was caused by fallow deer in our study area.

Keywords: browsing pressure; *Dama dama*; multipurpose management; Norway spruce; supplemental feeding

Introduction

Supplemental feeding of cervids has become a widespread management practice throughout northern Europe and parts of North America especially during winter time (Putman & Staines 2004). At the landscape scale, supplemental feeding contributes significantly to available forage stocks, to which deer might adapt their spatial feeding strategy (Côte et al. 2004; Sahlsten et al. 2010). Accordingly, the spatiotemporal distribution in deer might be influenced by forage availability as well as qualitative and quantitative forage characteristics (Moen et al. 1997; Côte et al. 2004; Newman 2007; Sahlsten et al. 2010). Supplemental feeding is primarily provided in order to support deer winter survival and enhance fitness when natural forage availability is scarce, often intending to maintain high densities of deer for hunting (Putman & Staines 2004). It is also used to mitigate or to reduce browsing pressure in production and conservation forestry and on agricultural systems (Gill 1992; Peek et al. 2002; Putman & Staines 2004). Such management actions are aimed at steering spatial movements of deer away from valuable tree stands and agricultural crops (van Beest et al. 2010). Supplemental feeding has been successfully applied in several studies for such purposes

(Steinn 1970; Ball et al. 2000; Peek et al. 2002; Sahlsten et al. 2010). However, some studies also report an effect of increased browsing pressure adjacent to supplemental feeding sites as a consequence of the redistribution of animals in the landscape and increased density of deer at these sites (e.g. Schmidt & Gossow 1991; Gundersen et al. 2004).

Supporting high abundances of deer is often favored by economic incentives related to hunting activities (Gordon et al. 2004). Landowners are often interested in managing both forest and deer, although research aimed at optimizing multiple uses of landscapes is missing, and applicable management tools seem to be lacking.

In Sweden, maintaining high densities of deer through supplemental feeding has become a common management practice across the southern part of the country (Carlström & Nyman 2005). Still, deer abundance and its impact on forestry has demonstrated a positive relationship (Gill 1992), i.e. high deer densities might obstruct forest regeneration by increased browsing (Angelstam et al. 2000; Fuller & Gill 2001; Bergqvist et al. 2003). In Sweden, planting Norway spruce (*Picea abies* (L.) Karst.), one of the least palatable tree species (Bergström & Hjeljord 1987; Gill 1992; Månsson et al. 2007), is an

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attempt to reduce browsing pressure on economically valuable tree species as well as a prevalent and increasing (Forest Statistics of Sweden, http://www.slu.se/riksskog-staxeringen) silvicultural strategy (Bergquist & Ölander 1998). Browsing pressure subjected by roe deer (*Capreolus capreolus* L.) on spruce seedlings in newly established plantations has been well documented (e.g. Bergquist & Ölander 1996; Kullberg & Bergström 2001). Yet, browsing by other cervid species on young spruce seedlings and trees is partly unknown and deserves further consideration. The introduced fallow deer (*Dama dama* L.) has increased in distribution as well as in numbers from approximately 7000 wild living animals in 1955, after harvest, to 110,000 deer in 2005 (Bergström & Danell 2009). The species is generally described as a potential problem in agricultural fields but not as a problematic deer species in forest plantations or browsing on spruce seedlings (Carlström & Nyman 2005; Nichols 2013). However, when fallow deer are offered supplemental winter food ad libitum, the species can become locally abundant. These conditions are becoming more and more common in southern Sweden, and knowledge-based solutions for multipurpose landscape management are highly desirable. In order to suggest plausible management alternatives aimed at maximizing game and timber yields, landscape and habitat characteristics potentially affecting fallow deer browsing patterns need to be considered.

The aim of this paper is to model fallow deer browsing pressure on young Norway spruce in relation to distance from supplemental feeding sites. According to the literature, a higher browsing pressure in the nearest vicinity of feeding sites is expected (Schmidt & Gossow 1991; Hörnberg 2001; Gundersen et al. 2004; Sahlsten et al. 2010; van Beest et al. 2010). Because available forage is considered important in understanding browsing patterns (Mitchell & McCowan 1986; Månsson 2007), we control in the model for a number of factors affecting food availability, and their interaction effect with distance. These factors are the distance from supplemental feeding site, proportions of Scots pine (*Pinus sylvestris* L.) and deciduous trees, and field layer (FL; amount of dry biomass), all of which previously have been identified as key factors in decreasing the deer browsing in coniferous tree plantations (Mitchell & McCowan 1986; Welch et al. 1991; Garrido 2011).

This information will help managers to identify locations for supplemental feeding sites for fallow deer, while minimizing browsing effects on young Norway spruce.

Materials and methods

The study was conducted within the boreonemoral zone (Bohn et al. 2004) at Koberg estate (58°N and 12°E) in southwestern Sweden (Figure 1). The area covers ca. 9000 ha with approximately 79% forest, 16% agriculture areas, and the remaining 5% consist of mires, small lakes or gardens (Winsa 2008). The average annual precipitation is around 700 mm, of which 15% is snowfall. The vegetative growth period calculated from daily mean temperature >5°C is 190 days (Swedish Meteorological and Hydrological Institute [SMHI] 2012). Tree coverage is dominated by coniferous tree species such as Norway spruce and Scots pine; however, other deciduous and hardwood species also occur in the study area (see Garrido 2011). The FL consists primarily of blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.) and heather (*Calluna vulgaris* (L.) Hull). The open arable and pastures lands are specially cultivated to sustain high population densities of sympatric large herbivore species (e.g. fallow deer, moose (*Alces alces* L.), and roe deer). Deer populations are artificially fed during winter with a total of 500–700 tons/year of silage at >50 supplemental feeding sites (Garrido 2011). Deer densities were estimated in 2007 by a distance sampling procedure (Buckland et al. 2001) based on observations along 85 transects each 1km long and randomly distributed within the study area. Fallow deer density was estimated at 327 (23%CV) animals/ 1000 ha, while roe deer and moose densities were much lower and estimated at 17 (24%CV) and 6.5 (40%CV) animals/1000 ha, respectively (Walander 2012).

Study design

The study was conducted during May–August in 2010. A total of 24 supplemental feeding sites was selected based on their location (Figure 1) to homogenously cover the study area available for research (i.e. varying property rights impeded coverage of the entire study area). At each feeding site, six plots (4 m radius) were systematically surveyed in every cardinal direction at 0, 50, 100, 200, 300, and 400 m from the feeding site, totaling 557 surveyed plots (some plots were removed when their location fell within open water, animal enclosures, etc.). Plot 0 was defined as the closest coniferous tree (i.e. trees ≥ 0.25 m height) at the surveyed direction. Once plot 0 was established, the remaining plots were defined using a hand-held GPS (Garmin 60CSx) in a 400-m long transect.

The term "browsing pressure" is defined as the proportion of browsed available twigs (Bergström et al. 1995; Hörnberg 2001). In order to estimate browsing pressure, all available and browsed twigs on Norway spruce trees (<1 m and/or 1–4 m height) closest to the plot center were counted. On trees 1–4 m high was the examination limited to only one branch for the browsing pressure estimate; hence, a browsing index per plot is considered as the statistical unit. Only winter feeding marks were assessed, i.e. twigs consumed or browsed during the previous winter (all but actual spring growth
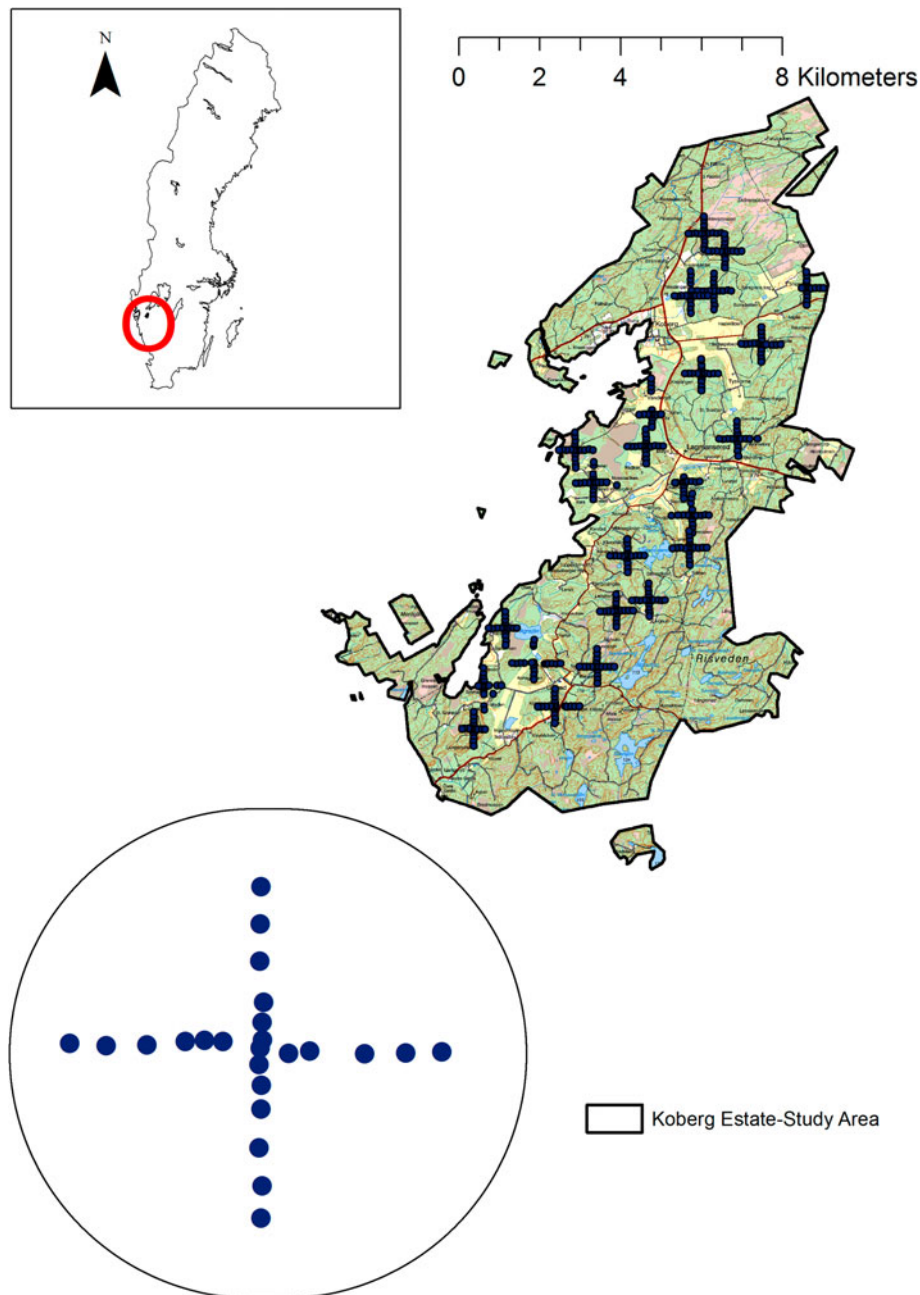
Figure 1. Location of the study area at Koberg estate in southwestern Sweden. Distribution of the selected supplemental feeding sites in the present study, including detail of study design around the feeding sites.

was assessed), although it is challenging to distinguish the feeding marks from different deer species (Månsson 2007). Therefore, it was assumed that if a strong spatial pattern of browsing pressure in relation to the feeding sites was found, it is likely that it was mainly caused by the abundant fallow deer population. This deer species represents more than 93% of the total number of animals of different deer species found in the study area (Walander 2012). However, we are aware of that both moose and roe deer could to some extent have affected the

found browsing pressure (Bergquist & Ölander 1996; Kullberg & Bergström 2001; Nichols 2013).

Explanatory factors

Alternative forage has been suggested as an important factor related to browsing occurrence (Mitchell & McCowan 1986). To examine to what extent alternative food availability affects the relationship between browsing pressure and distance, data on FL, as well as the

proportions of Scots pine and deciduous tree species, were estimated. The proportions of all pine and deciduous trees were visually estimated within a 20 m radius around each plot by approximating the relative abundance (%) of the mentioned tree species present in the spruce dominated forest matrix.

Sampling of FL biomass included blueberry, lingonberry, and heather. In the center of each plot, a 25 × 25 cm wooden frame was placed and all specimens of the three target species were cut, separated, and dried at 70°C for a minimum of 72 hours. Dry biomass was weighed to the nearest gram with a precision scale (Bergqvist et al. 1999).

Modeling procedure

Generalized linear mixed models (GLMMs; lme4 package; Bates et al. 2008) were used in order to assess the browsing pressure occurring on young Norway spruce trees (<1 m, 1–4 m height) and to estimate the extent of previously identified factors on browsing occurrence around supplemental feeding sites. Thus, no model selection procedure was utilized.

A GLMM can be explained as a combination of a general linear model and a mixed effects component, i.e. both accounting for fixed and random effects (Zuur et al. 2009). Briefly explained, fixed effects affect the mean of the population (y), while, in our study plots, random effects influence the variance of y (see also Crawley 2007). GLMMs are especially useful when collected data might suffer from spatial or temporal autocorrelation (Crawley 2007; Zuur et al. 2009). In our study area, neighboring supplemental feeding sites might attract the same deer. Hence, potential autocorrelation (Crawley 2007) between supplemental feeding sites was controlled for by their inclusion as random factors in our model.

All analyses were made using the free statistical software R version 2.15.1 (R Development Core Team 2012). GLMMs (Zuur et al. 2009) with binomial errors (logit link) were fitted to test the relationship between the browsing pressure on young Norway spruce as the response variable, and distance from supplemental feeding sites as the explanatory variable, plus the two way interactions between distance and the aforementioned alternative forage factors; distance × FL; distance × pine proportion (PP); distance × deciduous tree proportion (DP; see Supplemental data, Model S1).

FL was treated as a continuous factor [g/m^2] constituted by the total sum of available dry biomass of blueberry, lingonberry, and heather sampled at each plot. We model two different scenarios with "high" and "low" FL abundance. These scenarios can reflect either deep snow cover vs. no snow cover or other factors like the mere scarcity or abundance of the mentioned species. The proportion of Scots pine and deciduous trees were

treated as continuous factors as well as distance from supplemental feeding sites.

The Pearson's correlation matrix obtained from the fitted model output was used to avoid autocorrelation ($r \geq 0.7$; Stighäll et al. 2011) between the response and the different factors and interactions. Additionally, in order to express the amount of variation in the response variable explained by the model, the pseudo-R^2 parameter was calculated.

Results

In total, 557 plots were surveyed to assess browsing pressure on Norway spruce. The species was found in 319 plots. This number was considered our sample size for further analysis (Figure 2). Browsing occurred in 27.6% of the plots (88 out of 319) across the study area with a mean browsing pressure on spruce of 0.09 ± 0.15 (SD) of the available twigs per plot (arithmetic mean; $n = 88$). In 231 plots, browsing was not observed.

Browsing pressure around supplemental feeding sites

The distance from supplemental feeding sites had a highly significant effect on browsing pressure on young Norway spruce trees (Table 1). The estimated browsing pressure within the study area decreased with increasing distance from supplemental feeding sites (Figure 3). Distance appears to be the most important factor (z value = −16.35) in relation to the response variable (Table 1), although the relationship was also influenced by additional factors concerning other available forage resources, specifically the amount of FL (z value = −12.04) as well as the proportion of deciduous trees (z value = −4.19) and pine (z value = 3.89; Table 1). The interaction between distance and preferred food (FL and deciduous trees) was significant with positive effects, i.e.
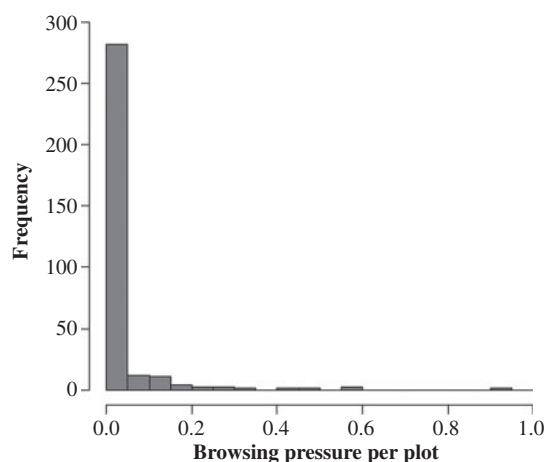

Figure 2. Histogram representing the frequency of surveyed plots ($n = 319$) at different intervals of browsing pressure. The X axis denotes upper interval limits of browsing pressure. Bars were generated in 5% intervals.

Table 1. The GLMM fitted model with browsing pressure as the response variable presenting degrees of freedom of each factor, estimates, standard error as well as z and p values of all model parameters.

	df	Estimate	SE	z value	p value
Intercept		−3.16	0.34	−9.36	<0.001
Distance	1	−0.01	8×10^{-4}	−16.35	<0.001
FL	1	−0.19	0.02	−12.04	<0.001
PP	1	0.61	0.16	3.89	<0.001
DP	1	−1.53	0.37	−4.19	<0.001
Interaction terms					
Distance: FL	1	5.5×10^{-4}	1.6×10^{-4}	3.51	<0.001
Distance: PP	1	−0.02	2×10^{-3}	−9.26	<0.001
Distance: DP	1	0.01	2×10^{-3}	5.34	<0.001
Model df	311				

Note: Three additional factors, namely, FL, PP, and DP, are presented. Further, the interactions between distance and previously listed parameters are also shown.

Table 2. The log-likelihood of the full model and null model (full model: see Supplemental data, Model S1; null model: $y = 1 + \varepsilon$, where 1 represents the intercept parameter) is presented.

	Log-likelihood	Pseudo-R^2
Full model	−1284	49.5%
Null model	−2543	

Note: The pseudo-R^2 of the full model is obtained by pseudo-$R^2 = 1 -$ (log-likelihood full model/log-likelihood null model). This is an approximation used to assess the explanatory power of the model when using GLMM.

reducing browsing on spruce at a given distance with increasing biomass, particularly in the FL. The effect of the interaction between distance and PP was also significant but negative (z value = −9.26). The variance of the random factor (supplemental feeding site) was 2.51 ± 1.58 (SD). In order to express the amount of variation in the response variable explained by the model, the pseudo-R^2 parameter was calculated (Table 2).

On average, browsing pressure gradually ceases and reaches zero (0) at around 205 m from a feeding site (see Supplemental data, Equation S1). In reality, the relationship varied greatly among different feeding sites as confidence intervals ranged from 0 to 0.36 (36%) of browsing levels at 0 m from supplemental feeding sites (Figure 3).

Factors affecting browsing occurrence in relation to distance

Estimated FL, PP, and DP averaged 3.52 (g/m² dry biomass; FL), 0.38 (PP), and 0.05 (DP), respectively. The size of these factors varied within and around the surveyed plots. Consequently, higher and lower values than average are plotted to elucidate the variation of browsing pressure in relation to distance from supplemental feeding sites.

FL (g/m² of dry biomass) was the second most important factor after distance to explain the browsing pressure on spruce. Effects of low 50% quintiles mean values compared to the grand mean correspond with an increased browsing pressure on spruce at 0 m from a supplemental feeding site of about 0.04 (4%; Figure 4A). This effect seems to cease at around 200 m from a feeding site under such conditions. In contrast, when FL values corresponded to the grand quintile mean, browsing pressure was minimal (Figure 4A). No strong interaction effects between PP and browsing pressure on spruce were found and varied between 0.02 and 0.04 (2–4%) in the low and high quintile mean scenarios (Figure 4B). At around 30 m, browsing levels equaled, irrespective of the PP occurrence (Figure 4B). The main difference was found in relation to the distance at which PP effects on browsing ceased, at around 200 m in the low, and approximately at 120 m in the high quintile mean (Figure 4B).

High proportions of deciduous tree species, 0.8 (80%), correlated with low levels of browsing (<0.01 [1%] at 0 m from supplemental feeding sites). At high proportions of deciduous trees, browsing levels on spruce constantly decreased throughout the 400 m surveyed. In contrast, lower levels (approx. 0.03) showed a steeper gradient from more than 0.02 of browsing (at 0 m) to no effect at around 300 m (Figure 4C). The influence of low proportions of deciduous trees appeared significant within the first 100 m.

Discussion

In this study, we confirm earlier findings about a locally high browsing pressure on natural vegetation adjacent to supplemental feeding sites (Sahlsten et al. 2010; van Beest et al 2010). Browsing pressure clearly declines with distance from feeding sites. Novel is that this pattern is also true for typically avoided or least preferred forage such as Norway spruce, and that there
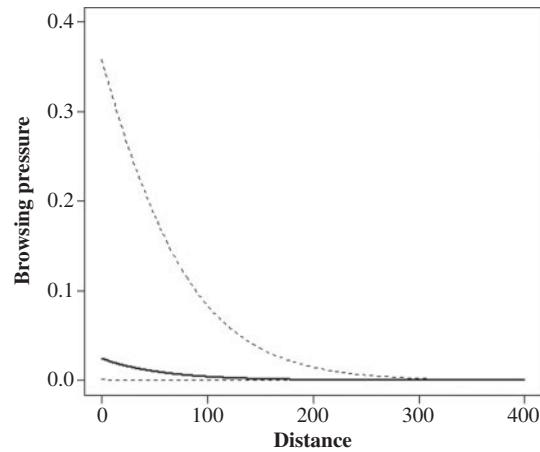
Figure 3. Relationship between estimated mean browsing pressure and distance from supplemental feeding sites, obtained from the full model including all factors and interactions (Table 1). 95% confidence intervals are also shown.

is an additive effect on spruce browsing of declining natural alternative food sources. In the area around the surveyed supplemental feeding sites, i.e. in a radius of 400 m from each feeding site, we found browsed spruce in 27.6% of the plots with a mean browsing pressure per plot of 9% of all available twigs. We suggest that most of this browsing on spruce is caused by fallow deer, since it is the totally dominant deer species in our study area. Similar browsing pressure by fallow deer has been reported earlier by Moore et al. (2000), but only on broadleaves at the peak of summer.

Norway spruce is considered an avoided forage species in moose (Månsson et al. 2007) as well as in fallow deer considering its morphophysiological adaptations as an intermediate-mixed feeder (Hofmann 1989), and because of possible effects of secondary metabolites, inhibiting or slowing down its digestion in ruminants (Harbourne 1991). On this basis, it is suggested that even a low per capita utilization of spruce in combination with low levels of preferred forage might result in the observed high browsing pressure assessed on spruce during winter. This might be related to the high fallow deer density occurring in the study area (Faber & Pehrson 2000; van Beest et al. 2010). Our results are also in accordance with other studies (e.g. Guillet et al. 1996; Doenier et al. 1997), showing that supplemental feeding sites represent a focal attraction for cervids, promoting a restricted spatial habitat use. The same pattern was pointed out by van Beest et al. (2010) who showed that moose concentrated their movements in a range of 1 km radius around supplemental feeding sites. In addition, it has been suggested that the temporal increase of spruce consumption around supplemental feeders could be related to a higher demand of roughage to offset the intake of forage supplied (Doenier et al. 1997). Consequently, supplemental food quality provided for deer along with habitat characteristics might help to induce the observed browsing pattern on young Norway spruce.
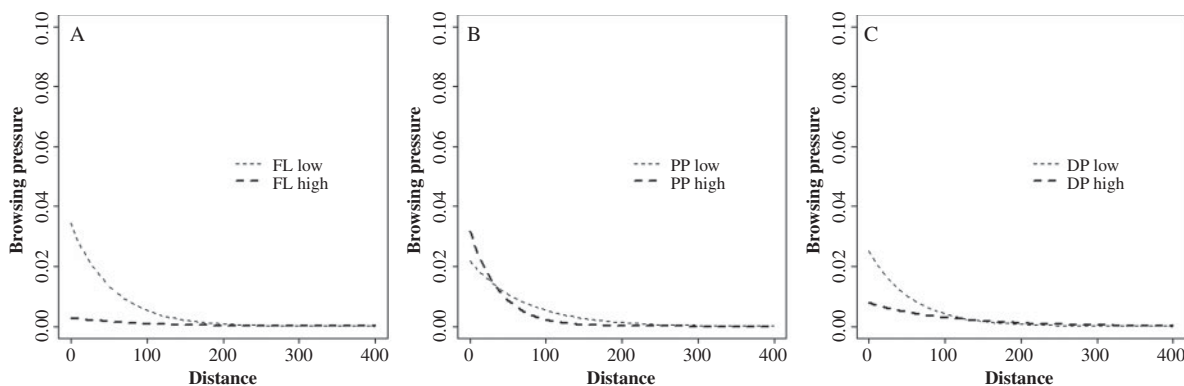

Figure 4. Graphical illustration of interaction effects of distance and (A) field layer (FL), (B) pine proportion (PP), and (C) deciduous tree proportion (DP), with predicted browsing pressure on spruce. The factors were kept at fixed low and high values, respectively, for FL, PP, and DP. Low and high values were obtained by averaging each factor from above and below the mean value (the upper or lower 50% quintiles). Low and high average records correspond to 1.69 g/m^2 ($n = 251$) and 14.56 g/m^2 ($n = 68$; FL), 0.19 ($n = 224$) and 0.84 ($n = 95$) (PP), 0.03 ($n = 311$) and 0.8 ($n = 8$; DP).

In a group living species as fallow deer, it is well known that social dominance affects the rate at which low ranked individuals access preferred food patches as supplemental feeding sites (Chapman & Chapman 1997). It is thus likely that low ranked individuals in our study, mostly fawns and females, gather in high numbers around winter feeding sites, waiting for high ranked individuals that despotically monopolize the station to leave. During that waiting time, spruce might also be consumed. If this hypothesis is true, it would be possible to avoid that kind of pattern by supplying food in many small patches over larger areas, which would unlikely be monopolized by a few high ranked individuals.

Availability of alternative forage significantly reduced browsing pressure on Norway spruce, irrespective of the distance from feeding sites. Our results suggest that the amount of available forage in the FL seems to be the factor of greatest importance in reducing browsing on spruce, followed by availability of deciduous trees and of least importance seems to be the availability of pine. The observed order of magnitude in the additive effect of alternative forage is not surprising and rather supports the general knowledge about ruminants where the most palatable forage, i.e. several FL species, will be consumed before less preferred as pine (Hofmann 1989; Månsson et al. 2007). Unpublished data from this study area based on rumen content analysis of 44 harvested fallow deer indeed supports the idea that the measured FL species are an important component of the winter diet, representing up to 16% of total consumption, while spruce only represents about 1.2% of total winter consumption (Kastensson unpublished). This could also explain why in areas where the FL was scarce, it had a quite modest effect on browsing pressure of spruce in relation to the distance to supplemental feeding sites.

The availability of deciduous trees had a similar but smaller effect as the FL on browsing pressure on spruce. Indeed, the deciduous tree species occurring in the study area are generally seen as more preferred forage than spruce (Gill 1992). However, this pattern does not explain why browsing pressure on spruce was slightly higher than 200 m from supplemental feeding sites when deciduous trees dominated the area compared to when deciduous trees were scarce in a spruce-dominated area. As suggested by Palmer et al. (2003), a preferred plant species attracts herbivores to a patch and as a consequence neighboring plant species, i.e. spruce in this case, is browsed more than expected a priori. Further, Bee et al. (2009) also suggest that a given plant is more likely to be browsed in areas containing high abundance of palatable forage species, thus supporting the observed browsing pressure on spruce in this study, despite the high occurrence of deciduous trees. Within the study area, such habitats were rare and spruce was the most common tree species. Even if our sample size is rather

thin to make any strong inference about pine, an interactive effect was also found here. Surprisingly, the more available pine, the more spruce was browsed up to 30 m from a feeding site, and after that distance, the opposite and expected pattern was found, i.e. the more pine, the less browsing on spruce, with increasing distance.

In Sweden, even-aged forest management practices (e.g. clear cutting) are utilized in ca. 96% of managed forests (Axelsson & Angelstam 2011). In these conditions, in order to determine the optimal location of supplemental feeding sites to minimize the browsing pressure on commercial forest stands, several parameters must be considered. Our results suggest that if supplemental feeding sites are to be located in forest stands, managers should base their decisions on two factors: FL abundance (also related to stand structure and tree density), and occurrence of deciduous tree species at stand scale (see Supplemental data, Table S1). Then deciduous trees occurrence in combination with a continuous FL should lead to a total browsing level on spruce to reach zero at ca. 80 m from supplemental feeders. However, residual browsing will likely occur due to fallow deer gregarious behavior and the attraction exerted by the supplemental feeding sites.

In conclusion, the current widespread strategy to change timber production from pine to spruce does not appear as the best possible alternative to avoid deer browsing on trees completely. In southern Sweden, where deer species commonly are fed artificially in order to maintain high game densities, browsing pressure even on less preferred tree species, in this case spruce, is significant under the studied conditions. Our model explains around 50% of the variation in the response variable, i.e. browsing pressure on spruce, as a consequence of distance and available alternative forage. Thus, 50% remains to be explained and other factors, such as small scale heterogeneity in deer density, social dominance factors in local deer populations, and habitat heterogeneity, i.e. stand structure and composition, should also be considered. We suggest managers should try to distribute supplemental food to avoid dominance despotic effects of monopolizing forage and make food available for lower ranked individuals.

Funding

Supplemental data

Supplemental data for this article can be accessed here.

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