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Managing landscapes for multiple objectives: alternative forage can reduce the conflict between deer and forestry

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Abstract. Deer (*Cervidae*) cause considerable damage to forest plantations, crops, and protected habitats. The most common response to this damage is to implement strategies to lower population densities. However, lowering deer density may not always be desirable from hunting, recreational, or conservation perspectives. Therefore, knowledge is needed about additional factors beyond deer density that affect damage levels, and management actions that consider competing management goals. We studied the relationships between levels of bark-stripping by red deer (*Cervus elaphus*) on Norway spruce (*Picea abies*) and (1) relative deer density indices (pellet group count and deer harvest data), (2) availability of alternative natural forage (cover of forage species) and (3) proportion forest in the landscape, both at a forest stand scale and at a landscape scale. Extensive variation in damage level was evident between the six study areas. On a stand scale, the proportion of spruce damaged was positively related to pellet group density, indicating the importance of local deer usage of stands. In addition, available alternative forage in the field layer within spruce stands and proportion forest surrounding stands was negatively related to damage level. On the landscape scale, damage level was negatively related to availability of forage in the field and shrub layers and proportion forest, but was not related to any of the relative deer density indices. Increasing alternative forage may thus decrease damage and thereby reduce conflicts. Additionally, the proportion of forest in the landscape affects damage levels and should thus be considered in landscape planning and when forecasting damage risk. The relationship between local deer usage of stands and damage level suggests that future studies should try to separate the effects of local deer usage and deer density.

Key words: *Cervus elaphus*; deer management; forest damage; habitat fragmentation; landscape structure; land use conflicts; large herbivores; Norway spruce; *Picea abies*; red deer; ungulates.

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INTRODUCTION

Deer (*Cervidae*) can have profound impacts on vegetation leading to conflicts with humans through damage to forest plantations and agriculture, but also through negative impacts on habitats of high conservation value, e.g., those with high biodiversity value or forests planted to avoid land slips and avalanches (Gill 1992*a*, Conover 1997, Reimoser and Putman 2011). It is widely accepted that there is a positive relationship between deer density and their impact on vegetation (McShea et al. 1997, Conover 2002, Månsson 2009). Therefore counter-measures commonly aim to limit or lower population densities (Brown et al. 2000, Côté et al. 2004). However, deer density is only one of many factors affecting browsing intensity and density may also be subordinate to other factors (Kuijper 2011, Putman et al. 2011*a*). Thus, if the relationship between deer density and browsing intensity is weak, a reduction in density may not result in the expected recovery of vegetation (Putman et al. 2011*a*, Tanentzap et al. 2012). Moreover, from hunting, recreational, or conservation perspectives (e.g., if the deer species is threatened) it is not always desirable to lower deer densities (Gordon et al. 2004, Sharp and Wollscheid 2009). Since deer range over large areas, their management commonly involves multiple, different human interests and conflicting goals, for instance between forestry and game management, but also more generally between land use and conservation interests (Bunnefeld et al. 2011, Putman et al. 2011*b*, Redpath et al. 2013). Furthermore, single landowners with interests in both forest production and in game management will also have conflicting management goals (Gordon et al. 2004, Mysterud 2006, 2010). Meeting these multiple objectives and tackling factors affecting herbivore impact on vegetation requires a comprehensive understanding about effectiveness of counter-measures as well as a landscape scale approach that integrates several potential land-use interests (Putman and Kenward 2011).

At a larger spatial scale, factors other than population density, such as landscape structure and forage composition can also affect the level of damage (for reviews, see Gill 1992*a*, Reimoser and Gossow 1996, Putman et al. 2011*a*). A general increase in forage availability within the managed landscape, e.g., higher densities of trees for timber and pulp production, can cause a decreased level of damage due to diffusion of browsing intensity (Månsson 2009), although tree species diversity and stand structure are also important factors (Reimoser and Gossow 1996, Kuijper 2011). Moreover, in line with the attractant-decoy hypothesis, damage limitation may be achieved by diverting browsing to more preferred plants (Hjältén et al. 1993, Gundersen et al. 2004). Field layer species (e.g., bilberry (*Vaccinium myrtillus*) are a preferred forage source for several deer species (Baskin and Danell 2003) and may therefore be one alternative forage that could function as an attractant to decrease browsing impact on trees (Putman 1989). Availability of field layer species is, amongst other factors, affected by forestry practices (Atlegrim and Sjöberg 1996, Bergstedt and Milberg 2001, Parlane et al. 2006). Therefore it may be possible to divert browsing intensity from targeted plants by changing forest practices to increase availability of alternative forage. Forage availability may also be affected on a landscape scale by intensive agriculture decreasing the proportion of forested area (Bélanger and Grenier 2002, Robinson and Sutherland 2002). Composition of the landscape, e.g., forest cover and fragmentation, has been shown not only to affect deer diet (Rouleau et al. 2002, Abbas et al. 2011) and movement patterns (Coulon et al. 2008), but also the availability of preferred forage in forests (Lesage et al. 2000, Rouleau et al. 2002). This suggests that damage level not only depends on local site conditions in forests but also on composition of land cover types. Here we compare damage level at different levels of forest cover and forage availability to evaluate the potential to mitigate conflicts between deer density and forestry.

We used red deer (*Cervus elaphus*) and damage level on Norway spruce (*Picea abies*) in Sweden, in six areas with a varying range of forest cover, as a model system to study the effects of availability of alternative forage and forest proportion on extent of deer damage. Red deer are increasing in many parts of Europe (Milner et al. 2006, Apollonio et al. 2010). The species ranges over large areas (Jarnemo 2008, Kamler et al. 2008) and can cause severe and costly damage to forest plantations—especially Norway spruce—through bark-stripping, mainly during winter (Gill 1992*a*, 1992*b*, Reimoser and Putman 2011) . As a response to human disturbance, red deer tend to adopt an activity pattern characterized by feeding in the open during night and seeking shelter in the forest during day (Georgii 1981, Pepin et al. 2009, Allen et al. 2014).

However, red deer, like most ruminants, have a feeding behavior characterized by periods of feeding interspersed with periods of rumination and resting throughout a 24 hour period and thus also need to feed during day-time (Bubenik and Bubenikova 1967, Georgii and Schröder 1978, Clutton-Brock et al. 1982), meaning the deer may be restricted in their food search to the forest interior. Bark can provide roughage and is comparable to other food items regarding nutritional value, water and digestibility, but nevertheless seems to be less preferred forage due to the energy consumption involved in removing the bark from the stem (Gill 1992*a*). The preferred winter diet of red deer in Sweden largely consists of species in the field layer such as bilberry, lingonberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*) (Lavsund 1976). We aimed to investigate the effect of alternative forage in the forest (field and shrub layer species) and proportion of forest in the landscape on the level of bark-stripping damage taking into account two spatial scales (small: stand; large: landscape).

METHODS

Study areas

Six study areas (Fig. 1) were selected with data available on forest stand characteristics and annual red deer harvest (Table 1). Harvest data for the hunting season 2009/2010 were retrieved from the estates comprising the study areas (1–4 estates per area). Three areas were situated in the south of Sweden (areas 1–3, 55°4 N, 13°40 E, nemoral zone). In this region the ratio of agricultural land to productive forest is 1.5, and the average forest productivity index is 11.1 $m^3ha^{-1}yr^{-1}$. The productive forest area consists of pine 10%, spruce 36%, mixed conifer 5%, mixed conifer/broadleaved 7% and broadleaved 37% (Nilsson and Cory 2012). Common crops are cereals (49% of arable land), ley (26%), oilseeds (11%), sugar beets (8%), potatoes (2%), leguminous plants (2%), green fodder (1%) and corn (1%) (Jordbruksverket 2013). The more northern region (areas 4–6, 58°48 N, 16°24 E, boreonemoral zone) has a ratio of agricultural land to productive forest of 0.5. Average forest productivity index is 7.9 $m^3ha^{-1}yr^{-1}$. The productive forest area consists of pine 33%, spruce 30%, mixed conifer 17%, mixed conifer/broadleaved 7% and broadleaved 9% (Nilsson and Cory 2012). Dominating crops are cereals (48% of arable land) and ley (43%), but there are also oilseeds (7%), leguminous plants (1%) and green fodder (1%) (Jordbruksverket 2013). Lynx (*Lynx lynx*) occur permanently but sparsely in the northern region, whereas visits in the southern study areas are rare. There are no wolf (*Canis lupus*) territories in any of the regions, just rare and occasional visits of long-straying single wolves. The main hunting season for red deer is from the second Monday in October to 31 January (loose dogs allowed). In the northern region females and calves are also allowed to be harvested from 16 August, but only by using a 'sit and wait' hunting technique or stalking. However, hunting disturbance continues during February as the hunting season for wild boar (*Sus scrofa*) lasts until 15 February and for fallow deer (*Dama dama*) until the end of February. In each of the six study areas, 30 stands of Norway spruce (minimum size 1 ha, age 20–40 years) were randomly selected for collection of field data during 13 May to 17 June 2010 (Månsson and Jarnemo 2013).

Level of damage

In each of the 180 spruce stands ten survey plots were systematically and evenly distributed (random starting point). Occurrence of fresh bark-stripping damage (i.e., wounds from preceding winter) was measured on the 10 spruce stems closest to the plot center (i.e., 100 spruce stems per stand) and stems were classified as damaged or not damaged (for details, see Månsson and Jarnemo 2013).

Pellet group survey

An index of red deer use within targeted spruce stands and forest stands in the surrounding landscape was estimated by counting the number of red deer pellet groups within a 100 m^2 circular plot, using a fecal standing crop (FSC) survey (species identification by size and shape of pellets, Mayle et al. 1999; for details see Månsson and Jarnemo 2013). Pellet groups were surveyed within the targeted spruce stands (pellet $groups_{std}$, i.e., same plot center as damage survey) and on plots distributed along transects (pellet $groups_{trct}$) in each of the cardinal directions from the targeted stand (Fig. 1). The first transect plot had the border of the plot tangential

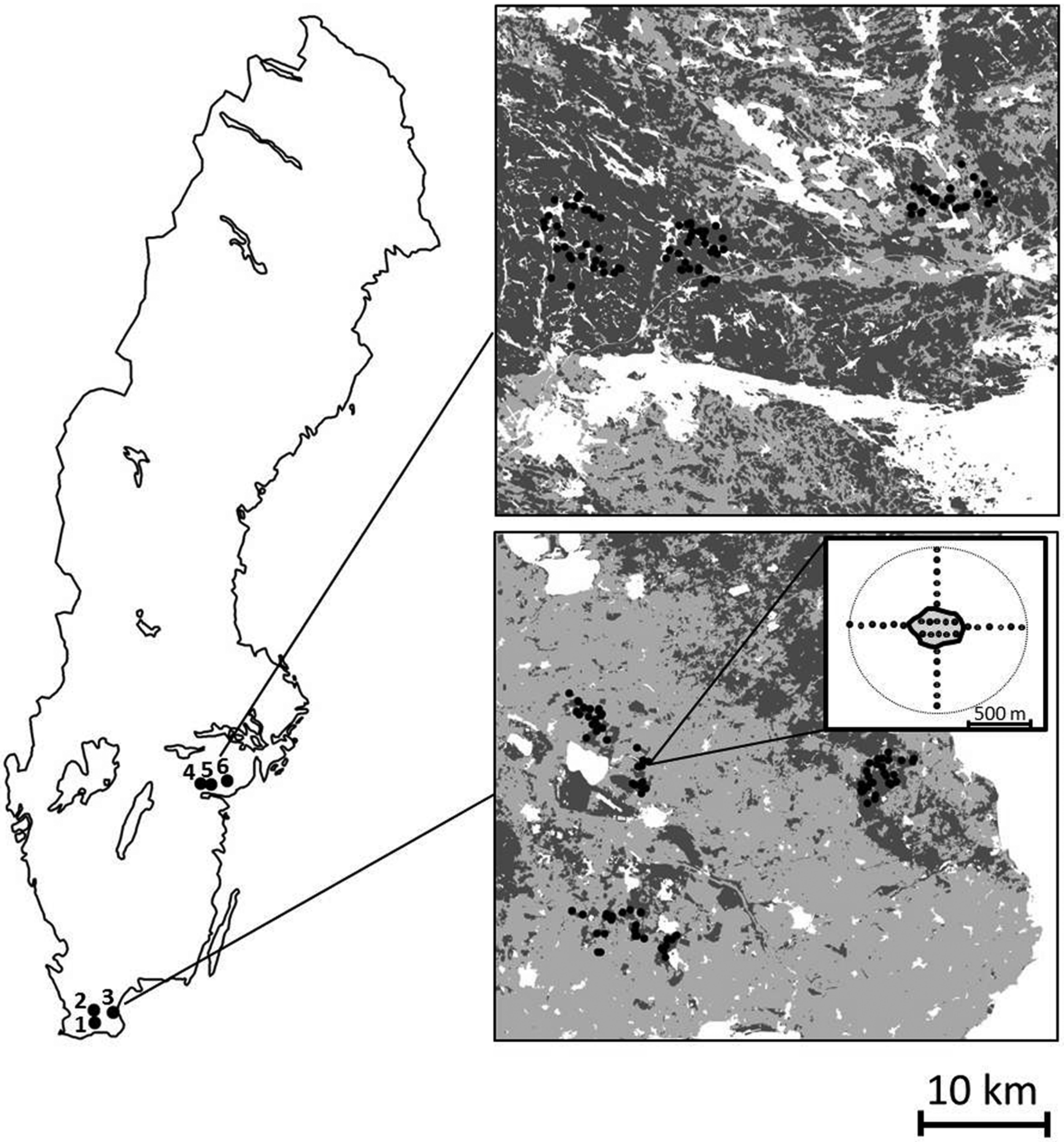

Fig. 1. Locations of the six study areas in Sweden and distribution of surveyed stands. Light grey indicates agricultural land, darker grey forest and white other land types (mainly water and urban areas). The sketch shows the principal of the distribution of the 10 sample plots within a forest stand (shaded area), and the transects reaching 500 m from stand border for estimating number of pellet groups, forage availability, and damage level. Proportion forest was estimated within an 800 m radius from stand center.

to the edge of the surveyed stand. The subsequent plots were distributed at 100, 200, 300, 400 and 500 m from the stand edge (in total 24 transect plots surrounding each stand). Because only forested areas were surveyed, the number of plots surveyed along transects was occasionally reduced. Stands with less than ten sample plots along transects were excluded in analysis. Only fresh (from preceding winter) pellet groups were used in analysis. Pellet groups were aged by color and position in relation to litter and old vegetation (Månsson and Jarnemo 2013).

Table 1. Descriptive data (mean values and SD within parentheses) for the six study areas and the variables used in analysis.

					Targeted spruce stands			Transects		
Study area	Stands (n)	Harvest (deer/km^2)	Forest†	Fresh damage‡	Field layer§	Shrub layer§	Pellet groups¶	Field layer§	Shrub layer§	Pellet groups¶
1	20	0.2	0.60 (0.13)	0.21 (0.23)	0	1.12 (3.66)	1.75 (2.36)	0.01 (0.04)	0.62 (0.8)	0.53 (0.51)
2	17	0.5	0.53 (0.19)	0.15 (0.18)	0.01 (0.02)	1.67 (4.57)	1.39 (1.56)	0	1.75 (2.5)	0.34 (0.27)
3	30	1.2	0.82 (0.11)	0.12 (0.08)	0.02 (0.08)	0.08 (0.33)	2.75 (1.79)	1.23 (1.94)	3.16 (3.61)	1.15 (0.54)
4	28	0.8	0.83 (0.11)	0	3.65 (4.46)	4.59 (8.41)	0.89 (0.48)	14.38 (7.34)	6.18 (2.98)	0.97 (0.77)
5	26	2.3	0.85 (0.11)	0.01 (0.03)	3.06 (4.53)	5.08 (11.53)	1.62 (1.9)	12.26 (7.37)	8.7 (5.48)	0.92 (0.69)
6	22	0.8	0.66 (0.14)	0.08 (0.11)	0.75 (1.13)	0.49 (0.61)	0.72 (0.67)	7.14 (5.17)	5.07 (3.95)	0.55 (0.59)

† Proportion forest within an 800 m radius from stand center surrounding targeted stands.
‡ Proportion trees with fresh damage.
§ Percentage of 20 m^2 plot covered by field and shrub layer species.
¶ Number of pellet groups per plot.

Forage availability

We measured two indices of forage availability in forest stands by visually estimating cover of browse in the shrub layer and field layer projected onto the horizontal plane in 20-m^2 plots (Hörnberg 2001, Månsson et al. 2012). The shrub layer forage index consisted of the sum of the cover of aspen (*Populus tremula*), ash (*Fraxinus excelsior*), birch (*Betula* spp.), oak (*Quercus robur*), rowan (*Sorbus aucuparia*), willows (*Salix* spp.), juniper (*Juniperus communis*), Scots pine (*Pinus sylvestris*), and Norway spruce within browsing height, 0.3–3 m, encompassing the browsing range of red deer (Renaud et al. 2003, Kuijper et al. 2013). The field layer forage index consisted of the sum of the cover by field layer species such as bilberry, lingonberry, and heather irrespective of height. Two forage indices were estimated, within the targeted spruce stands (field layer$_{\text{std}}$ and shrub layer$_{\text{std}}$) and within stands surrounding the targeted stands, i.e., the transect plots (field layer$_{\text{trct}}$ and shrub layer$_{\text{trct}}$).

The proportion of forested land

Around each surveyed spruce stand, within an area with a radius of 800 m (i.e., an area of 201 ha) from stand center (Fig. 1), the proportion of land classified as forest was estimated by using a digital land-use and vegetation map (geographical data of Sweden, GSD, produced by the Swedish National Land Survey [Näslund-Landenmark 1997]). Spatial analyses were conducted in ArcMap (version 9.3.1). The 800 m radius enabled that all sample plots along the transects radiating from the edge of the selected stands were included within the area.

Statistical analysis

All statistical analyses were carried out in the open source program R (version 3.0.2; R Core Team 2013). We used generalized mixed effects models (GLMMs, function glmer in lme4 package, Bates et al. 2013) with a logit link and a binomial error structure to model occurrence of bark-stripping damage (damage evident = 1 or not evident = 0). Explanatory variables were proportion of forested land within the buffer zone, proportion of ground covered by field layer, proportion of ground covered by shrub layer, and number of pellet groups (log + 1 transformed). Explanatory variables (pellet group counts and forage availability) were estimated both within targeted stands and along transects, and were included in the model as separate variables. All proportions were arcsine transformed. Although some of the explanatory variables naturally are correlated, these correlations did not adversely affect the analysis as shown by low levels of variance inflation of the model containing all variables (Zuur et al. 2010) as well as stability of the parameter estimates in the top models (see below and Table 2). Study

Table 2. Parameter estimates from the top five (delta AICc < 2) best fitting GLMMs for the probability of fresh damage as a function of different combinations of proportion forest ('Forest'), and (1) proportion shrub ('Shrub layer'), (2) field layer, and (3) number of pellet groups on both stand level and transect (landscape) level. Model structure is indicated by the parameters included (no value = not included in given model). Also shown is the percentage of variation (POV) explained by the random effect of study site, number of fixed effect parameters (df), the AICc and the difference in AIC between each model and the top model (ΔAICc).

			Targeted spruce stands			Transects						
GLMM no.	Intercept	Forest†	Shrub layer‡	Field layer‡	Pellet groups§	Shrub layer‡	Field layer‡	Pellet groups§	POV study site	df	AICc	ΔAICc
1	4.2	−4.3		−8.2	2.2				87	5	86.8	0.00
2	3.8	−4.4			2.3				78	4	87.8	0.97
3	4.4	−5.2		−8.7	2.5		3.6		88	6	88.5	1.64
4	−0.1			−8.9	2.1				91	4	88.5	1.68
5	3.8	−4.0	2.7	−9.8	2.2				86	6	88.6	1.73

† Proportion forest within an 800 m radius from stand center surrounding targeted stands.
‡ Proportion of 20-m^2 plot covered by field and shrub layer species.
§ Number of pellet groups per plot.

area ($n = 6$) was added as a random effect.

The most parsimonious model was found using an information theoretic approach (Burnham and Anderson 2002). A difference of AIC $>$ 2 indicates some support and of AIC $>$ 4 substantial support that the model with the lower AIC is the better model. The function dredge in the package MuMIn (Barton 2013) was used to compare all model combinations with variables mentioned above as main effects as well as a model with an intercept only ($N = 128$ models in total); no interactions were tested. Because the five top models showed less than 2 AIC difference, we present parameter estimates averaged over the top five models (weighted by their AIC weight; Burnham and Anderson 2002).

The percentage variance explained by the random effect (study area) was calculated for all top models (ΔAIC < 2). To illustrate the differences between sites, we present the mean predicted damage probability in each site as a function of relevant explanatory variables, in addition to the mean predicted damage probability across sites.

To investigate which factors affect damage level at the landscape scale (above deer home range level) we tested the correlation between the grand mean of the response variable (damage level) with the grand mean of the same explanatory variables as included in the analysis at the stand scale (i.e., $n = 6$). Given the limitation of only six data points we used Spearman's rank correlation and only included the explanatory variables one at a time. In addition to the explanatory variables earlier included in the stand scale analysis, we also included harvest data. Harvest data can be used as indices of relative deer abundance at a landscape scale (Ueno et al. 2014). The pellet group count can be used as an overall proxy of relative deer abundance within the forest stands within the landscape (Mayle et al. 1999).

RESULTS

The proportion of trees with fresh damage in the six areas varied between 0 and 21% (Table 1). The best model (lowest AIC) for the proportion of damaged trees at stand scale contained field layer$_{\text{std}}$, number of pellet groups$_{\text{std}}$, and the proportion of forested land surrounding the stands as explanatory variables (Table 2). This was closely followed by models that contained field layer$_{\text{trct}}$ and shrub layer$_{\text{std}}$ (Table 2). The model with only an intercept ranked poorly (rank: 80th, delta AIC = 9.7). Across all models, the variation between the study areas was relatively large and explained between 78 and 91% of the random effect variation (Table 2).

Model averaged parameter estimates showed that damage probability decreases with both increasing proportion of forested land and with increasing field layer on a stand level (field layer$_{\text{std}}$), but increases with higher numbers of deer pellet groups (pellet groups$_{\text{std}}$; Table 3, Fig. 2). Moreover, model predictions for individual

Table 3. Model-averaged parameter estimates (and their standard error and significance level) from a mixed-effect model for the probability of fresh damage as a function of the five most important explanatory variables (proportion forest within the 800 m radius from stand center (Forest), number of pellet groups in the stands (Pellet groups (stand)), and field layer in the targeted stands (Field layer (stand)), field and shrub layer in the surrounding forest stands (transect)) as determined by model selection (Table 2).

Variable	Estimate	SE	z	P	Relative variable importance
Intercept	3.5	2.9	1.2	0.231	1.00
Forest	−4.4	2.4	1.9	0.063	0.85
Field layer (stand)	−8.7	5.1	1.7	0.085	0.79
Pellet groups (stand)	2.3	0.8	2.7	0.006	1.00
Field layer (transect)	3.6	4.0	0.9	0.372	0.15
Shrub layer (transect)	2.7	3.9	0.7	0.490	0.14

sites show that study areas 4 and 5 had consistently low damage, whereas areas 1, 2, 3 and 6 had consistently higher damage than the estimated overall mean damage level (fixed), irrespective of proportion forest, field layer at stand level or number of pellet groups (Fig. 2).

At the landscape scale the damage level was negatively correlated to availability of forage within the field layer independent of where it was estimated, i.e., within targeted stands or within surrounding forests (Fig. 3). Also the shrub layer available in surrounding forests and the proportion of forested land were negatively correlated to damage level. However, no correlation was found between damage level at a landscape scale and harvest data or pellet group indices independent of where it was estimated, i.e., within targeted stands or within surrounding forests (Fig. 3).

Discussion

Our study showed that damage level was negatively related to available forage in the field layer within stands and to the proportion of forested land surrounding the targeted stands, independent of spatial scale. In addition to field layer within stands, field layer and shrub layer within forests surrounding targeted stands were negatively related to damage level on a landscape scale. These results support the hypothesis that availability of alternative forage is a key factor that must be considered when evaluating effects of deer browsing on commercial plants and native vegetation (Reimoser and Gossow 1996, Kuijper et al. 2010, Garrido et al. 2014). Our results also comply with studies requesting that landscape composition and land use practices should be given higher priority in the study of damage caused by deer (Kuijper 2011, Putman et al. 2011*a*).

On a stand scale, level of damage was positively related to number of pellet groups within the stands. However, there was no effect of pellet groups in the surrounding forests, suggesting that it was the relative use by deer of the targeted stands that was affecting the damage level i.e., the local usage. None of the relative indices of deer density (pellet group numbers and harvest) showed a significant relation to damage level at the landscape scale. Local usage of deer, which is affected by landscape structure (i.e., distribution of forage and shelter), thus had a strong impact on damage level, whereas the impact of population density (as inferred from the relative indices) seemed less important, suggesting that merely focusing on overall deer density may misdirect conclusions and mitigations.

The activity pattern commonly shown by red deer of spending the night-time in open areas and seeking shelter in forest habitats during the day-time (Georgii 1981, Godvik et al. 2009, Pepin et al. 2009), is also displayed by the red deer in our study areas (Allen et al. 2014). During the day-time feeding bouts, the deer are thus largely dependent on available forage inside the forested habitats that offer cover. Our results showed that the availability of natural forage species in the field and shrub layers, highly favored by deer (Lavsund 1976, Baskin and Danell 2003), decreased the level of bark-stripping. The results are thereby in line with the suggested food resource hypothesis stating that deer eat bark when the availability of other more palatable food resources is limited (Ueckermann 1956, Gill

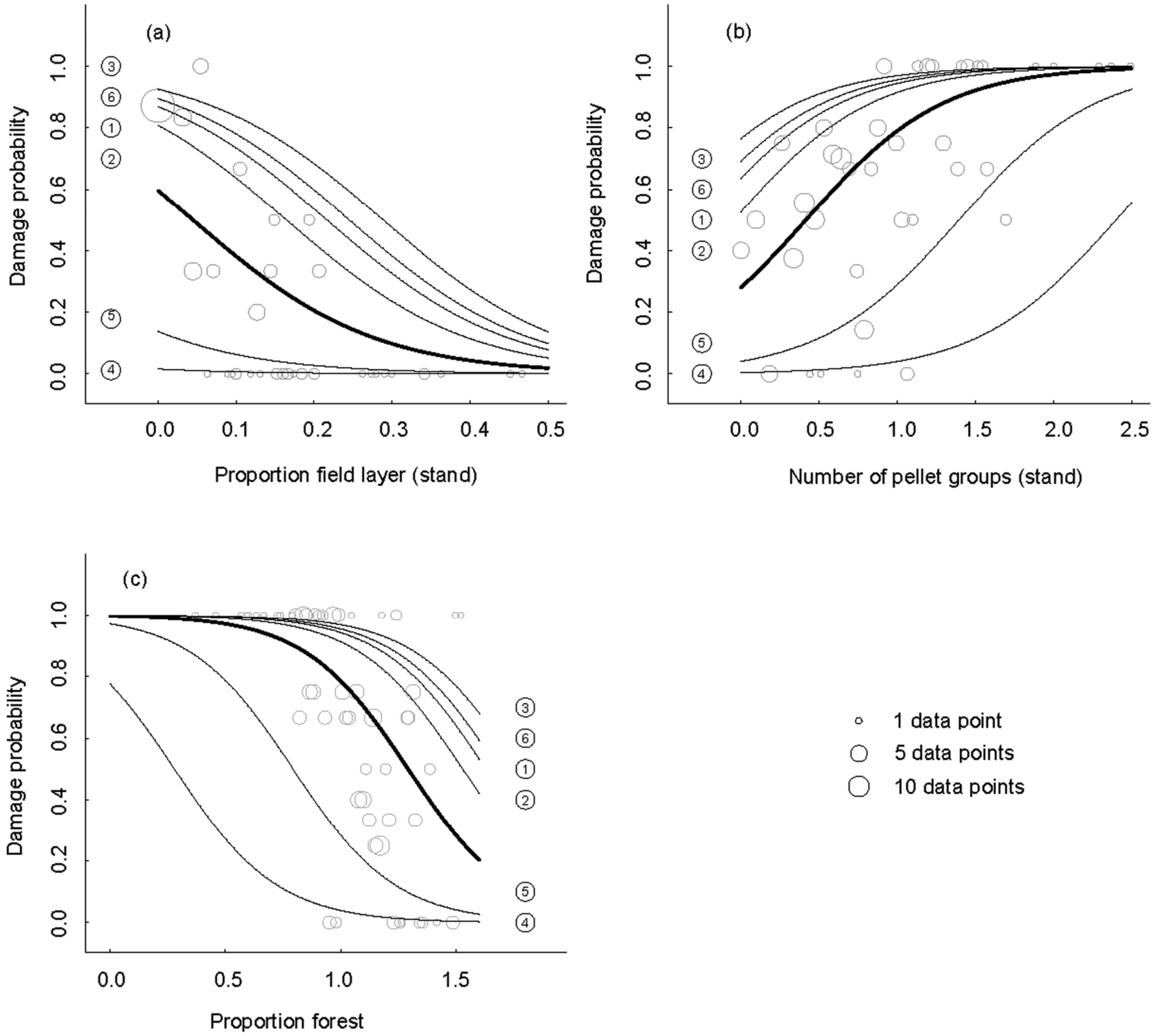

Fig. 2. Predictions from a GLMM for damage probability as a function of (a) proportion cover of field layer (arcsin transformed), (b) number of pellet groups (log transformed), and (c) proportion cover of forest (arcsin transformed). Thick black lines are mean predictions across all sites, thin black lines are the predicted means for each site (labelled using circled numbers). Circle sizes reflect the log-transformed number of data points.

1992*a*, Verheyden et al. 2006). Studies directly relating bark-stripping to natural food availability, however, are rare (Verheyden et al. 2006, but see Ligot et al. 2013). There are studies that have related level of bark-stripping to supplemental feeding (Ueckermann 1984, Jerina et al. 2008, Masuko et al. 2011), but a direct comparison between these studies and ours may be hampered because of differences between supplemental feeding and natural forage. Whereas supplemental feeding generally is concentrated at feeding stations and restricted to one or a few types of feed, natural forage can be expected to be more evenly spread in the landscape and probably consists of several species with differing availability, palatability and nutritional value (Putman and Staines 2004).

Our study revealed large differences in bark stripping damage level between areas diverging in land use and landscape composition. In the study areas with low proportion forest and high proportion agriculture, damage levels were

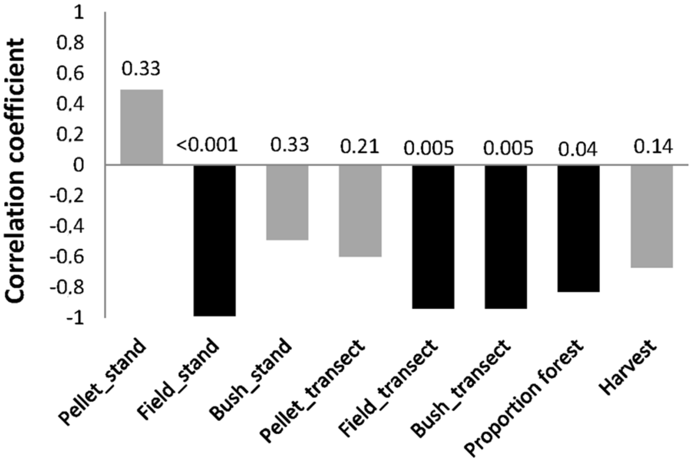

Fig. 3. Correlation coefficients (Spearman's rank) and P values (above bars) between damage level at a landscape scale and eight explanatory variables within the six study areas ($n = 6$). Black bars indicate $P < 0.05$ and grey bars $P > 0.05$. Indices of forage availability and pellet groups represents survey estimates both within targeted spruce stands (stand) and within forest stands surrounding the targeted stands (transect). Harvest size was used as a proxy for relative deer abundance within the six areas.

higher, even relative to previous studies (Verheyden et al. 2006, Månsson and Jarnemo 2013), whereas damage level was low in the forest-dominated areas, despite seemingly high relative densities of red deer as indicated by harvests and pellet group counts. In areas with less forest and more fragmented forests, the deer are restricted to fewer and smaller forest stands for protection and foraging during the day-time. Since the areas with low proportion forest in our study coincided with low availability of alternative forage in the forests deer not only have to cope with forests offering less available day-time forage, but also a limited amount of forest in the landscape. Leaving the forest before dark in this fragmented landscape often means entering open habitats and equates to an increased risk of being shot. It is suggested that damage increases when deer are restricted in their movements, either by snow or by human disturbance (Van de Veen 1973, Maizeret and Ballon 1990). Red deer seem sensitive to disturbance (Sunde et al. 2009, Sibbald et al. 2011, Jarnemo and Wikenros 2014) and bark-stripping level has already been related to human activity (Petrak 1998, Ligot et al. 2013). The intensity of damage thus likely depends both on the availability and the quality of day-time security cover (Borkowski and Ukalski 2012). Therefore it will probably be even more important to increase availability of alternative forage in forests within a fragmented landscape and if possible increase availability of habitats offering high-quality day-time security cover to counteract damage.

Within the given range of deer density in our study, the level of damage was not related to any of the relative indices of deer density (i.e., harvest data or pellet groups along transects). A weak relationship between ungulate density and damage level is, however, far from unique (Putman et al. 2011*a*, Reimoser and Putman 2011) and even though several recent studies have shown a positive relationship between bark-stripping level and deer density (Jerina et al. 2008, Kiffner et al. 2008, Ligot et al. 2013), this pattern is not consistent Verheyden et al. (2006). Our study supports the conclusion that this inconsistency depends on other factors such as landscape structure, forage availability, winter severity, forest block size, and stand character (i.e., high damage levels in even-aged monocultures [Vospernik 2006, Kiffner et al. 2008, Jerina et al. 2008] and lower levels in multi-specific stands with different storeys [Szczerbinski 1959, Reijnders and Van de Veen 1974, Reimoser and Gossow 1996]) (Verheyden et al. 2006, Kuijper 2011, Tanentzap et al. 2012). Moreover, we found a relationship between local usage of stands and damage level. This relationship could thus also weaken the relationship between deer density and damage level, suggesting that future studies should try to separate the effects of local usage and density.

Recommendations for management and research

The red deer in our three southern areas is red-listed as a nominate sub-species (Höglund et al. 2013) and thus serves as a good example of conflicting goals between conservation efforts, game management, and forestry, emphasizing the need for a management strategy that must attempt to integrate different land-use interests (Putman and Kenward 2011). The differences in sensitivity to damage between our study areas suggest that land use and deer management needs to be adapted accordingly. In forest-dominated landscapes with sufficient alternative forage, red deer seem to exist without causing large bark-stripping problems and are potentially valuable game animals. In mixed forest-agricultural landscapes the risk of damage seems higher. Here, existing high-quality day-time cover should be managed with caution. It may be difficult to increase the amount of forest patches, but, at least in the southern areas, energy crop plantations of *Salix* spp. seem highly used by deer, and may thus offer one possibility of such cover. However, to reduce conflicts between deer management and forestry, our results mainly suggest that measures increasing availability of alternative forage in the field and shrub layers may decrease damage. Distribution and composition of the field layer is highly dependent on land use, therefore forage availability is affected by forest practices (Atlegrim and Sjöberg 1996, Reimoser and Gossow 1996, Bergstedt and Milberg 2001). Mixed stands and stands of varying age generate a more heterogeneous habitat which results in more preferable light conditions for field layer vegetation compared to mono-specific and even age stands (Atlegrim and Sjöberg 1996, Lieffers et al. 1999, Parlane et al. 2006). The effect of forestry on field layer vegetation and damage level needs high priority in research, but silvicultural practices (Reimoser and Gossow 1996, Völk 1999), establishment of preferred forage, and supplemental feeding have been shown to divert deer browsing from valuable trees (Campbell and Evans 1978, Nolte 1999, Gundersen et al. 2004) and to affect deer distribution (Pérez-González et al. 2010). Forage-increasing measures may thus also be used to attract ('pull') deer to sites where their presence is acceptable. As disturbance can cause red deer to leave sites (Sunde et al. 2009, Sibbald et al. 2011, Jarnemo and Wikenros 2014), an additional step could be to divert ('push') deer from sites where damage is undesirable (Cromsigt et al. 2013). This combination of forage-increasing measures and disturbance actions—so called 'push-pull strategies' (Cook et al. 2007)—merits further study.

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