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Factors affecting bark-stripping by red deer (*Cervus elaphus*)

–the importance of landscape structure and forage availability

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Abstract

Bark-stripping by red deer (*Cervus elaphus*) cause extensive damage to economically valuable spruce trees (*Picea abies*) in Swedish forests. The underlying causes for bark-stripping are not fully understood, and the frequency and severity of damage unpredictably differ between regions. In this study, I investigated if landscape structure (e.g. agricultural dominated landscape opposed to forest dominated landscape), forage availability, population density and disturbance (e.g. roads and settlements) affect bark-stripping frequency. The study was carried out in two Swedish regions, Skåne and Södermanland/Östergötland and included 180 spruce stands.

Bark-stripping frequency was explained by proportion agricultural land in the area, forage availability and the distance to agricultural land. Areas with a high proportion agricultural land had significantly more damage than forested areas. Areas with high abundance of available winter forage had significantly less damage than areas that lacked alternate forage. Disturbance by roads and settlements did however not seem to influence the amount of bark-stripping. There was a significant difference in bark-stripping frequency between the regions. Skåne had 87 % damaged trees, while Södermanland/Östergötland only had 18 % damaged trees. The damage frequency was higher in Skåne despite a lower population size. Furthermore damage did not differ between study sites in Skåne even at different densities. Because bark-stripping seems to be dependent on landscape structure and forage availability, habitat management rather than increased red deer culling may be a possible way to reduce damage.

Key words: bark-stripping, Cervus elaphus, red deer, forestry, Picea abies, spruce, wildlife damage, ungulates

Sammanfattning

Kronvilt (*Cervus elaphus*) orsakar allvarliga skador på gran (*Picea abies*) genom att gnaga eller flänga av barken. Skadorna kan i sin tur kan ge upphov till svampinfektioner som kan leda till röta, vilket då resulterar i nedklassning av virket; stammen blir dessutom mer känslig för stormbrott efter skada. Följaktligen orsakar dessa skador skogsägare stora ekonomiska förluster.

För att bättre kunna förutse och förhindra skador krävs en ökad förståelse av orsakerna till barkskalning. I den här studien har jag undersökt hur landskapssammansättning, alternativ föda, mänsklig störning och populationstäthet påverkar omfattningen av barkskalning.

Det fanns inget samband mellan populationstäthet och antal skadade träd; skadorna var till och med betydligt fler i Skåne (87 %) som har en relativt låg täthet, medan det var väldigt sparsamt med skador i Södermanland/Östergötland (18 %) där tätheten är betydligt högre. En åtgärd som ofta föreslås för att försöka minska barkskador är en ökad avskjutning för att minska stammen. Resultatet från den här studien tyder dock på att avskjutning inte alltid behöver ge önskad effekt.

Studien visade att andelen jordbruksmark i landskapet påverkar mängden barkskalning; mer skador uppträdde i områden med mer jordbruksmark. Detta kan ha tre förklaringar. En möjlig förklaring är att kronviltet behöver äta bark efter en diet med näringsrika grödor som saknar fiber. Barken kan då fungera som fiberersättning och hålla igång matsmältningen. En annan möjlighet är att kronviltet i det jordbruksdominerade landskapet tvingas söka skydd i de jämförelsevis få och små skogspartier som finns. Täta skogar ger skydd från störning, vind, låga temperaturer och djup snö, därför kan det tänkas uppstå höga koncentrationer av kronvilt i de skogar som finns tillgängliga. Om kronviltet dessutom har svårt att hitta föda i dessa skogar kan skadefrekvensen öka.

Studien visade också att det var betydligt mer skador i de områden där det var brist på alternativ föda. I områden där markvegetationen var rik var skadefrekvensen också lägre. Bark är en fullt acceptabel energikälla men det är tidskrävande att äta bark, därför kan man anta att det är en lågt prioriterad födoresurs. Åtgärder som ökar mängden tillgänglig föda kan därför tänkas minska skadorna. Genom att plantera granbestånd i glesare förband och genom att gallra tidigt kan mer ljus nå marken och markvegetationen stimuleras. Dessutom har andra studier visat att träden blir mer kvistiga och får grövre bark om man planterar i glesare förband; det kan också skydda träden från barkskalning. Dessutom har andra studier visat att olikåldriga och flerskiktade blandbestånd inte drabbas lika hårt som likåldriga granmonokulturer; troligen på grund av en bättre födotillgång. Andra trädslag kan därför med fördel planteras tillsammans med gran.

Jag fann inget samband mellan störning (bebyggelse och vägar) och omfattning av barkskalning.

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*"Yea, like the stag, when snow the pasture sheets
The bark of trees thou browsed'st"*

/ Shakespeare, W. 1607

Introduction

Ungulates are becoming gradually more important in Sweden, as well as in the rest of the world, not just for hunting, recreation and biodiversity, but also because of their negative effect on forestry, agriculture and biodiversity (Mitchell et al. 1977, Côte et al. 2004, Akashi & Terazawa 2005, Danell et al. 2006). Consequently, management is necessary for nearly all ungulates in their habitats (Danell et al. 2006). Whether the aim of management, is to ensure yield of game or to protect economically valuable crops or forest plantations, it is of great importance to understand ungulates' foraging behavior and ultimately its effects on ecosystems (Senft et al. 1987, Augustine & McNaughton 1998, Coulson 1999, Reimoser 2003, Côte et al. 2004, Danell et al. 2006, Jarina 2006, Vospernik 2006).

An animal's foraging strategy will determine the daily and annual energy balance of the animal (Moen et al. 1997, Newman 2007) and is decided by a complex combination of factors. Besides availability and quality of forage, factors such as predation risk, available shelter, weather conditions, social interactions and human disturbance also affect the decisions (Pierce & Peek 1984, Grover & Thompson 1986, Senft et al. 1987, Morrison et al. 2003, Jerina 2006, Newman 2007). For large herbivores, the available forage is widely dispersed in the landscape and is of variable quality, quantity and structure, depending on season (Senft et al. 1987, Jefferies et al. 1994, Moen et al. 1997, Côte et al. 2004) and even time of day (Newman, 2007). As seasons change, herbivores need to adapt their foraging strategy accordingly (Moen et al. 1997, Jarina 2006).

Red deer expansion

Red deer (*Cervus elaphus*) has successfully spread all over the world and are increasing considerably in abundance (Côte et al. 2004). At present it is the second most abundant cervid species in Europe (Gill 1992a, Appollonio et al. 2010). The red deer has reached a post harvest population of nearly 10 000 individuals in Sweden (Appollonio et al. 2010) and are established in all Swedish regions except in Norrbotten, Halland and Gotland (A. Jarnemo, unpubl. data). Large thriving populations can be found in several places in south and central Sweden (A. Jarnemo, unpubl. data).

The successful expansion of red deer can be explained by high survival, because of increased forage and reduction in hunting and natural predators (Reimoser 2003, Côte et al. 2004). Red deer also show excellent adaptability to different environments (Geist 1998).

Bark-stripping

Bark-stripping damage caused by red deer has been observed throughout Europe (Lavsund 1968, Mitchell et al. 1977, Jarina 2006, Verheyden et al. 2006). Mitchell et al. (1977), presents several studies that show the occurrences of bark-stripping, dating all the way back to the 19th century, but he also reveal earlier texts that mention bark-stripping, such as Shakespeare's *Antony and Cleopatra* (1607) and Turberville's *Noble Arte of Venerle or Hunting* (1576).

Though bark-stripping is not a new phenomenon, it has become a growing problem, since the forest industry has grown (Lavsund 1968).

Bark is stripped in two ways, gnawing (winter) or tearing (vegetation period). During the vegetation period red deer can easily remove bark by tearing the bark of the trees in large chunks. However, during winter the bark is strongly adhered to the stem, and the deer can only gnaw smaller pieces of bark, leaving teeth marks on the stem (Lavsund 1968, Welsh et al. 1987).

When red deer strip bark from trees they leave wounds that lead to discoloration and stem deformations. The wounds also become susceptible to fungal infection, which can lead to rot (Lavsund 1968, Gill 1992b, Putman & Moore 1998, Vasiliuska & Stenlid 1998). Trees show different propensity to degrading fungi, where Norway spruce, Lodgepole pine (*Pinus contorta*) and Scots pine (*Pinus sylvestris*) are highly susceptible, and for instance Sitka spruce (*Picea sitchensis*) is not (Gill et al. 2000). Old wounds may also become the point of breakage during wind or snow storms (Gill et al. 2000).

Previous studies have shown that the forest industry is experiencing economic loss because of bark-stripping damage (Gill 1992b, Gill et al. 2000). Several studies (for review see Lavsund 1968) show crucial reductions in income because of bark-stripping. In a review, Gill et al. (2000) found that there is a significantly greater loss of yield in Norway spruce because of bark-stripping than in other species.

Species and morphology

No less than 21 tree species in Europe have been reported with bark-stripping damage (Mitchell 1977, Gill 1992a). Which species that are most subjected, seems to vary in different parts of Europe (for review see Lavsund 1968, Vospernik 2006). Among the more subjected species, we find Norway spruce, Lodgepole pine, rowan (*Sorbus spp.*) and willow (*Salix spp.*, for review see Lavsund 1968, Welsh et al. 1987, Gill et al. 2000).

The age at which trees are most vulnerable to damage varies between species, and can be explained by differences in morphology, such as: bark thickness, roughness and the bark's attachment to the tree (Lavsund 1968, Mitchell et al. 1977, Gill 1992a, Kiffner et al. 2008). Red deer will strip bark of trees from the time the stem become unbending, until the bark is too tough and thick to remove (Gill et al. 2000, Vospernik 2006). Most tree species are susceptible at an early age (7-20 years, for review see Mitchell 1977). However, Welsh et al. (1987) found that Norway spruce was most susceptible to damage between 9 and 44 years (the longest period compared to other trees species). Damage is made on stems with variable diameter. However, larger wounds are made on trees with larger diameter (Welch et al. 1988, Gill 1992a). Damage is mostly made at the tree trunks between 50 and 100 cm above ground (Welch et al. 1988, Gill 1992a).

Theories on bark-stripping

A number of theories are proposed to explain the occurrence of bark-stripping (Lavsund 1968, Mitchell 1977). One theory suggests that bark is eaten when other resources are scarce (Gill 1992a, Vospernik 2006, Verheyden et al. 2006). Other theories suggest mineral deficiencies, parasite control or digestion improvement by the bark's roughage after an over-rich diet (Mitchell 1977, for review see Gill 1992a, Verheyden et al. 2006). There has been some consensus about the nutritive value of bark and its use as food source during winter (Lavsund 1968, Mitchell 1977, Vospernik 2006, Verheyden et al. 2006, Kiffner et al. 2008). However, Gill (1992a) state that these types of studies has failed to give an uncomplicated correlation between bark-stripping and nutrient content.

Supplemental feeding during winter has proved to be counterproductive in preventing bark-stripping (for review see Reimoser 2003, Jerina 2006, Verheyden et al. 2006, Jerina et al. 2008). Red deer become concentrated in areas with supplementary feeding stations and change their habitat use by occupying the same area all year (Reimoser 2003, Jerina 2006). The feeding stations only account for a small portion of their diet and therefore the surrounding area becomes even more subjected to damage (Jerina 2006, Jerina et al. 2008).

Forest susceptibility to bark-stripping

It is commonly believed that there is a correlation between amount and severity of damage and animal density (Lavsund 1968, Verheyden et al. 2006, Kiffner et al. 2008). However, Gill (1992a) points out the fact that most of these studies used unreliable or rough methods of estimation of density, and therefore believes that they can only give a rough estimate of the influence density has on bark-stripping. A great variation in frequency and gravity of bark-stripping has been reported, with periods of fairly constant damage and then additional sudden outbreaks (Welsh et al. 1987, Gill 1992a, Verheyden et al. 2006). Reimoser (2003) proposed that the severity of damage depend on forest attractiveness rather than on the abundance of red deer. According to Reimoser (2003), Gossow (1986) found that intensified hunting efforts have failed to decrease damage. Furthermore, Ahlén (1965) found high frequencies of damage already at low densities of deer' suggesting that population density may be of secondary importance.

Reimoser (2003) suggest that susceptibility to damage is dependent on both forest distribution in the landscape and the forest structure. He argues that small areas of forest in agricultural land are more prone to damage because of higher concentrations of ungulates. He also suggests that monocultures should be rehabilitated to a more natural state, thereby giving ungulates alternate forage. Stands with more than one dominating tree species seem to have less damage than monocultures (for review see Gill 1992a, Verheyden et al. 2006) and some authors have argued that monocultures may force the red deer to new habits such as bark eating (for review see Lavsund 1968).

In this study I will examine the influence of environmental factors e.g. forest dominated landscape opposed to agricultural dominated landscape, forage availability and red deer density on bark-stripping on Norway spruce. I will also consider the influence disturbance from roads and settlements has on bark-stripping frequency.

Hopefully, an understanding of the factors behind bark-stripping can be used to suggest countermeasures and foretell the risk of bark-stripping when red deer establish in new areas. This knowledge will help to achieve an improved management of red deer populations.

Material and methods

Study area

This study was implemented in two Swedish regions, Skåne and Södermanland/Östergötland, hereafter referred to as S and SÖ. Characteristically, S has predominantly open landscape with agricultural land (45%) and pastures (5%), forest, cover only 35% of the area (Skogsdata 2009). The most common tree species is spruce (37.5%) followed by hardwood (20%) and foliage (18.1%, Skogsdata 2009). SÖ, on the other hand hold, mostly forest (57%) with a small fraction of agricultural land (20%). In SÖ, both pine and spruce are frequent with 27.4% and 31% respectively (Skogsdata 2009). Climate data from 1961-1990 show that the mean number of days per year with snow is 25-50 days in S and 75-100 days in SÖ. The annual mean snow cover in S range between 0-20 cm and 30-40 cm in SÖ (SMHI 2009).

In each of the two regions, three study sites were chosen. In S the study sites were chosen over a range of population densities (Table 1). In SÖ areas were chosen with varying landscape features, ranging from homogeneous forest to a mixed forest-agricultural landscape as well as over a range of population densities (Table 1, Appendix 1).

Table 1. Study locations in S and SÖ

Region	Area	Name	Size (ha)
S	1	Krageholm, Bellinga, Rydsgård, Ågerup	6238
	2	Christinehof, Kronovall	10200
	3	Övedskoloster, Hjularöd	4865
SÖ	4	Holmen, Stavsjö, Virå	5617
	5	Holmen, Simontorp, Brevik	7210
	6	Fjällskär, Tista, Christineholm	4350

Data collection

Spruce stands -damaged trees

Data on bark-stripping damage was collected between the 12th of April to the 12th of May 2010 in the S region and between the 18th of May to the 19th of June 2010 in the SÖ region. By using forest maps and land owners' management plans, appropriate spruce stands were chosen (e.g. stands with trees at a susceptible age to bark-stripping (20-36 years), stands > 1 hectare to fit ten sample plots and stands that contained at least 80 % spruce, to be classed as a spruce stand in this study). Thirty stands per study area were then randomly selected, adding up to a total of 180 investigated stands.

In each stand, ten plots were placed according to the size and shape of the individual stand. The distance between sample plots (> 15 m to avoid overlapping plots) was set to get them as evenly distributed in the stand as possible. Placement of plots was decided before arriving to the stand to assure objective placement. All plots were placed at least 15 meters from the edge of the forest to avoid edge effects.

In each plot, the ten trees closest to the center point were examined regarding bark-stripping damage. The ten trees had to be found in the radius 11.28 m to be investigated. Number of injured (both old and fresh injuries) and non-injured trees was counted.

Transect plots –forage availability

Forage availability was measured in transect plots in the surrounding area. Six plots were placed along transects (500 m) heading in the four cardinal directions (North, South, West and Eastward). The zero point was placed 15 m from the edge of the forest.

To get an index of available winter forage, the cover of palatable food was estimated. Estimates of cover (in percent), projected vertically in the range 0 to 2 meters were made in 20m² large circular plots with a radius of 2.52 m. Species monitored were: ash (*Fraxinus excelsior.*), birch (*Betula sp.*), juniper (*Juniperus communis*), oak (*Quercus sp.*), bilberry (*Vaccinium myrtillus.*), lingonberry (*Vaccinium vitis-idaea*), heather (*Calluna vulgaris* and *Erica tetralix*), pine, rowan, spruce, willow, other foliage and other rice's. For the statistical analysis the available forage was divided into the following groups: *field layer* (bilberry, lingonberry, heather and other rice's), *tree/bush layer* (ash, birch, juniper, oak, pine, rowan, spruce, willow and other foliage), *foliage* (ash, birch, oak, rowan, willow and other foliage).

Data analysis

ArcGIS

Layers for landscape structure (e.g. roads, buildings and land cover) for the study areas were defined by the Swedish mapping, cadastral and land registration authority (Lantmäteriet), GSD-road map "Blå kartan" (Appendix 1). To analyze the influence of disturbance and stand closeness to agricultural land, the shortest distance to roads, buildings and agricultural land were measured from the stands centre (ArcGIS 9.3). Roads and buildings in the analysis were

selected to fit the criteria of possible red deer disturbance (e.g. *Buildings*: houses, castles and mansions, *Roads*: interstate, motor-traffic-, national-, country- and good quality roads).

The proportion of forest and agricultural land around each stand was estimated within buffer zones around the stand. The size of the buffer zone was based on the yearly home ranges (Minimum Convex Polygon) of hinds in the areas e.g. 2862 ha in S and 1057 ha in SÖ (A. Jarnemo, unpubl. data).

Statistical analysis

Out of 180 stands, 143 were used for all analysis including forage availability. Removed stands (23 in S and 14 in SÖ) had a low number of transect plots (< 10 plots) resulting in insufficient amount of data. I used spruce stand (opposed to individual trees) as the statistical unit (n = 180) to avoid dependent samples. Histograms showed distributions divergent from the normal distribution, therefore I used non-parametric tests to analyze differences between and within the two regions. The effects of the independent variables on bark stripping were analyzed with multiple regressions (the backward algorithm). As a proxy for red deer density in each study area I used culling statistics from 2009/2010 (collected by A, Jarnemo). To control for the effect of red deer population density in the multiple regressions, I weighed the damage estimate by deer numbers harvested in each study area, hereafter termed damage per animal. Fresh damage per animal and total damage per animal were analyzed separately. Scatter plots were analyzed to see if the variables needed to be transformed to meet the assumptions of regression analyses. I normalized the data by transforming the dependent variable with a square root transformation.

A correlation analysis (Pearson's) showed correlation between some of the independent variables (Table 2). The test showed a very strong negative correlation between proportion forest and proportion agricultural land ($r = -0.97$, $p < 0.01$, $n = 180$,) and a strong positive correlation between mean bush/canopy layer and mean foliage ($r = 0.77$, $p < 0.01$, $n = 143$). These correlations show higher r-values than the level (0.50) recommended for regression analyses (e.g. Edge et al. 1987). Therefore the variables proportion forest and foliage will be excluded from the regression.

All statistical tests were performed in the Windows software package SPSS 19.0.

Table 2. Correlation between independent variables.

	A	B	C	D	E	F	G	H
A: Proportion forest	1							
B: Proportion agricultural land	-0.97**	1						
C: Distance to agricultural land	0.05	-0.06	1					
D: Distance to buildings	0.07	-0.03	0.10	1				
E: Distance to roads	0.36**	-0.34**	0.26**	0.21**	1			
F: Bush/canopy layer	0.20*	-0.22**	0.32**	0.04	0.23**	1		
G: Foliage	0.10	-0.11	0.46**	0.04	0.12	0.77**	1	
H: Field layer	0.21*	-0.21*	-0.02	0.00	0.26**	0.25**	0.047	1

** Correlation is significant at the 0.01 level, *Correlation is significant at the 0.05 level.

Result

In total, 180 stands were visited in this study and up to 18 000 trees scanned for fresh and old damage. The total number of damaged trees (old and/or fresh damage) in both study areas combined was 9611 (7934 in S and 1677 in SÖ).

Distance to roads ranged from 53 m to 5662 m (mean 1310 m) from studied stands; distance to buildings ranged from 80 m to 1522 m (mean 482m) from studied stands; distance to agricultural land ranged from 0 m to 1372 m (mean 245 m) from studied stands.

The non-parametric tests (Mann Whitney) showed that there was a significant difference in fresh damage (Mann Whitney, $U = 1117.5$, $p < 0.01$, $n = 180$) and total (old + fresh) damage (Mann Whitney, $U = 317$, $p < 0.01$, $n = 180$) between the two regions. The S region had a high level of both total and fresh damage compared to the SÖ region (Fig. 1). In the S region, 87 % of the trees were damaged compared to 19 % in the SÖ region. In the S region 17 % of trees had fresh damage compared to 3 % in the SÖ region.

The frequency of fresh damage (Kruskal-Wallis, $H = 44.1$, $p < 0.01$, $df = 2$) and total damage (Kruskal-Wallis, $H = 39.5$, $p < 0.01$, $df = 2$) differed significantly between the study sites in the SÖ region (Table 3).

There was however no significant difference between study sites in the S region for either fresh damage (Kruskal-Wallis, $H = 1.1$, $p = 0.57$, $df = 2$; Table 3) or total damage (Kruskal-Wallis, $H = 5.5$, $p = 0.06$, $df = 2$; Table 3).

Table 3. Index for red deer density (number of culling/1000 ha, 2009/2010) and mean fresh and total (fresh + total) damage at three sites in the Skåne and Södermanland/Östergötland regions respectively, in Southern Sweden during 2010.

Region	Area	Size (ha)	Index of red deer density (Culling/1000ha)	Total damage % (mean)	Fresh damage % (mean)
S	1	6238	2.2	83	9.0
	2	10200	12.2	92	12.0
	3	4865	4.9	89	20.0
SÖ	4	5617	23.9	7.7	0.9
	5	7210	7.9	1.9	0.1
	6	4350	8.0	46.0	9.0

A correlation analysis (Spearman's rho) showed no significant correlation between mean fresh damage for the study sites and the index used for red deer density (Spearman's rho = -0.54, $p = 0.27$, $n = 6$) or between mean total damage for the study sites and the index used for red deer density (Spearman's rho = -0.14, $p = 0.79$, $n = 6$).

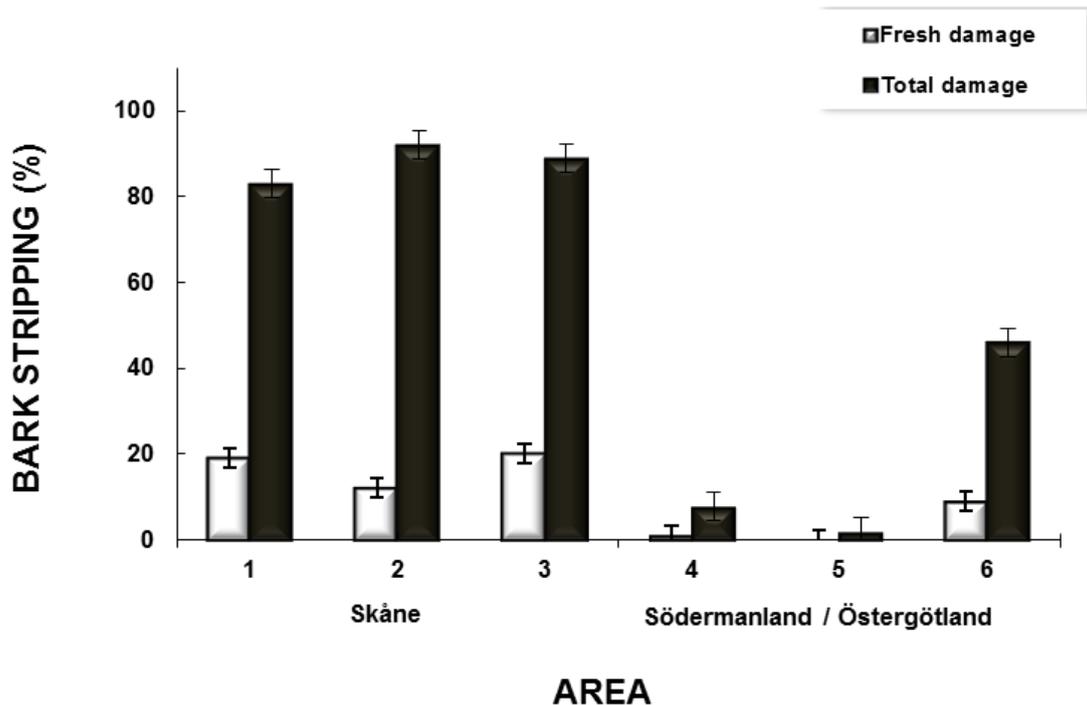


Figure 1. Fresh and total (fresh + old) estimated bark stripping damage (%) at three sites in the Skåne and Södermanland/Östergötland regions respectively, in Southern Sweden during 2010. Error bars show SE.

The landscape structure differed significantly between the two regions as recognized by the design; the difference was significant for both proportion forest (Mann Whitney, $U = 745$, $p < 0.01$, $n = 180$; Fig. 2) and proportion agricultural land (Mann Whitney, $U = 716$, $p < 0.01$, $n = 180$; Fig. 2). In the SÖ region forest cover was dominating the landscape (69 %) and consequently the cover of agricultural land was low (17 %). The S region displayed the opposite relationship with low forest cover (38 %) and high cover of agricultural land (58 %).

In the S region, there was a significant difference between the study sites in proportion forest (Kruskal-Wallis, $H = 6.1$, $p < 0.05$, $df = 2$) and proportion agricultural land (Kruskal-Wallis, $H = 11.3$, $p < 0.01$, $df = 2$).

In the SÖ region there was a significant difference in proportion forest (Kruskal-Wallis, $H = 28.1$, $p < 0.01$, $df = 2$) and proportion agricultural land (Kruskal-Wallis $H = 16.4$, $p < 0.01$, $df = 2$) between study sites. Area 6 had considerably more agricultural land than area 4 and 5 (Fig. 1).

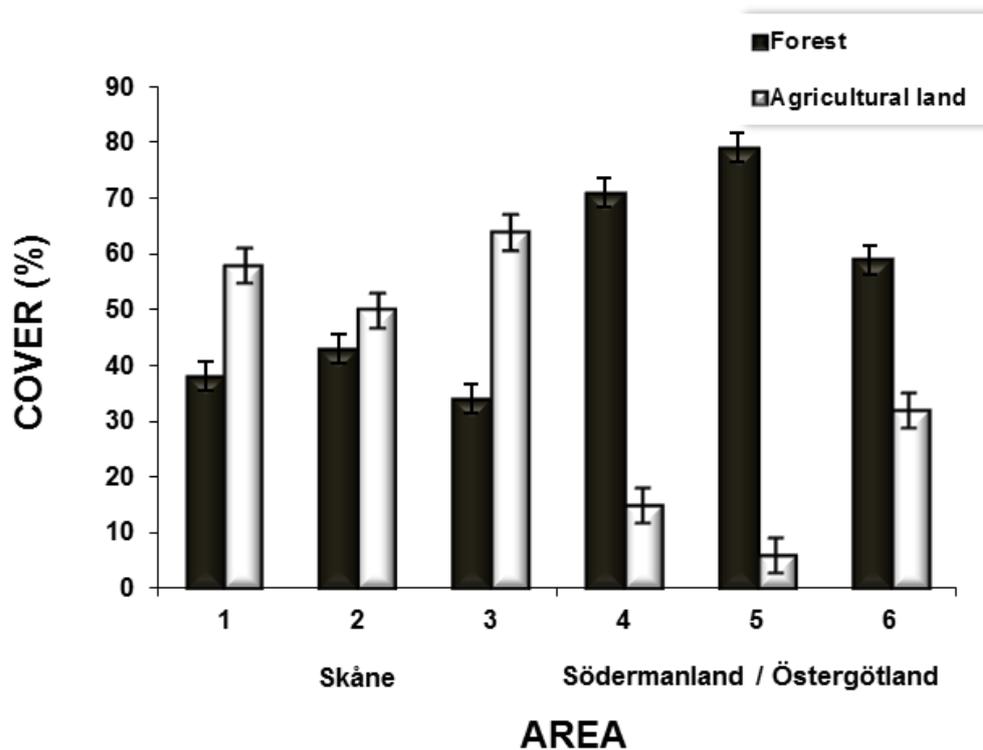


Figure 2. Landscape features (% cover) at three sites in the Skåne and Södermanland/Östergötland regions respectively, in Southern Sweden during 2010. Error bars show SE.

Available forage in the field (Mann Whitney, $U = 79$, $p < 0.01$, $n = 143$; Fig. 3) and bush/tree layer (Mann Whitney, $U = 1216$, $p < 0.01$, $n=143$; Fig. 3) differed significantly between regions. The available alternate forage in the SÖ region were rich (14 %) compared to the S region (1 %).

The final analysis; the multiple regression (backward algorithm) retained the variables proportion agricultural land, field layer and distance to agricultural land and excluded the variables tree and bush layer, distance to roads and distance to buildings explaining the level of fresh bark stripping damage per animal. Using the backward model a significant model emerged (adjusted R square = 0.33, $p < 0.001$, $df = 3$) see the significant variables below (Table 4).

Table 4. Significant variables contained from the multiple regression (backward algorithm) for fresh damage/animal.

Predictor variables	Beta	p
Proportion agricultural land	0.255	< 0.005
Field layer	-0.303	< 0.001
Distance to agricultural land	-0.211	< 0.005

The regression analysis showed that fresh bark stripping damage per animal might be explained by increasing proportion agricultural land and decreasing amount of forage in the

field layer and the stands closeness to agricultural land. When analyzing the fresh bark-stripping damage per animal the model explained 33 % of the total variance.

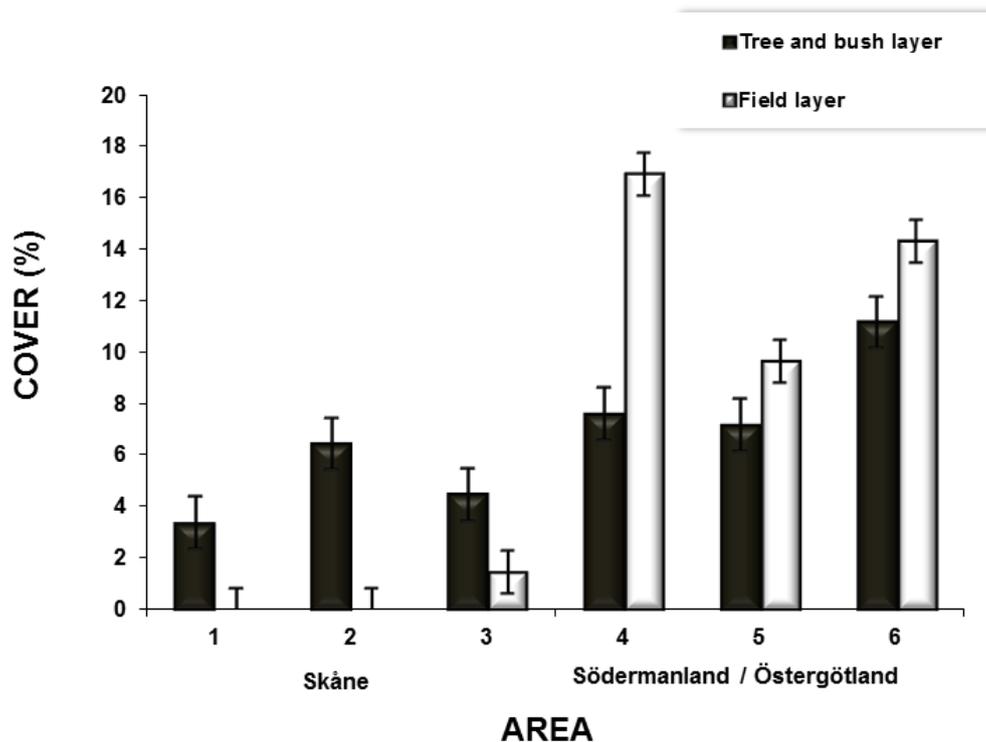


Figure 3. Forage availability (% cover) at three sites in the Skåne and Södermanland/Östergötland regions respectively, in Southern Sweden during 2010. Error bars show SE.

The multiple regression retained the variables agricultural land, field layer, tree and bush layer and distance to agricultural land and excluded the variables distance to buildings and distance to roads explaining the level of total bark stripping damage per animal. Using the backward model a significant model emerged (adjusted R square = 0.61, $p < 0.001$, $df = 4$) see the significant variables below (Table 5).

Table 5. Significant variables contained from the multiple regression (backward algorithm) for fresh damage/animal.

Predictor variables	Beta	p
Proportion agricultural land	0.417	< 0.001
Field layer	-0.301	< 0.001
Distance to agricultural land	-0.234	< 0.001
Bush/tree layer	-0.138	< 0.05

Total damage per animal were explained by increasing proportion agricultural land (Fig. 4) and decreasing field layer (Fig. 5), decreasing tree and bush later and the stands closeness to agricultural land. When analyzing the total bark-stripping damage per animal the model explained 61 % of the total variance.

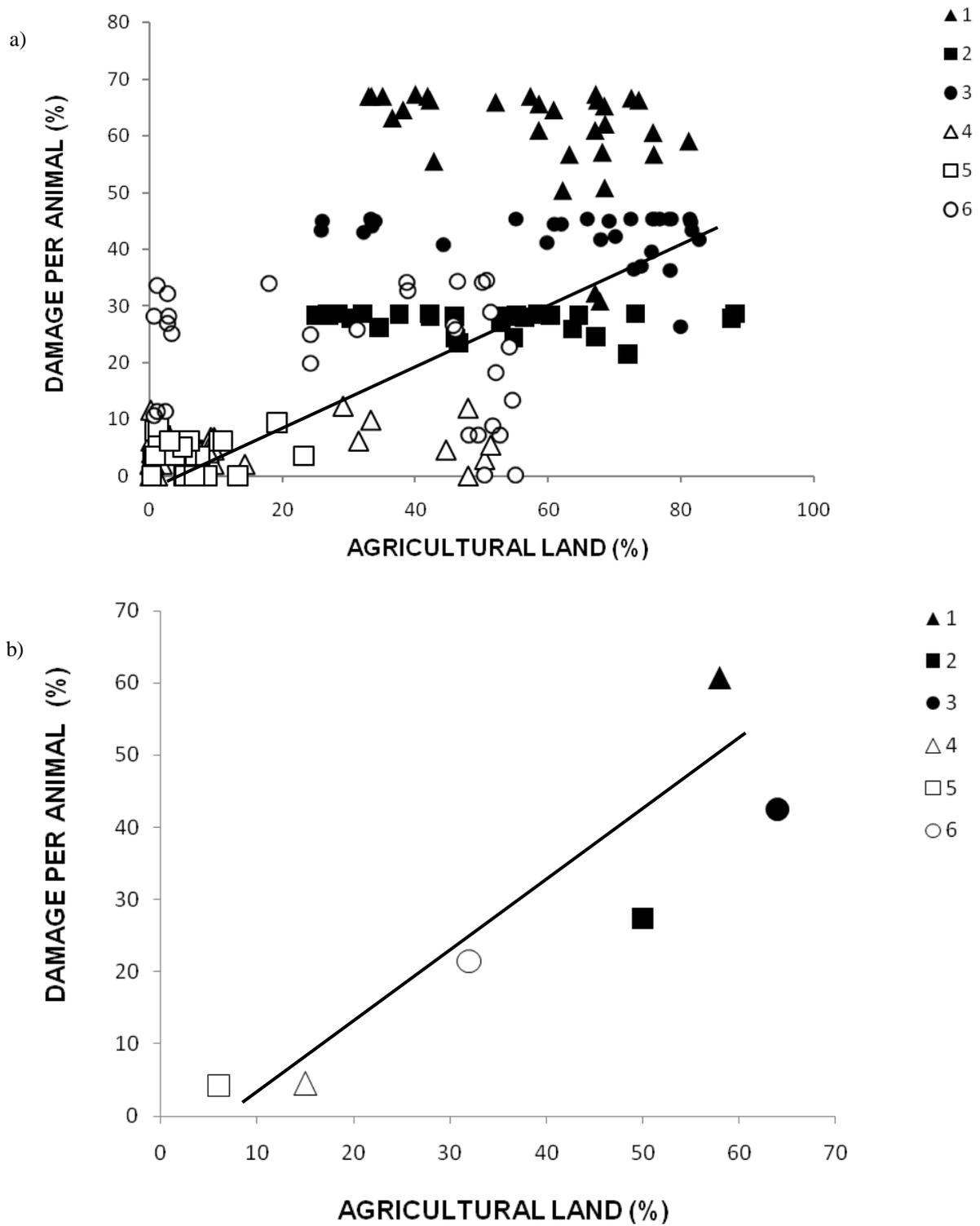


Figure 4. Total damage per animal (% , square root transformed) vs. cover of agricultural land (%). In (a) all stands (n = 180) and (b) as mean for each area (n = 6) in two regions (filled symbols: Skåne and open symbols: Södermanland/Östergötland) of southern Sweden, 2010. There was a significantly higher level of damage in areas with high percentage of agricultural land ($p < 0.01$). See Appendix 1 for location reference.

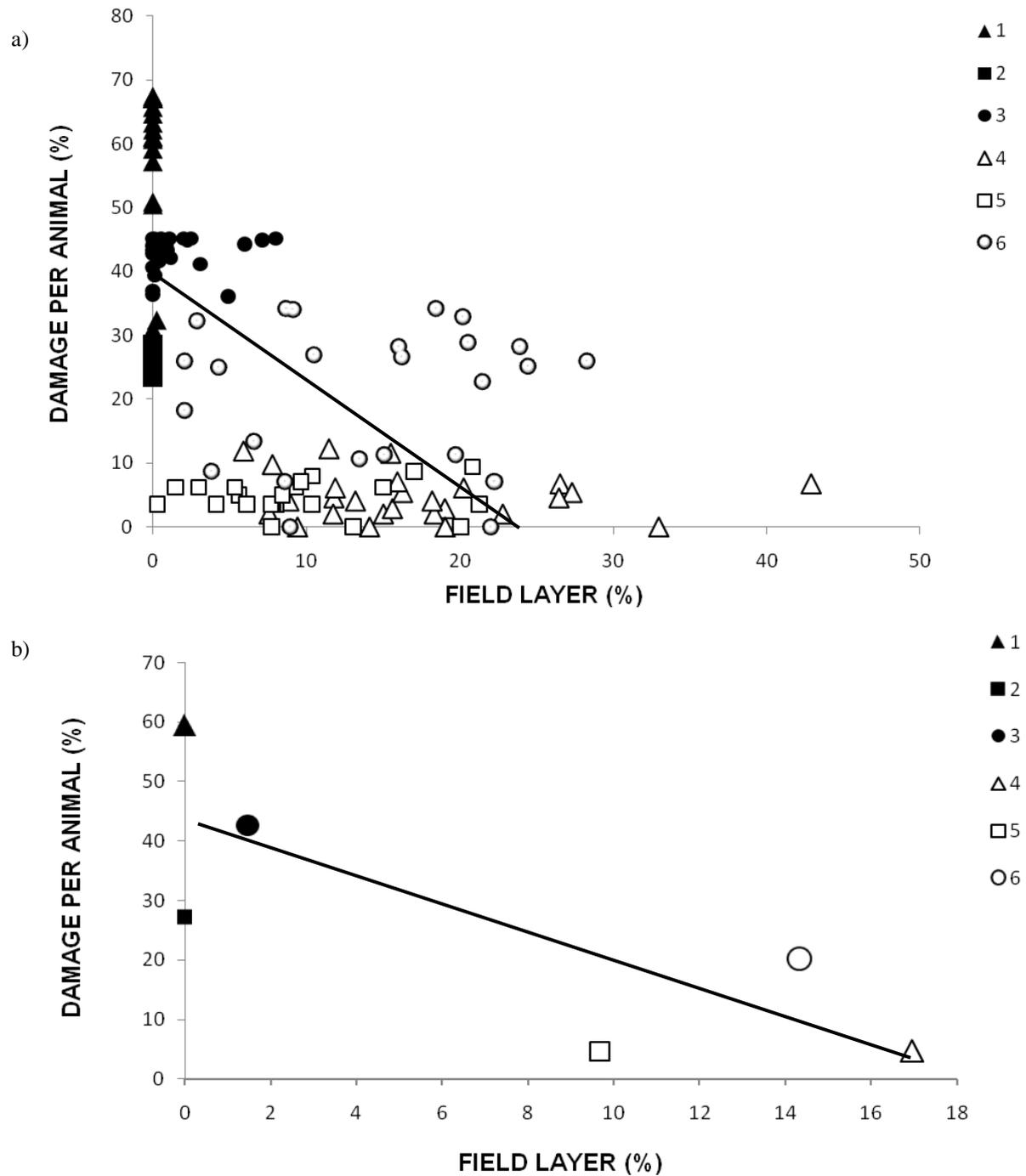


Figure 5. Total damage per animal (% , square root transformed) vs. cover of field layer (%). In (a) all stands (n = 143) and (b) as mean for each area (n = 6) in two regions (filled symbols: Skåne and open symbols: Södermanland/Östergötland) of southern Sweden, 2010. There was a significantly lower level of damage in areas with plenty of available forage in the field layer ($p < 0.01$). See Appendix 1 for location reference.

Discussion

Red deer density

Quantity and severity of bark-stripping does not appear to be easily explained by the number of red deer inhabiting a region. In the Skåne region, 87 % of trees were stripped even though that region only has a moderate population size of red deer. Even more convincing, bark-stripping was lower in the Södermanland/Östergötland region where the density of deer is very high, as only 18 % of trees were damaged there. Furthermore, there were high frequencies of damage in all study sites in the Skåne region, even at different densities, while the highest damage level in the Södermanland/Östergötland region were found in one of the study site with the lowest red deer density. Additionally there was no correlation between the index used for density and the frequency of damage. The same pattern has been observed previously by Völk (1999) in Austria, where he found low frequencies of damage in an area with a large red deer population.

Verheyden et al. (2006) found a positive correlation between bark-stripping and red deer density when they looked at several European studies on stand level and larger scale studies. The study concluded that more animals create shortage of alternate forage, suggesting that density may influence forage availability. The lack of forage that results from high densities of red deer may therefore, as a consequence, result in more bark-stripping. However, in a previous study in Skåne, Ahlén (1965) reported that while the influence on vegetation abundance was highly correlated to red deer density, bark-stripping was not; a small group of red deer had been observed to damage several hectares of spruce trees in in a short period of time. Reports of sudden outbreaks (Welsh et al. 1987, Gill 1992a, Verheyden et al. 2006) also indicate that damage may be the result of other factors than deer density.

Consequently, deer density seems to explain only a little of the variation in bark-stripping between areas. Nevertheless it is still a fairly common belief among foresters that increased culling of red deer will reduce damage (Reimoser 2003). However, increased hunting has failed to reduce damage (for review see Reimoser 2003) and even though population size probably is of some significance (several deer' can consume more bark than one deer), an increased hunting pressure may not be the key solution to decrease bark-stripping damage, unless the majority of the red deer population is harvested.

Landscape structure and forage availability

The main objective of this study was to examine the significance of landscape structure and forage availability on the occurrence and severity of bark-stripping. The study confirmed that both these variables affected bark-stripping frequency, and thereby suggests that habitat management may help to reduce, and perhaps even prevent damage.

The results showed that bark-stripping increased significantly with proportion agricultural land in the landscape. There was a clear difference in landscape features between the two regions and damage was more frequent in Skåne, where agricultural land dominates the landscape. The same pattern could be seen in Södermanland/Östergötland, where study sites had

been selected with varying landscape features e.g. the study site with the highest proportion agricultural land was the area with most damage.

The importance of agriculture activities on bark-stripping can be explained by several possible factors. Agricultural land offers easy accessible nutritious food that is available most of the year, even during winter, if snow cover is not too extensive (Ahlén 1965). Winter grain is palatable food that usually stands one decimeter high during winter months (Ahlén 1965) and because snow cover is rarely constant in Skåne, red deer are not restricted to forage in the forest during winter (Ahlén 1965), which may be the case in Södermanland/Östergötland. It is possible that bark is eaten to retain the rumen function after eating such concentrated food (for review see Gill 1992, Verheyden et al. 2006). In a study from 1973, bark-stripping was more frequent in areas where alternate roughage was absent (for review see Gill 1992a). The multiple regressions also showed that damage were more frequent in forests close to agricultural land which might also support this hypothesis.

If lack of fibre in the diet does create a need to eat bark, feeding stations that offer easy digestible forage may also result in more bark-stripping (see Putman & Staines 2004 for review). Winter feeding practices are common in many countries and indeed, supplemental feeding has been used as a measure to prevent damage, but has often had the opposite effect (for review see Reimoser 2003, Jerina 2006, Verheyden et al. 2006, Jerina et al. 2008). Planting shrubs and trees as winter forage or offering well-adjusted forage in feeding stations could therefore possibly decrease damage. However, because the consequence of rich food has not been investigated thoroughly, experimental studies may be needed to test if lack of roughage makes red deer compensate for that deficiency.

Feeding stations has also been reported to restrict red deer movement (Jerina 2006) and could therefore be used to direct the deer to areas less susceptible to damage.

It may however not be the proportion of agricultural land that result in more bark-stripping, but the configuration e.g. the level of fragmentation of forest in the landscape. In agricultural landscapes with only few, fragmented forests, higher concentrations of red deer will gather in small areas (Reimoser 2003). Forests are crucial habitat for red deer, and telemetry studies even show that red deer spend up to 80 % of their time in forests (Jerina 2006). A spruce stand will offer shelter from wind, low temperatures (Conradt et al. 2000, Jerina et al. 2008) and disturbance in the surrounding area, and present a thinner snow cover in severe winters (Jerina 2006) and will therefore be attractive to red deer. However these small fragmented spruce monocultures offers nothing palatable to eat except bark (for review see Jerina et al. 2008) and may therefore be exposed to high frequencies of damage.

Previous studies on moose (*Alces alces*) in Sweden and the occurrence of bark-stripping on pine (*Pinus sylvestris*) showed a weak correlation between bark-stripping and forest productivity (Faber & Thorson 1996). The fact that areas with agricultural land most likely have forests with higher productivity may therefore be a possible contributing factor explaining the high occurrence of bark-stripping by red deer in agricultural dominating landscapes.

The multiple regressions showed that bark-stripping decreased significantly with increasing forage availability in the field and bush/tree layer in the surrounding area. The results showed that especially the field layer was of importance. There were higher damage levels in the Skåne region, and Skåne has a fair amount of bush/tree layer but has little field layer. This is also supported by the fact that the study site in the Södermanland/Östergötland region with the most abundant field layer had low damage levels while the study site with the most abundant bush/tree layer had the highest frequency of damage in that region.

Several authors support the food resource hypotheses; that lack of alternate forage result in bark-stripping (e.g. Völk 1999, Reimoser 2003, Jerina 2006, Vospernik 2006, Verheyden et al. 2006). Spruce monocultures provide nothing to eat except bark (For review see Jerina et al. 2008) and even though bark is a perfectly adequate food source, with satisfactory energy value (Gill 1992a, Verheyden et al. 2006), it is time-consuming to eat bark and consequently it is probably just eaten as a last resort (Jerina et al. 2008). The flexible feeding behavior seen in red deer (alternate grazers and browsers depending on season) could also clarify the occurrence of bark-stripping behavior when other recourses are lacking (Verheyden et al. 2006). Spruce bark is also eaten by moose during periods of food deficiency (Randveer & Heikkila 1996).

Some authors (for review see Gill 1992a, Verheyden et al. 2006) have also stated that mixed stands with more than one dominating tree species display less damage than monocultures which could be explained by more available forage in these forests. In fact, Völk (1999) established that low frequencies of damage were correlated with near natural forests (multi-layered, mixed and thinned stands) e.g. forests with high abundance of available forage.

Jerina et al. (2008) found the highest amount of damage in young thick spruce monocultures (e.g. tight crown closure, high tree density, and low species diversity) where the only available food source is bark. As mentioned earlier, young thick forests are attractive to red deer because they offer milder temperatures, less snow cover and winds during winter when extreme winter conditions limit red deer movement (Jerina et al. 2008). A forest with high tree density will also have thinner bark for a relatively longer time making the bark easier to remove (Vospernik 2006). High frequencies of damage can therefore be the result of forest attractiveness in combination with a lack of alternate forage (Reimoser 2003).

Rehabilitating forests to a more natural state with abundant forage can therefore probably help decrease damage. To increase forage, monocultures should be replaced with mixed stands with wintergreen and deciduous species (see also Reimoser 2003). Spruce stands should be planted with a lower plant density and be thinned at an early stage; letting more light in through the canopy will allow a rich field and shrub layer. In addition it will allow trees to become more branched, protecting them from bark-stripping (Reimoser 2003, Jerina et al. 2008).

As well as improving the spruce stands, areas outside the stand can be improved to help the overall feeding conditions.

It has also been observed that bark-stripping is worse in severe winters (Jerina 2006), however winter conditions in Södermanland/Östergötland are generally far worse than in Skåne. Thus, the high proportion of forests with abundant field and shrub layer seem to keep red deer

from bark-stripping even during severe winters. Nevertheless, clearing of snow may be one way to help red deer reach the field and shrub layer during winters with substantial long-lasting snow cover (Ahlén 1965).

Disturbance

There was no significant effect of disturbance (e.g. roads and buildings) on bark-stripping damage on spruce. This is contradictory to a previous study by Jerina (2006) in Slovenia where damage increased with distance to both roads and buildings. It is possible that single isolated buildings, as are seen in the Swedish countryside, do not disturb red deer to the same extent as more gathered communities that are seen in Europe, and could therefore be a possible explanation to why buildings did not influence bark-stripping in my study.

It is also possible that red deer, to some extent, habituate to human settlements and roads which could also be a contributing factor for these results.

Because the mean stand damage level was used as the statistical unit, I did not investigate how damage was distributed within the spruce stand. It is possible that there are patterns of avoidance on a local scale where red deer avoid bark-stripping close to houses and roads but start stripping bark further inside the same stand. Jerina et al. (2008) found damage to increase with distance from forest edge, with the highest frequency of damage at 800m. Further studies in these regions may therefore be needed to examine the influence of disturbance on bark-stripping frequency.

In conclusion, this study highlights the importance of habitat management to reduce bark-stripping in spruce stands. By replacing monocultures which offer nothing palatable to eat, except bark, we may be able to reduce or even prevent damage. Suggested measures include: sparse plantation and thinning of spruce stands to create more natural forage in the field and shrub layer, as well as mixing in deciduous trees in spruce stands. Within the range of densities included in this study, red deer density does not seem to influence bark-stripping in a conclusive way, therefore increasing culling is probably not the best measure to prevent bark-stripping in most areas.

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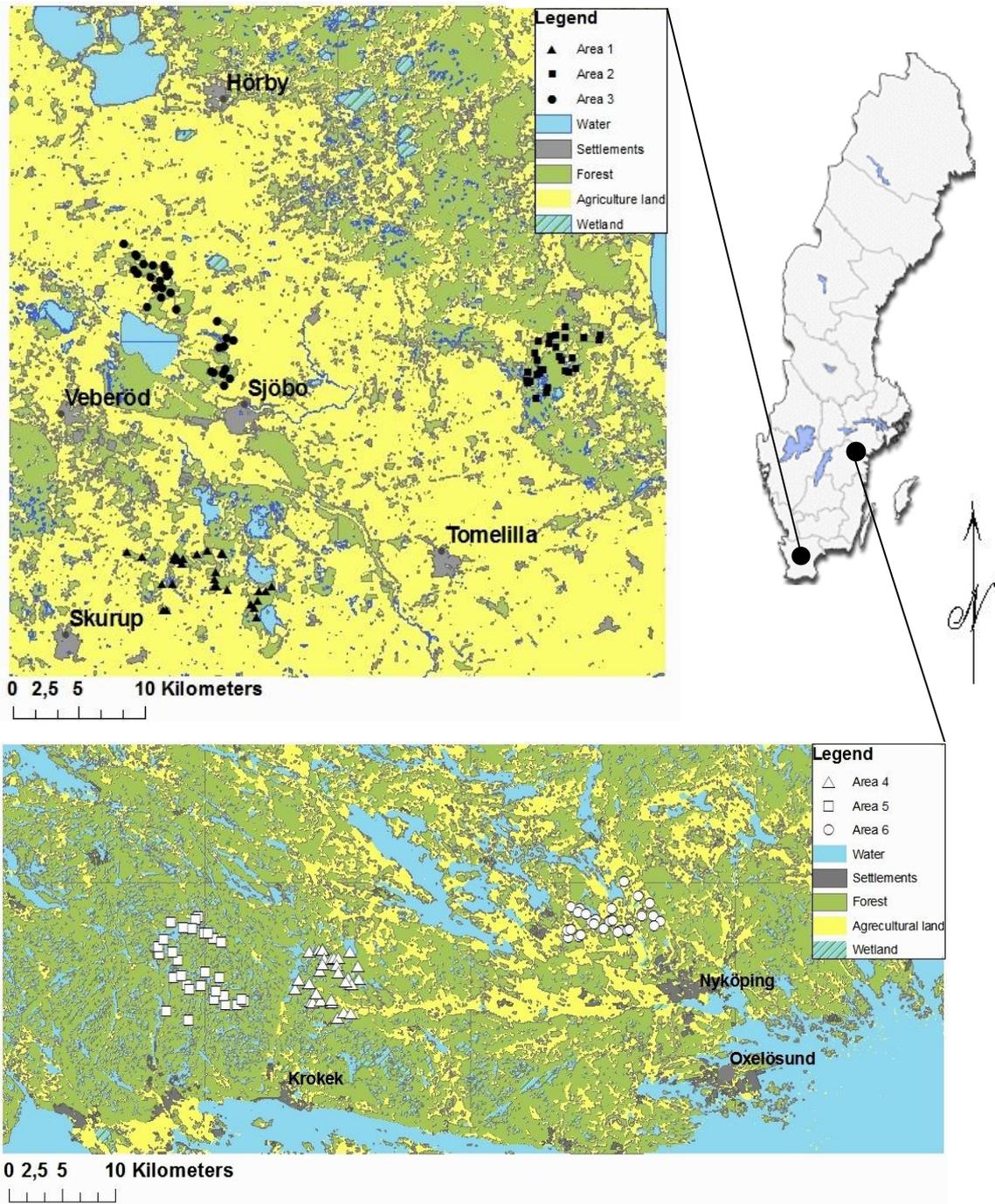
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Appendix 1



The location of the study areas and individual stands in the Skåne region (at the top) and the Södermanland/ Östergötland region (at the bottom).