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Factors affecting damage to Scots Pine in a multiple ungulate species system

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Abstract

Managing browsing impacts on commercial forestry is one of the main aims of ungulate management in Sweden, with Scots Pine being one of the major forestry species. Moose is the ungulate species with the greatest management focus, although in parts of Sweden it forms a multiple ungulate species system, along with red deer, roe deer and fallow deer. Land use is also thought to be a significant factor on ungulate behaviour and resulting feeding impacts. But which species, and which land uses, result in increased economic damage to pine trees? By monitoring ungulate density, land use and browsing damages across multiple years and at locations across Sweden, these relationships were modelled using generalised linear mixed effect models. The results indicate that moose densities are a significant factor in levels of browsing damage, with roe deer having some impact, but that increases in red deer densities produced possibly the biggest impacts of all. Increased use of land for agriculture also leads to greater browsing damages. Although much of the physical browsing may be conducted by moose, competition from the other ungulates may be leading to increased browsing on pine. While increased disturbance from agricultural land, and the restrictions to daytime movement that result, may also be driving increased browsing damages. Further studies are needed to confirm the drivers behind the browsing damages, but these results will provide a better framework for landscape scale management that considers both the presence of multiple species, and the use of the surrounding landscape.

Introduction

Deer populations have increased across Europe over the past few decades (Kuijper et al 2009). A number of factors have contributed to this, including milder winters, management actions, and changes to forestry practices (Kuijper et al 2009). They play a significant role in forest ecosystems and can have negative impacts on vegetation such as forest plantations and agriculture that places them in direct conflict with humans (Jarnemo et al 2014). Although it is accepted that as deer density increases so does their impact on vegetation, too many measures seeking to manage ungulate impacts focus purely on density. It is in fact only one of many factors affects damage levels, with food availability, site quality, habitat characteristics, silvicultural methods, deer ranging behaviour and actions such as artificial feeding all suggested to affect the pattern of browsing and resulting levels of damage (Månsson and Jarnemo 2013). Deer density may well be secondary in affect to some of these other factors, and where the relationship between deer density and browsing intensity is weak, a reduction in density may not result in the expected reductions in browsing damages (Jarnemo et al 2014). In areas where multiples ungulate species occur together, it also can be difficult to even tell apart damage from different herbivore species. Estimates are often made based on the relative population size of each herbivore population, more often placing blame on the more abundant species (Nichols and Spong 2014). To enable effective management it is important to know the relative contribution of each species to browsing damages, though there has been very limited studies showing this in multi-species situations (Putman et al 2011).

Across Sweden there have been both increases in both density and range of deer species. Due to changes in the hunting laws and management systems, moose, *Alces alces*, numbers have increased dramatically since the beginning of the last century (Liberg et al 2010). Adoption of clearcut practices in forestry, and the transition of agricultural land to forest plantations provided plentiful deciduous browse for moose (Ahlen 1975). Forests in early successional stages having been shown to be one of the most forage rich habitats in boreal forests, and the favoured winter habitat of moose (Bergström and Hjelford 1987). The population increase was paralleled by increasing damage to forestry, especially young Scots pine, *Pinus sylvestris*, as it is quantitatively the most important winter food species for moose in Sweden (Cederlund et al 1980). Scots pine is a very economically important species in Swedish forestry, and excessive moose browsing is problematic as it reduces wood quality and volume, and the resulting economic value of the timber (Bergquist et al 2014).

In contrast to moose, red deer, *Cervus elaphus*, populations have been far slower to recover after more protective hunting laws have been put in place (Liberg et al 2010). Red deer are known to damage forest plantations, particularly by stripping bark from trees in spruce plantations, *Picea abies*, and this may well be the reason they have been historically restricted from expanding (Ahlen 1965). Genetically native Swedish red deer are still restricted to the south, though escapes or releases from game farms have resulted in new populations of introduced red deer across Sweden (Liberg et al 2010). In total, red deer populations are thriving, now being found in nearly all counties in Sweden, and increasing in number in most areas (Månsson and Jarnemo 2013).

Roe deer, *Capreolus capreolus*, populations expanded over the last century due to the benefits to them from restrictive hunting laws, removal of domestic stock from the forest, eradication of large predators, and improvements to their habitat due to changes in agricultural and forestry practices (Liberg et al 1994). Supplementary feeding in particular has been of great benefit, which coupled

with milder winters has allowed roe deer to expand northwards, being now found everywhere except alpine areas and the extreme north. Densities are however highest in mixed agricultural/forest habitats in the south of Sweden (Liberg et al 2010).

The fallow deer, *Dama dama*, though an exotic introduction to Sweden, is now well established as wild populations around its sites of release or escape, with these populations increasing in number and distribution (Liberg et al 2010). Their population is however extremely fragmented, remaining in close proximity to each point of release, as they have very slow rates of dispersal (Liberg and Wahlstrom 1995).

Both roe deer and red deer, although being classed as browsers and intermediate feeders respectively, have not traditionally implicated to a large extent in damage to trees in clearcuts. They have been shown however to occur in higher densities in clearcuts and may preferentially forage within them. Spending more time feeding in these gaps may result in higher browsing intensity to the young plantation trees (Kuijper et al 2009). Current management frameworks in Sweden are however significantly biased towards management of moose, with the now highly organised implementation of moose management areas being highly successful, but limited in their focus on a single species and purely on its density. Red deer management units have more recently now been formed in a similar manner. While for roe deer and fallow deer there is no coordinated management at a larger scale (Liberg et al 2010). As the multiple deer species found within Sweden often coexist in the same location, the current management that is seen focussed on moose, and to some extent on red deer, should not focus on managing their populations in isolation, but needs to be considered and integrated within a wider framework of multiple ungulate species and their management, and differing land use and management aims and objectives (Putman et al 2011).

Especially at large scales, factors other than population density, such as the amount of forage available, and the structure of the landscape can have effects on levels of damage occurring. Generally an increase in the amount of forage available, as would be found in clearcuts, can cause a decrease in damage due to diffusion of browsing. Intensive agriculture can also impact on forage availability as it decreases the proportion of forested area (Jarnemo et al 2014). In addition, where habitat structure is attractive to deer, yet natural food supply is sparse, more damage may be anticipated to occur. Distributions of deer are not purely determined by aspects such as food, but also suitable cover, sheltering them from aspects such as predation and inclement weather (Reimoser and Gossow 1996). Additionally, naturally evasive behaviour of deer to hunting, forestry operations or tourism may cause them to spend more time in stands which offer them cover, if this cover offers little forage, more damage can further occur (Gerhardt 2013). By understanding which aspects of the landscape can influence levels of deer damage, it may be possible to change land uses to alter damage on a landscape scale, or better indicate which aspects of management might be altered to work best with how deer utilise the existing landscape.

This study aims to use a standard measure of browsing damage of economic importance to pine trees, ungulate density, types of land use and weather data to study:

1. How year to year changes in winter weather affect the intensity of browsing damage of economic importance to pine.
2. How the density of each of four species of ungulates affect the intensity of browsing damage of economic importance to pine.
3. How different land uses affect the intensity of browsing damage of economic importance to pine levels of browsing damage to pine trees to pine.
4. When all factors are combined, which types of measures best explain browsing damages to pine.

I predict that:

1. As winters become colder and have greater levels of snow, that browsing damage of economic importance to pine trees will increase.
2. Moose density will have a strong positive relationship with browsing damage of economic importance to pine trees, with the other deer species having smaller impacts relative to the amount of pine in their diets.
3. There will be a negative relationship between young forest in the landscape and browsing damages of economic importance to pine, a positive relationship between pastures and fields and damage, and that marsh and wetlands will have a positive relationship to browsing damages to pine.

Methods

Study Locations

The study data utilised here was collected from between 2012 and 2016 at three different locations in north, central and southern Sweden (Fig. 1).

The northernmost location is situated around the town of Nordmaling in Västerbotten county (63°34'N 19°30'E). It is in the boreal zone and is characterised by high levels of forestry. The climate is cold and temperate, with an average annual temperature of 2.9°C, with the coldest month January having an average of -9.7°C, and the warmest month July having an average of 16.0°C. There is a significant amount of rainfall with an annual precipitation of around 581mm (Climate-Data.org 2017). Along with the four species of wild cervids of focus in his study, reindeer herding also occurs, and there is not yet any wild boar this far north.

The central Sweden study location was at Öster Malma in Södermanland county (58°57'N, 17°9'E). It is in the boreonemoral zone and consists of small scale agriculture and forestry in a fragmented landscape. It has a warm and temperate climate, with the temperature averaging 6.8°C, with



Figure 1. The location of each of the three study locations across Sweden.

the highest average temperature of 17.2°C occurring in July, and the coldest month being February with an average of -2.6°C. Annual precipitation is about 560mm (Climate-Data.org 2017). It is intensively managed for wildlife, with dense populations of game species, and with wild boar now present in the area.

The final location is in southern Sweden, north of the town of Växjö in Kronoberg county (56°52'N 14°48'E). It is also in the boreonemoral zone, with more forestry than agriculture. It is warm and temperate with an annual average temperature of 6.5°C, the warmest month of July being on average 16.1°C, and January the coldest month being 2.3°C. Average annual rainfall is 649mm (Climate-Data.org 2017). Here game populations are less dense, and the landscape was heavily affected by the winter hurricane Erwin in 2006, creating a large spontaneous regeneration of broadleaves in the landscape over the following years.

Data use for each study locations does not cover the entire period. Öster Malma has the greatest number of survey years, 2012 -2016, while Växjö is from 2012-2015, and Nordmaling data collection began later with data only from 2015-2016.

Pellet Counts

Ungulate density was determined as an index based on pellet counts, in the same manner as described in (Pfeffer 2016). At each location annual surveying was conducted using point inventory at 50 sites, each with ≤16 points (Fig. 2), as not all points are able to be surveyed where they fell on lakes, flooded areas or private gardens. Nordmaling was however initially surveyed at 75 sites in 2015, being subsequently reduced to 61 in 2016. At each point all dung pellet groups of moose and red deer were counted that fell within a 5.64m radius (100m²), and roe deer and fallow deer were counted within a 1.78m radius (10 m²). A GPS unit was used to find the exact locations, which when within 10m of the required coordinate location, the position where the right heel of the field surveyor next hit the ground was selected as the middle of the survey circle. A string of 5.64m, and with a marking at 1.78m was attached to a stick and dung groups were then counted that fell within the circle of the correct radius. Pellet morphology, particularly size and shape, was used to identify it to species level. Roe deer and fallow deer dung is particularly difficult to identify and as such the number of pellets per dung group was used as the distinguishing feature between the two: roe deer with <45 pellets per group and fallow deer >45 pellets per group (Eckervall 2007).

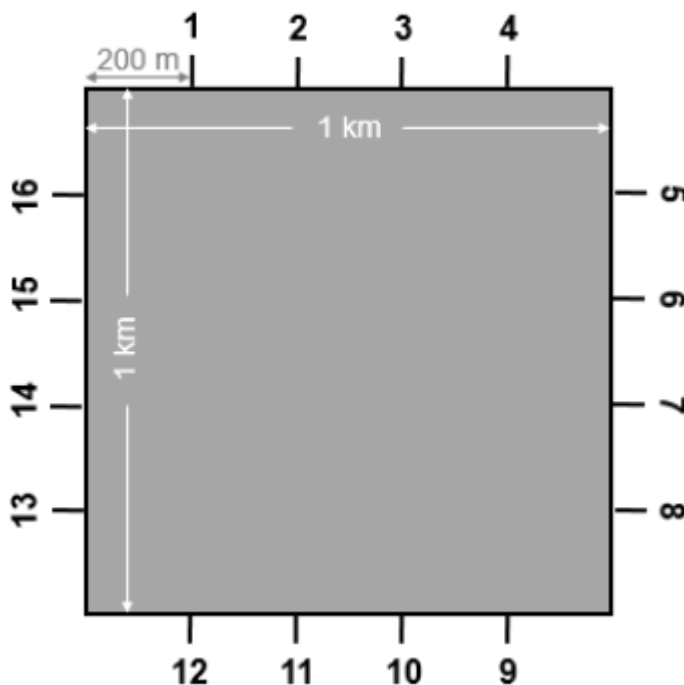


Figure 2: The design of the pellet count sampling tracts. Each tract consisted of 16 coordinates, the individual sample locations, evenly distributed at 200m intervals along each side of a 1km square (Pfeffer 2016).

For each pellet count survey the total number of pellet groups of each species that were found was totalled. As not all sample sites were always possible to be surveyed, the percentage of sample area that was actually surveyed was calculated. The total number of pellet groups was then divided by the area surveyed to give an average pellet group count per sampling site for each tract. The coordinate of this tract average was then taken as the average of each of the 16 sample sites, which gave the location of the middle of the 16 sample sites. As the pellet count tract locations were not at the same location as the ABIN surveys, the pellet count at the ABIN location was estimated using an inverse distance weighting interpolation. The interpolation was conducted using default settings on ArcGIS (Environmental Systems Research Institute 2012) (variable distance, 12 points, cell size varied: Nordmaling=234, Väjö=115, Öster Malma=154).

Browsing Damages

Assessment of browsing damages to Scots pine was conducted using the standardised method used by the Swedish Forest Agency (Skogsstyrelsen) to measure impact by moose (Älgbetesinventering or ÄBIN) (Skogsstyrelsen 2016) . Sampling squares of 1km² were randomly selected from the landscape and all young forests stands in the height range 1-4m were sampled within it. These plots were not the same as those used for pellet counts, but were however overlaid within the same survey area. In each young forest stand 10 sample plots were distributed evenly along transects following the longest diagonal in each stand, with each plot being a circle of radius 3.5m (38.5m²). To assess damage, the height of the two tallest pines in the plot was measured and an average taken. All pines above half this height were counted and screened for fresh browsing damage. The three types of damage counted were: 1) browsing of the apical shoot 2) breakage of the main (i.e. stem broken below the apical shoot and 3) bark stripping.

For analysis any pine tree that had suffered apical shoot loss, stem breakage or debarking was considered as have been browsing damaged. The total number of browsing damaged pine trees per sampling tract was totalled and divided by the total number of pine trees surveyed in the sample tract, to give a percentage of trees suffering from game damage. Since pine density varied between stands and locations, a percentage value gave the best means of comparison, and as it is economic damages that are being considered, the absolute measures of numbers or biomass per ha is not required as it is the percentage of the forest crop affected that is important. Any ABIN points that lay further outside the pellet count sampling grid than half the maximum distance from one pellet count tract to the next were excluded from the dataset as being too far away from pellet count data for reliable estimates (Nordmaling=3km, n=13, Väjö=2.12km, n=3, Öster Malma=2.12km, n=10).

Land Use

Land use was determined from the most recent CORINE land cover dataset (Copernicus Land Monitoring Service 2012). This most recent dataset was produced in 2012, and classifies the vegetation and land use types across the whole of Sweden into 35 classes. Classification was produced from satellite data, with images from 2011-2012, with image resolution from 10x10m up to a max of 25x25m, and an geometrical accuracy between +/- 5m to +/-12.5m (Copernicus Land Monitoring Service 2015).

From the coordinate of each ABIN sample tract the land use within a 1km radius was extracted. The total area of each land use was divided by the total area extracted to give a proportion of each land

use type. The three main land use types to be investigated were created by summarising multiple CORINE land use categories into functional categories for analysis (Tab.1)

Table 1: The original land use classifications as found in the CORINE land use data, and how these have been combined into categories for analysis in this study.

SMD Name	SMD Code	Combined Category
Clearcut	3242	Young Forest
Young Forest	3243	
Cropland	211	Pasture and Fields
Pasture	231	
Limnogenous Wetlands	411	Marsh and Wetlands
Saltwater Wetlands	421	
Wet Marsh	4121	
Other Marsh	4122	
Peat	4123	

Weather Data

Both snow depth and temperature data were taken from the database of the Swedish Meteorological and Hydrological Institute. For each study location data was taken from the nearest weather station that had a continuous dataset across the study period. All weather data for each survey year was taken January-March. Snow depth data was taken from the following weather stations: Nordmaling - Torrböle D, Växjö - Moheda D and Öster Malma - Gnesta. While monthly temperature data was taken from these stations: Nordmaling - Järnäsklubb A, Växjö – Berg and Öster Malma – Floda A (Swedish Meteorological and Hydrological Institute 2017).

The snow and temperature data was used as the following metrics (Tab. 2). With a sample size of n=11, weather data was not able to be included in models alongside the species density and land use data. A Shapiro test showed that not all weather metrics were normally distributed, so the relationship between each of the metrics and browsing damage was done using Spearman’s rank correlation coefficients.

Table 2: Metrics of weather data used for analysis. All weather data was taken during each study year between the periods of January 1st – March 31st, in the winter prior to the ABIN assessments it is compared to.

Weather Data Name	Description
Mean Snow Depth	The mean snow depth recorded
Maximum Snow Depth	The highest recorded snow depth
Number of Snow Days	The number of days with snow recorded as >0cm
Number of Snow Days ≥ 20 cm	The number of days with snow recorded as ≥ 20 cm
Mean Temperature	The weighted mean of the monthly mean temperatures (weighted for the variable days in Jan-Mar)

Statistical Modelling

The relationship between species density, land use and browsing damage was analysed using multiple generalised linear mixed effects models (GLMM), using R Studio (R Studio Team 2016). Proportion of pine tree browsed vs total number of pine trees surveyed was entered as a binomial value. From an initial sample size of n=383 ABIN survey locations, all ABIN locations with no pine in the survey were removed from the sample, leaving a final sample size of n=185. Areas with no pine were removed as these areas can not show any pine damage, and hence could not show any relationship between damage and other factors.

Placing both land use and species densities in the same model to begin with would have been the most efficient way to model the data, but the GLMM was not able to run all the full set of variables at once, so species density and land use were first ran as separate models. Initially models were run with data from all study locations together, with each of the four species densities in the model, with location as a fixed effect, and year as a random effect. The model was simplified by stepwise selection, removing the term with the greatest p-value, until all terms were either significant, or none remained in the model. This was then repeated for each location in turn, with each of the four species included initially in the model, with year as a random effect.

The same process was then conducted with the three land use terms replacing species densities in the models. The significant species and land uses from each of the all locations combined, and single location models, were combined and simplified using step selection once again, to produce final models of effects on browsing damages for all study locations together, as well as location specific models for Nordmaling, Våxjö and Öster Malma.

The levels of browsing damage at each of the three locations were also tested for differences using a t-test.

Results

Locations

The samples were unevenly distributed across the study locations, due to differences in the number of years that data was available for each site, as well as the proportion of browsing damage assessment locations that contained pine. (Nordmaling: years=2, n=63, Våxjö: years=4, n=23, Öster Malma: years=5, n=99). The sites also varied in the mean proportion of pine damaged each year (Fig.3). Nordmaling (mean=0.010, var=0.000) had significantly less damage each year than Öster Malma (mean=0.277, var=0.022)(two sample $t(4)=-4.031$, $p=0.016$). While Våxjö (mean=0.225, var=0.052) did not differ significantly from Nordmaling (two sample $t(3)=-1.874$, $p=0.157$), and there was very little difference between Öster Malma and Våxjö (two sample $t(5)=0.395$, $p=0.709$).

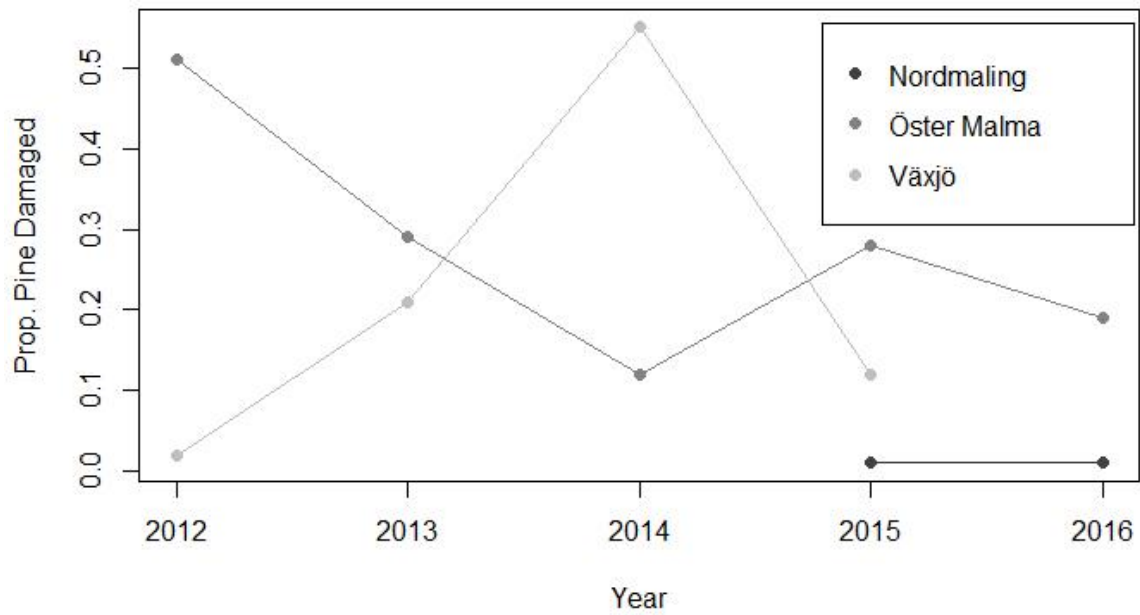


Figure 3: The mean proportion of pine damaged each year for each of the three study locations. Note the large between year variation at both Öster Malma and Växjö.

Weather

When tested for correlation between weather conditions and the proportion of pine trees damaged, weather conditions were for each survey year, giving a total of only n=12 weather recordings. None of the variables was found to be significant in either a combined model, or with Öster Malma and Växjö modelled separately or as with just them together without the Normaling results. Nordmaling was not modelled on its own due to n=2 (Tab. 3).

Table 3: Spearman's rank correlation coefficients and p-values for weather data metrics. None are significant results.

Locations	Mean Snow Depth		Max Snow Depth		Prop. Snow Days		Prop. Snow Days >20cm		Mean Monthly Temp	
	<i>rho</i>	<i>P-value</i>	<i>rho</i>	<i>P-value</i>	<i>rho</i>	<i>P-value</i>	<i>rho</i>	<i>P-value</i>	<i>rho</i>	<i>P-value</i>
All	-0.31	0.36	-0.43	0.10	0.00	1.00	-0.37	0.26	0.25	0.46
Öster Malma	0.60	0.35	0.20	0.78	0.80	0.13	0.20	0.78	-0.30	0.68
Växjö	-0.40	0.75	-0.63	0.37	-0.40	0.75	-0.45	0.55	0.40	0.75
Öster Malma & Växjö	0.27	0.48	0.05	0.90	0.29	0.44	0.16	0.68	0.04	0.91

Species

Species - all locations:

With all locations combined in the model, moose (p=0.025), red deer (p<0.001) and roe deer (p=0.022) were significant factors, all showing a positive relationship between density and damage. Also significant were the locations of Öster Malma (p<0.001) and Växjö (p<0.001) (AIC=1040.8, df =178) (Fig. 4).

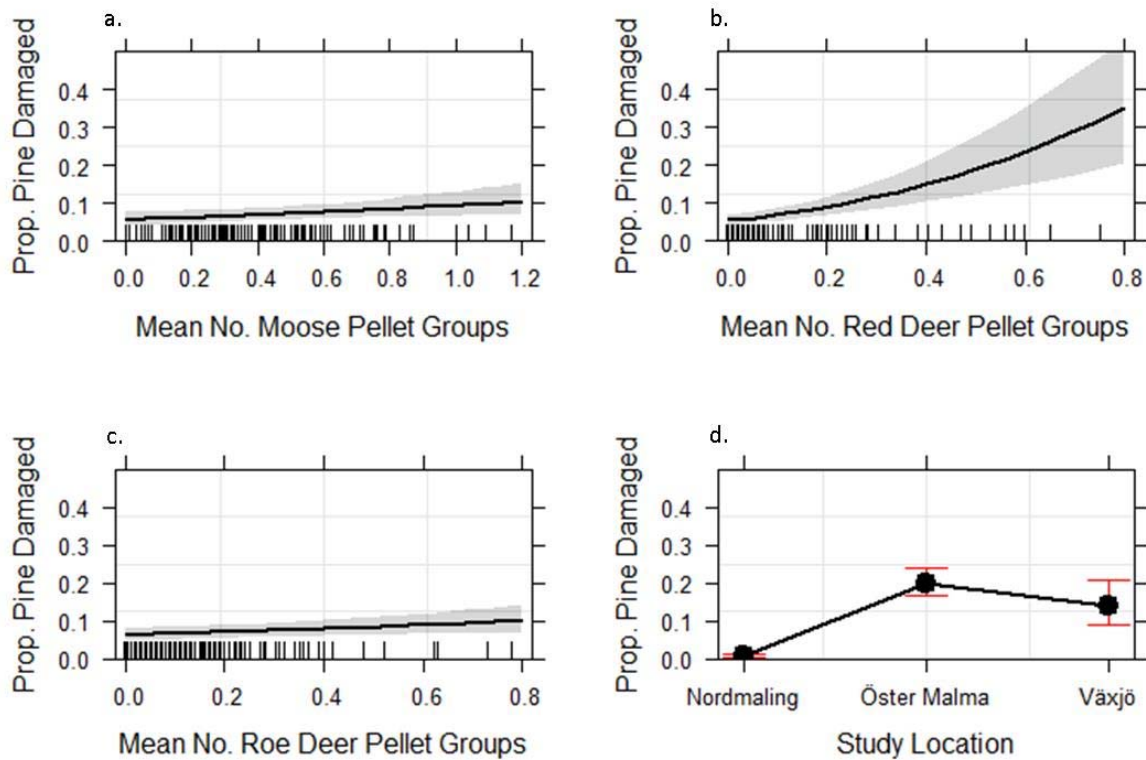


Figure 4: Final model for effects of ungulate species density across all study locations.

Fallow/Roe methodology:

Roe deer and fallow deer are discriminated in the methods using only pellet group number rather than morphology, and the counts are somewhat correlated ($r=0.335$, $df=381$, $p<0.001$). Due to the collinearity, and possible overlap of species counts, it was prudent to check which of the two species is more appropriate in the final model as one may be displacing the other. With just roe deer in the model, the variable is significant ($AIC=1040.8$, $df=179$, $p=0.0146$), with just fallow deer in the model it is not significant ($AIC=1045.5$, $df=179$, $p=0.4656$), and if the two are combined, assuming that they can't be accurately identified in the field, the combined value is also not significant ($AIC=1042.8$, $df=179$, $p=0.1262$). The only approach that is significant, and with the lowest AIC, is to retain just roe deer in the final all species model, matching the initial results of model simplification.

All species as a combined variable:

With all species combined together into an all species index, it is a significant factor in the model. The resulting model has a much higher AIC ($AIC=1064.6$, $df=180$, $p<0.001$), than the simplified model with all species included ($AIC=1040.8$, $df=178$). The effect sizes for each of the significant species (moose=0.5538, red deer=2.8181, roe deer=0.6342) in the model including all separate species are all greater than that of the all species value in its model (0.4978).

Species - Nordmaling:

In Normaling only fallow deer and roe deer were significant in the final model ($AIC=102.5$, $df=59$), with a negative effect for fallow deer and positive for roe deer on damage (Tab. 4).

Table 4: Final model for effects of ungulate species in Nordmaling.

Fixed Effect	Estimate	Std Error	z value	Pr (> z)
Intercept	-5.059	0.306	-16.517	<0.001
Fallow Deer	-56.5260	24.756	-2.283	0.022
Roe Deer	13.6532	3.554	3.842	<0.001

Species – Växjö:

In Växjö, both fallow deer and roe deer were once again the only significant species in the final model (AIC 780.1, df=23), although they were in the opposite direction of effect as to that found in Nordmaling, with fallow deer showing a positive effect, and a negative effect of roe deer on damage (Tab. 5).

Table 5: Final model for effect of ungulate species in Växjö.

Fixed Effect	Estimate	Std Error	z value	Pr (> z)
Intercept	-0.830	0.862	-0.962	0.336
Fallow Deer	23.002	5.755	3.996	<0.001
Roe Deer	-8.229	3.129	-2.630	0.009

Species - Öster Malma:

In Öster Malma all ungulate species were significant, with moose ($p<0.001$), red ($p<0.001$) and roe deer ($p<0.001$) showing a positive effect of density on damage, while fallow deer ($p=0.028$) showed a negative effect (Fig. 5) .

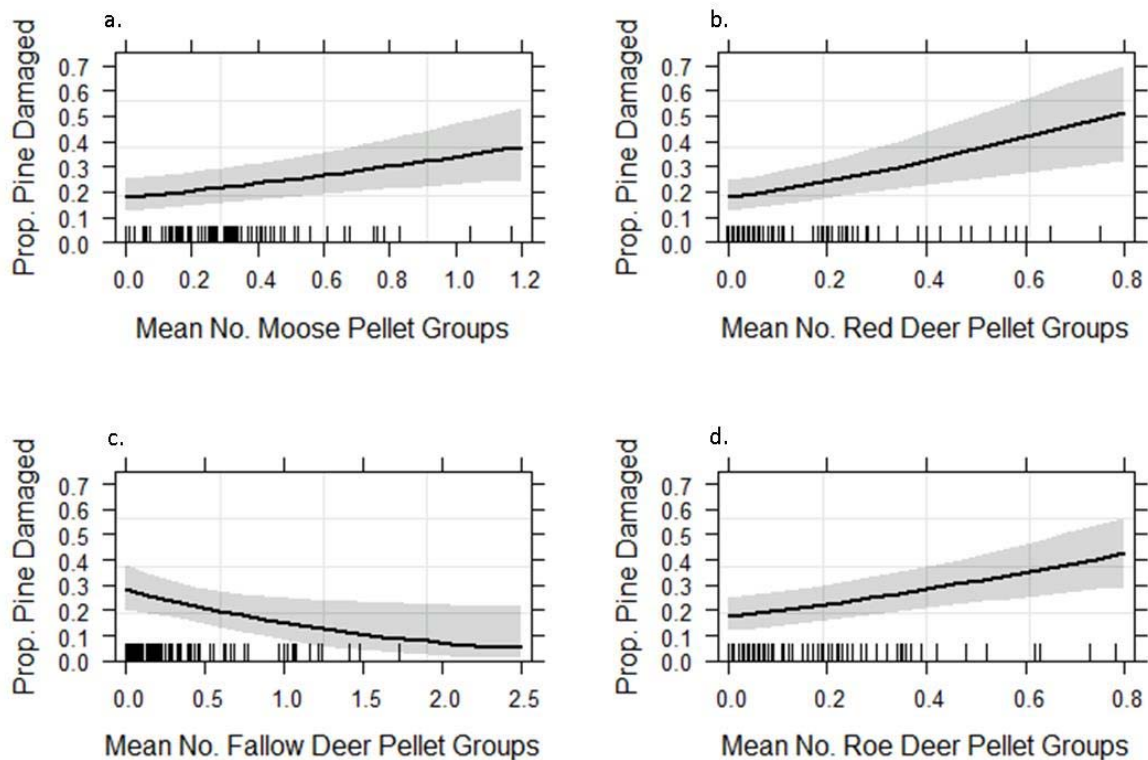


Figure 5: Final model for effects of ungulate species in Öster Malma.

Interaction between fallow deer density and other deer density:

Fallow deer density had a negative effect on browsing damages across two of the three study locations. To assess whether there a negative correlation between fallow deer and the other deer species could cause this, correlation tests were conducted between fallow and each of the other species. Deer density was highly variable between study sites, shown by the all species index (0.12 – 4.30), and there were significant positive correlations between fallow deer density and all deer density at all locations combined ($r_s=0.652$, $p<0.001$), Nordmaling ($r_s=0.353$, $p=0.005$) and Öster Malma ($r_s=0.589$, $p<0.001$), while Väjö also showed a positive correlation, though it was non-significant ($r_s=0.364$, $p=0.088$).

To control for fallow deer numbers therefore being correlated with overall deer density between sites the pellet count index for each species was standardised by dividing each species by the all species index for each location. There were many significant correlations between fallow and other species with these standardised values (Tab. 6).

Table 6: Spearman’s rank correlation coefficients and p-values for fallow and each of the other ungulate species. Each species density was divided by the all species index for its location, producing a density standardised for local density. Significant results are in bold.

Location	Fallow /Moose		Fallow/Red		Fallow/Roe	
	rho	p-value	rho	p-value	rho	p-value
All	-0.670	<0.001	0.421	<0.001	-0.132	0.010
Nordmaling	-0.492	<0.001	0.049	0.704	0.272	0.031
Väjö	-0.219	0.314	0.143	0.514	-0.284	0.189
Öster Malma	-0.754	<0.001	-0.551	<0.001	0.030	0.766

Land Use

Land use and all locations:

With all locations combined in the model only pasture and fields was a significant land use type as well as the locations of Öster Malma and Väjö ($p<0.001$)(AIC=1076.7, df=80) (Tab. 7).

Table 7: Final model for effect of land use across all study locations

Fixed Effect	Estimate	Std Error	z value	Pr (> z)
Intercept	-5.088	0.287	-17.753	<0.001
Pasture and Fields	1.061	0.352	3.015	0.003
Location: Väjö	3.005	0.329	9.121	<0.001
Location: Öster Malma	3.673	0.237	15.485	<0.001

Land use – Nordmaling:

There was no significant effect of land use in the model for land use in Nordmaling (AIC=116.9, df=60) (Tab. 8).

Table 8: Final model for effect of land use in Nordmaling. While this is the most simplified model possible for Nordmaling, it still does not have any significant land uses.

Fixed Effect	Estimate	Std Error	z value	Pr (> z)
Intercept	-4.573	0.319	-14.344	<0.001
Pasture and Fields	-4.796	4.0783	-1.176	0.240

Land use - Växjö:

There was also no significant effect of land use in the model for Växjö (AIC=116.9, df=60) (Tab. 9)

Table 9: Final model for effect of land use in Nordmaling. While this is the most simplified model possible for Växjö, it still does not have any significant land uses

Fixed Effect	Estimate	Std Error	z value	Pr (> z)
Intercept	-0.856	0.9569	-0.895	0.371
Young Forest	-6.2917	5.1439	-1.223	0.221

Land Use - Öster Malma:

All of the land use types were significant from the initial model, young forest ($p=0.021$), pasture and wetlands ($p=0.002$) and marsh and wetlands ($p=0.035$) (Fig. 6).

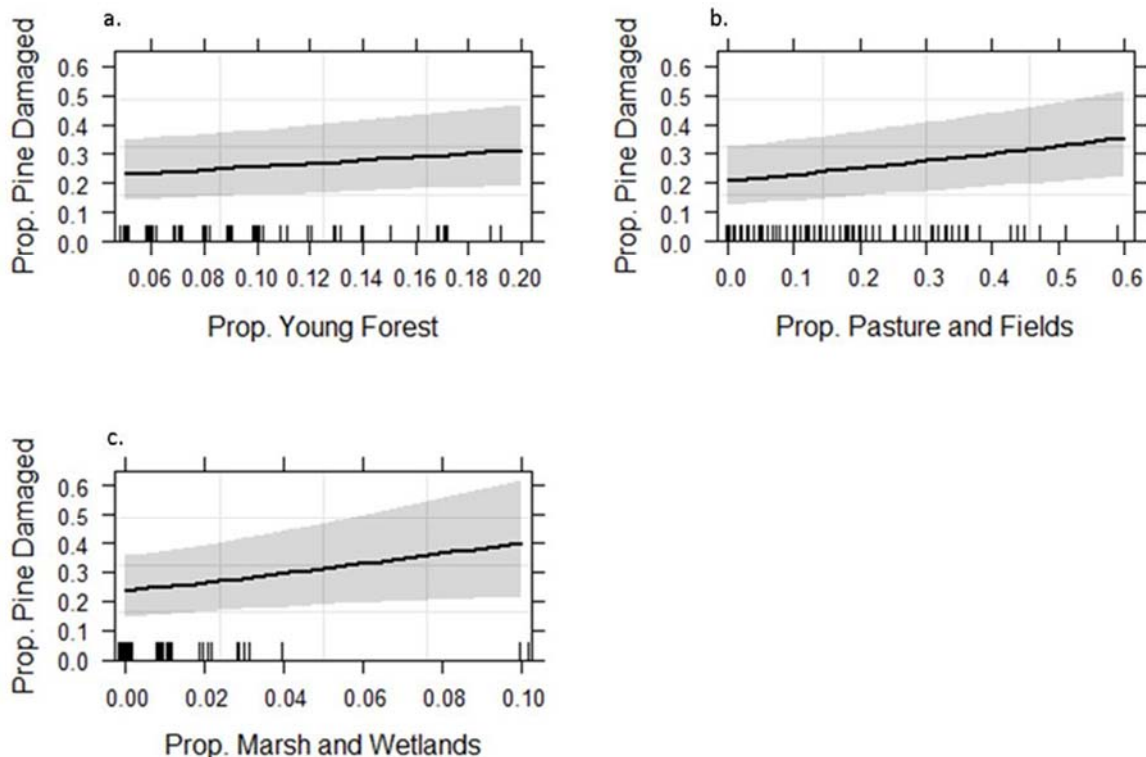


Figure 6: Final model for effect of land use in Öster Malma.

Species and Land Use Combined

Combined – All locations:

The significant terms from both the species model and the land use model are combined into a single model, all remain significant still. Moose ($p=0.002$), red deer ($p<0.001$), roe deer ($p=0.003$) and pasture and fields ($p<0.001$) being included in the final model, along with the locations Våxjö ($p<0.001$) and Öster Malma ($p<0.001$) also being significant (AIC=1029.2, $df=177$) (Fig. 7)

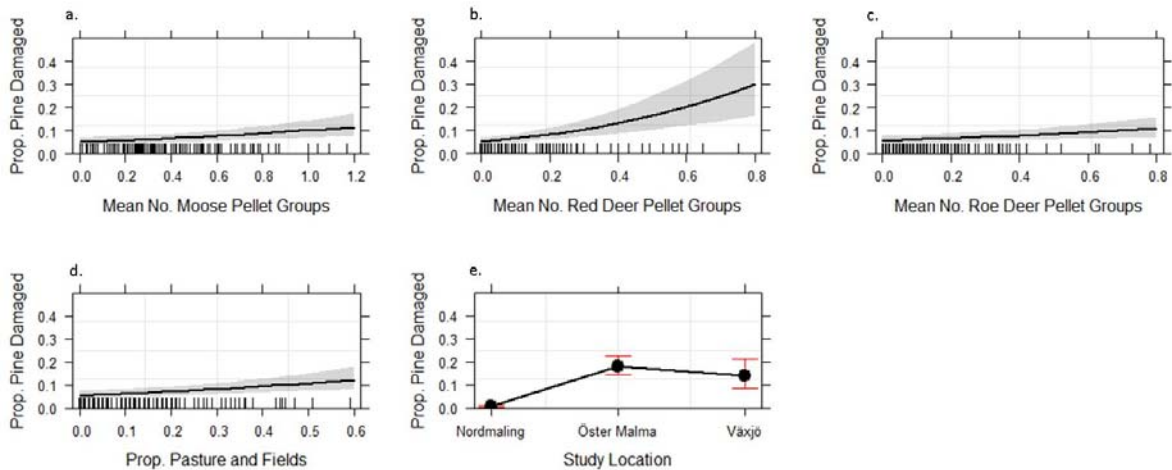


Figure 7: Final model for the combined effect of species density and land use across all locations

Combined - Öster Malma:

In Öster Malma moose ($p<0.001$), red deer ($p<0.001$), roe deer ($p<0.001$) and pasture and fields were found to be significant (Fig. 8).

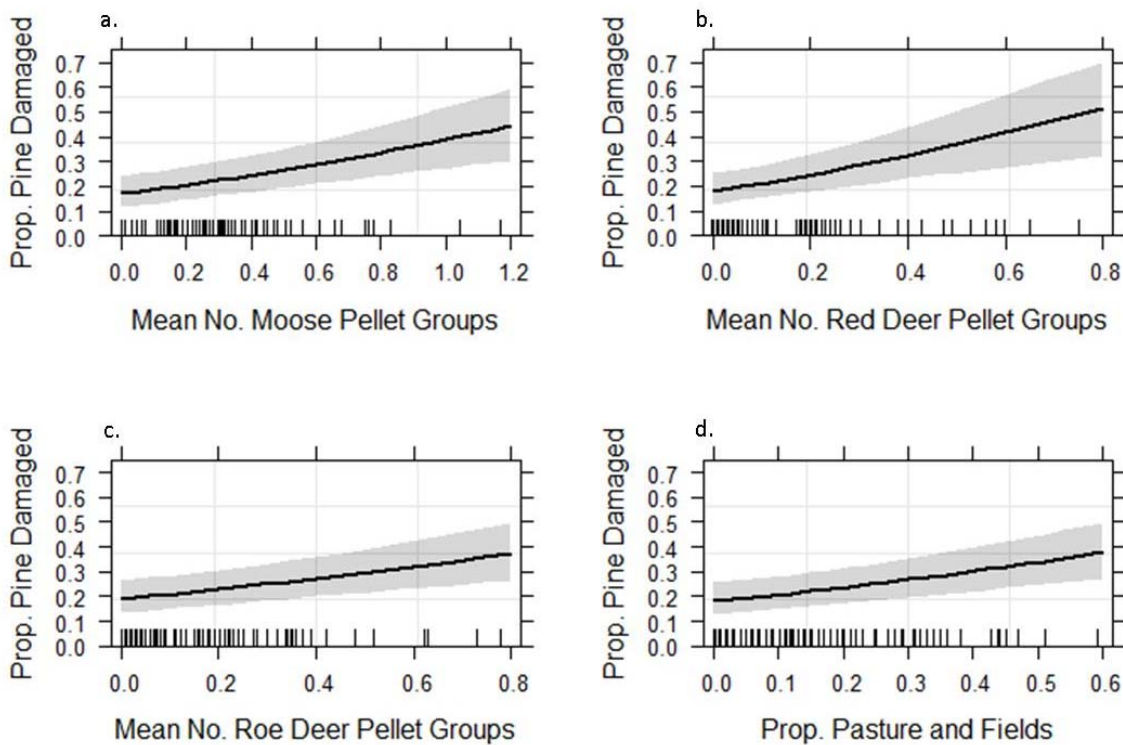


Figure 8: Final model for the combined effect of species density and land use in Öster Malma.

Discussion

Location

There was a very large variation in damage levels between the northernmost study location in Nordmaling, and the other two field sites. In the north densities of the study species, as determined by harvest statistics, are far lower than in the south of the country (Liberg et al 2010). When coupled with greater area covered in forest, particularly coniferous forest, it follows that the browsing damages are reduced. The increased number of survey blocks that contained pine also was far higher in Nordmaling, due to the increase presence of pine in the landscape, providing a greater sample size. Expanding on the current two years of survey data will greatly improve the results from Nordmaling and give stronger conclusions as to how the species and land uses might act differently in the north.

Växjö had a very small total number of survey plots over the four study years which contained pine (n=23). Coupled with only a small number of areas with high numbers of fallow, this resulted in particularly high errors in the model. The site also showed inverse trends in roe deer and fallow deer relationships to browsing than the rest of the models. This may be due to unique factors in the land management in Växjö, but due to the low sample size at this location the results are far less certain than the rest of the model results. They may therefore not show a genuine trend at this location, and as such won't be discussed further on their own.

Öster Malma was the study location that gave the most complete set of data for analysis (n=99), and therefore allows the strongest conclusions to be drawn from it. Much of the rest of this discussion is therefore weighted heavily towards the results shown from Öster Malma. It must however be remembered that the landscape in that location is subject to heavy game management, and as such the knowledge gained from it needs to be considered carefully before being applied elsewhere.

Weather

As each study year produced only a single weather value, the total sample size of n=11 was much too small to show any significant results, while what trends were apparent varied in direction between locations. It may also be that snow and temperature recordings from the nearest weather station were too broad to accurately reflect impacts of weather at the study locations, as in the case of snow, it is localised snow depth compared to snow conditions at larger scales that impacts most on pine browsing (Herfindal et al 2015). Weather should be expected to play a role in controlling browsing damages, and often determines when measures such as supplementary or diversionary feeding are implemented. It is as such something that needs to be looked at further, and with these being only the initial results from these study sites, a greater sample size is possible as further data is collected.

Species

The effects of each of the different study species on browsing damages to pines broadly follows that expected from their biology (Hoffman 1989) and from initial studies identifying responsible species in a multispecies system (Nichols and Spong 2014). Though in this study the relationships of each species' density to browsing damages, rather than which species is actually inflicting the browsing, places each species in a different importance ranking.

As large concentrate selectors (Hoffman 1989), and the target of much of the ungulate management in Sweden aimed towards limiting browsing damages (Liberg et al 2010), one would expect moose density to have the greatest impact of browsing damages. Moose density did show a significant relationship to browsing damages in the model for all sites, and in Öster Malma, as predicted, though wasn't found to be a significant driver of damages in the other two locations. Indices of moose density have been previously shown to be positively correlated to increased browsing on Scots Pine (Månsson 2009, Hörnberg 2001). Although this relationship appears to only exist at smaller scales, with environmental factors having more impact at large scales (Bergquist et al 2014). While the moose has been shown to be more of a browser on pine than the other species (Nichols and Spong 2014) with damages in multispecies systems often attributed to it (Ligi and Randveer 2012), this is not directly represented in the relationship between its density and damages in this study, with changes in both red deer and roe deer densities having a greater positive effect on pine damages.

With the red deer digestive system lying between the moose or roe deer and that of a fallow deer (Obzidinski 2013), they have been generally classified as having a mixed diet, with grasses being an important part of the diet alongside browsing (Nichols and Spong 2014). Like moose they were found to have a significant positive effect on browsing damages to pine in the model using all sites, and that of just Öster Malma. More surprisingly they have far larger effect sizes than did moose on browsing, having over five times greater effect size than did the moose in the all sites model, and over twice the effect size at Öster Malma. Most of their feeding however is on deciduous trees, grasses and forbs, with only small amounts of conifers in their diet (Gębczyńska 1980, Ligi and Randveer 2012), and when shown to feed on pines, they have done so at a much lower level than moose (Nichols and Spong 2014). As red deer are known to concentrate their feeding in forest gaps (Kuijper et al 2009), it may well be that the feeding of red deer on the more palatable deciduous trees is actually pushing moose from their more preferred food sources and onto the pine (Månsson et al 2007) as there is an overlap in moose and red deer diets (Myrstad 2000). The same overlap is also present between red deer and roe deer (Myrstad 2000), and competition has been suggested to likewise push the roe deer to feed on alternative species, (Putman et al 2011) including possibly pine. This then could lead to the strong positive relationship between red deer and pine damage.

Roe deer are concentrate selectors (Hoffman 1989) with a digestive tract best suited to digesting forbs (Obzidinski 2013). They have been shown to include woody plant material as an important source of food within their diet (Gębczyńska 1980), and have been observed to be a major contributor to browsing of conifers in clearcuts in some studies (Bergström and Bergquist 1997). Though there has also shown to be negligible feeding impacts on pine in others (Nichols and Spong 2014). Here roe deer density had a significant impact on browsing damage at all locations, as well as where all locations were combined in the model. All of these relationships were positive, except for the Växjö model, with roe deer having a similar effect size to moose in the final models where they were both present. This suggests that the roe deer might have a greater impact on pine damages than previously thought. In addition to some direct feeding on pines, there may also be a degree of competition between roe and moose (and also red deer) as they do also have a small overlap in diet (Myrstad 2000), further enhancing the impacts of increasing roe deer density on browsing damages.

Fallow deer in contrast to the other species have a diet more similar to grazing species such as bovines or equids (Putman 1986). They therefore generally avoid browse, but can feed on it in winter, especially where winters are long of fallow deer populations are high. This could result in competition with other deer species (Obzidinski 2013), or direct browsing damage to pine by the fallow deer (Nichols and Spong 2014). However results from all models except that of Våxjö, indicate that increasing presence of fallow deer not only does not increase browsing damage to pine, but seems to reduce it. Fallow was not a significant factor in the all location model, while in Nordmaling and Öster Malma there was a negative relationship between fallow deer density and browsing damage. This matches my prediction that increases in fallow deer density would have the least increase in damage to pine of all the deer.

How, however, can the presence of one species of deer seem to reduce browsing damage at greater levels the more deer there are? One possibility is that fallow deer are negatively correlated with the other deer species that do cause browsing damages. At all sites, and them all combined, there was a negative relationship between the standardised numbers of fallow deer and moose, being significantly so in the all locations, Nordmaling and Öster Malma models. As moose appear to be the main species actually feeding on the pine (Nichols and Spong 2014), this negative relationship could explain the trend for fallow deer. This may well be due to differences in habitat use by each species. The relationships between fallow and red deer, and fallow and roe deer were less certain with both positive and negative relationships shown across the models. A number of studies have shown interspecific interference to occur from fallow deer towards roe deer, causing roe deer to avoid areas with high densities of fallow deer (Ferreti, Sforzi and Lovari 2011, Ferreti et al 2010, Focardi et al 2006), but this does not seem to be the case in this instance.

Land Use

Young forest was only a significant factor in the model for Öster Malma, where there was a positive relationship between the amount of young forest and the levels of browsing damage. Rather than provide a possible dilution effect as predicted, where the more available young forest to browse spread damages more thinly, the inverse seems to possibly be the case. This has been previously shown for moose, where the area of damaged pine stands was related to the available proportion of pine in the environment (Hörnberg 2001), with moose causing more damage, the greater the amount of pine in the landscape. It has been shown that for the other deer species, that these gaps of young forest in the landscape are attractive foraging patches that attract them, in particular red deer, resulting in visitation rates of about twice that of the surrounding closed forest. With red deer even staying in these areas seven times longer than patches in closed forest, both resting and feeding within clearcut and young forest, as they provide increased amounts of both food and cover at the same location, reducing the need for a trade-off between the two (Allen et al 2014). The result is an uneven distribution of browsing, with increasing damage to the young trees planted there (Kuijper et al 2009). Areas with higher proportions of young forest may well also be more intensively managed by forestry practices that also reduce the availability of food in the surrounding forest, resulting in an even greater susceptibility to damage of the trees growing in the clearcuts (Reimoser and Gossow 1996).

Pasture and fields was the only factor significant in the model for all locations, and was also among the land uses having a significant impact on browsing damages in Öster Malma. These agricultural

land uses can offer provide forage in the form of grass, arable crops and other vegetation found within the fields themselves (Thirgood 1995, Allen et al 2014, Putman 1986) as well as at the ecotones between the forest and agricultural land (Torres et al 2011, Catt and Staines 1987). The downside is then that pastures and fields are very open habitats, which then force the deer to trade-off between available forage and cover. As a result deer avoid the open pasture and fields, particularly during daytime where they used forest habitats instead, and then only leaving shelter of the forest between sunrise and sunset (Jarnemo et al 2014, Tufto et al 1996, Thirgood 1995, Allen et al 2014). This effect is seen most where there are higher levels of disturbance (Allen et al 2014), which in the absence of large predators, is as a result of human activities such as hunting (Heurich et al 2014, Jarnemo et al 2014). During the daytime deer are therefore confined to the forest areas, and must utilise the forage found within them. As they are ruminants their feeding behaviour consists of feeding interspersed by rumination, throughout the day and night, requiring them to search for food while restricted in the forest areas during the day. Since with a higher proportion of pasture and fields in the landscape, the forested areas available for browsing in the daytime are reduced, browsing impacts are concentrated. This has been shown to result in higher damages in areas with more agricultural land (Jarnemo et al 2014), as seen in this study.

While traditionally considered an important habitat for moose (Olsson et al 2011), marsh and wetlands, which included mires, was only a significant factor in Öster Malma. This may be the result of a number of changes to habitats since the 1960s, which alongside the increase in the moose population, have now been suggested to now shift the moose preferences away from mires (Olsson et al 2011). With marsh and wetlands also existing at very low proportions across most of Öster Malma, with only a few areas having large amounts, it is difficult to say why and how much marsh and wetlands can impact on browsing damages, albeit that they still seem to be indicated to some extent in Öster Malma.

Combined

As models for both all locations together and just Öster Malma had significant species and land use factors, these were combined allowing the most important aspects overall to be concluded. The final models had the same factors, with moose, red deer, roe deer and pasture and fields being shown to have a positive relationship to browsing damages. This supports the conclusions from the previous models that the density of all the deer species except from fallow deer are implicated in browsing damages, either directly through browsing, or indirectly, possibly through competition. Young forest was no longer in any of the models, indicating that once species densities are taken into account, the proportion of young forest is less important. This does not give clear support to my initial prediction that there is a positive relationship between young forest and browsing damage. This left pasture and fields as the only significant land use factor having a similar effect to the species densities on changes in browsing damages.

Conclusions

By better understanding the effects on browsing damages at the landscape scale, we can be better placed to make accurate management decisions in the future. This doesn't have to involve simply lowering deer densities further, but can look at specifically which species can be reduced for the biggest impact, and can even extend to using non-lethal way of damage reduction (Putman et al 2011). This study has shown quite clearly that it is the impact of many deer species together that

result in browsing damages, regardless of which species is actually undertaking the browsing. Red deer especially have been highlighted as having a much larger effect than initially expected. Knowing also that landscape structure, particularly in the case of proportions of agricultural land could have such a marked effect, can also be taken into account for future management. Land uses may be a harder element to change, but by altering silvicultural practices to perhaps make forest gaps containing young pine trees less attractive within the landscape (Kuijper et al 2009), or changing our own behaviour and resulting disturbance effects on deer populations (Cromsigt et al 2013), we may alter the impacts of land use on deer populations. One thing is for certain, that reducing damages to pine trees in Swedish forests goes well beyond moose management, with further study onto browsing impacts within multiple ungulate systems a promising area of research.

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