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Browsing behaviour in complex ungulate multi-species systems in southern Sweden

*Betesbeteende i komplexa flerartssystem av klövvilt i södra
Sverige*

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Abstract

In recent years several of the ungulate species present in Sweden have increased in both densities and distribution. Browsing pressure has mainly been attributed to moose but recent research shows that with more complex ungulate ecosystems new interactions and connections might emerge. This thesis serves to investigate the impact of multi-species ungulate communities on browsing pressure in boreal forests and semi-open landscapes in southern Sweden. In this study the effect of ungulate species densities, richness and feeding strategy on browsing pressure were analyzed. This study uses data collected within the ongoing environmental analysis project “reference areas for management of ungulates in southern Sweden”. Total weighted browsing pressure, tree species specific browsing pressure and ungulate densities were monitored. The data was analyzed using generalized linear mixed models. Final model selection was done using Akaike information criterion (AIC). In order to include different ungulate species in the same models ungulate densities were transformed into moose equivalents. GLMM models showed that ungulate species richness, ungulate density and ungulate feeding strategy all have a significant effect on browsing pressure. Ungulate species richness had a negative impact on browsing pressure which likely means that increased interspecific competition could cause a decrease in browsing pressure. Ungulate total density had a positive effect on browsing pressure, which was not unexpected given previous research on the subject. Feeding strategy was found to have some, although weak indications that it could be a contributing factor to browsing pressure. In all the final models moose had a relatively large positive estimate, which agree with previous studies that moose is one of the main perpetrators behind browsing pressure carried out by ungulates in Sweden. To conclude there are clear indications that new interactions and connections will emerge with changing ungulate populations.

Keywords: browsing pressure, interspecific competition, multi-species

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1 Introduction

The forestry industry in Sweden is an important revenue stream for the Swedish economy (Skogsindustrierna 2015). Forests in Sweden cover 28.3 million hectares of which 23.6 million hectares are productive woodland (Skogsdata 2017). Fifty percent of the forest is owned by private landowners, 25 percent owned by companies and the rest by the state and other private owners (Skogsdata 2017). Private owners stand for 66% of clear cuts annually (Skogsdata 2017), for a majority of the private landowners' forestry used to be an important part of their economy and would offer a financial security (Lönstedt 1987) but with increased urbanization and increasing life standards other values take place among the economic aspects (Mattila et al. 2014).

Forestry in Sweden underwent a paradigm shift in the 1940-1950's when it went from small-scale to the industrial and intense process it is today (Ericsson et al. 2000; Östlund et al. 1997). This paradigm shift meant an increase in clear-cut areas where the food available for ungulate browsers increased enormously while the forest regenerated. Around the same time there was a change in hunting policy into new hunting practices such as a decreased harvest of female moose compensated by an increased harvest of bulls and calves. These new hunting practices combined with increased forage availability contributed to sharp increases in ungulate populations, especially moose (*Alces alces*) responded quickly (Figure 1; Hörnberg 1991; Cederlund et al. 1987). In recent decades, populations of red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) have increased in both densities and distribution (Bergström et al. 2009; Apolonio et al. 2010). Red deer and fallow deer have been slowly increasing while roe deer had a strong increase mainly caused by declining fox populations because of Sarcoptic mange, increased supplementary feeding by hunters and mild winters which increased survivability (Apolonio et al. 2010). With harder winters, recovering fox populations and increasing lynx populations during the later 90's the roe deer population have decreased and is today roughly on the same level as moose (figure 1).

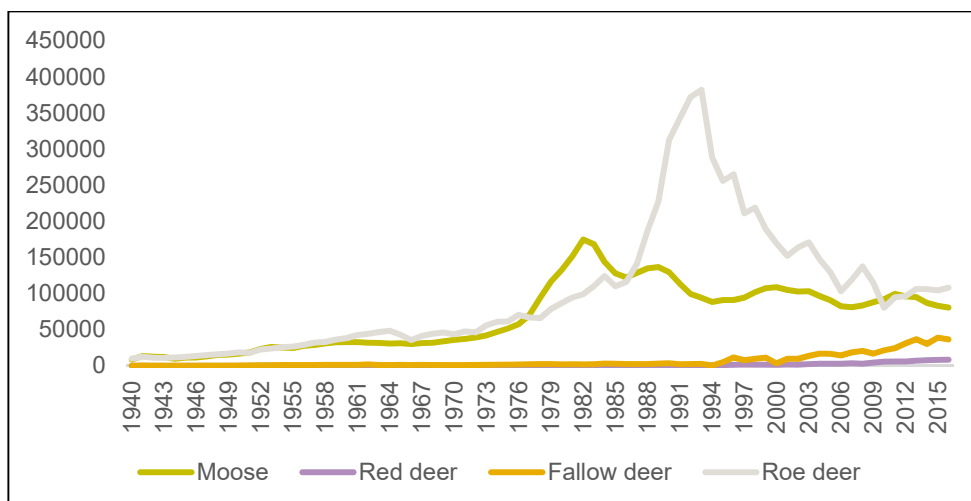


Figure 1. Swedish hunting bag statistics 1940-2016 (SJF Viltdata 2017).

According to Hofmann (1989), ungulates can be classified depending on their feeding strategy; Swedish ungulates can be divided into browsers and grazers; moose and roe deer are classified as concentrate selectors which are characterized by a diet consisting of mainly highly digestible content. Red deer and fallow deer are classified as intermediate grazers, which are characterized by a selective diet with a substantial fiber tolerance (Hoffman 1989; Bergqvist et al. 2002). Browsers have a high rate of reproduction and dispersal, allowing them to take quick advantage of disturbances in the forest ecosystem while grazers have a slower rate of reproduction and dispersal as an adaptation to open or semi-open landscapes which are characterized by a slower change and higher stability than the forest ecosystem (Bergqvist et al. 2002).

Moose food preferences in Sweden are thoroughly studied; during summer moose prefer plants in the field layer, shrubs and deciduous trees such as rowan, willow, aspen and oak, while during winter it prefers shoots and twigs of mainly pine but also birch, partially depending on forage availability (Månsson et al. 2007; Bergström et al. 2010). Roe deer have similar diet as moose; during winter roe deer will mainly browse shoots and twigs of coniferous trees, heather and berry shrubs, during summer they switch the coniferous trees for deciduous trees and also include herbs and grass in their diet (Bergström et al. 2010; Nichols et al. 2015).

Red deer and fallow deer prefer grazing on grass, herbs and shrubs during summer, they also feed on twigs and shoots of the same substrate as roe deer and moose if the forage availability is high (Bergström et al. 2010).

Wildlife is an ecosystem service that offer and affect a large number of factors. For example, ungulate browsing cause large monetary damages for landowners by negatively affecting reforestation, timber quality (Bergqvist 2011) and cause harm to biodiversity by disfavoring biologically important species such as oak or aspen (Bergqvist et al. 2002; Ericsson et al. 2001; Angelstam et al. 2000). Ungulates can also create dangerous situations in traffic for railway (Seiler et al. 2011) and car

traffic (Seiler et al. 2004). The actual monetary cost of ungulate damages is hard to assess, but an estimate by Seiler (2004b) places the cost of vehicle damages by collision with ungulates in Sweden to 100 million Euros annually. Kempe (2012) estimates the future forest production loss in Sweden caused by current damages to 1 million m³sk if current damage-levels are retained (93.3 million m³sk were gross felled in Sweden during 2016, Skogsstyrelsen 2017)

On the other hand, wildlife is a great resource to natural tourism, provides hunting experiences, climate neutral meat and can also positively affect biodiversity by increasing structural heterogeneity (Edenius et al. 2002) and by increasing light exposure to the ground by browsing in tree canopies (Mathisen 2011). According to an estimate by Kindberg et al. (2010), moose provides approximately 8.5 million kg meat annually. Boman et al. (2011) places the value on moose hunting to 1.45 billion sek.

Wildlife in Sweden hence offers many possibilities and potential problems, and the debate in Sweden have been heated since Sweden have many strong stakeholder groups involved, e.g. Swedish Hunters' Association, the forest industry, Swedish Environmental Protection agency, farmers, landowners, traffic, etc.

In order to strike a balance between the moose population, available food resources and damages on forest, a new moose management system was implemented in Sweden in 2012 (Regeringen 2009). The new system is an ecosystem-based adaptive management system that implements iterative decision making and learning on a regional level.

Since focus have mainly been on moose, little is known about ungulate browsing in multi-species systems where both intraspecific and interspecific competition can be contributing factors to size and variation in browsing pressure. With the appearance of new multi-species ungulate communities, new connections and interactions might emerge. There are few studies regarding browsing in areas with a high richness and densities of ungulate species (Gordon et al. 1989; Nicols et al. 2015; Månsson et al. 2015; Ånöstam 2017).

1.1 Aim

The aim of my thesis is to investigate the complex conditions that affect browsing pressure in forest landscapes with multiple ungulate species in Sweden by investigating browsing pressure by large mammalian herbivores in relation to their occurrence, densities and feeding strategy.

I aim to answer the following question:

- *Is browsing pressure on tree saplings more strongly related to the number of ungulate species than to their combined densities?*
- *To what extent is browsing pressure influenced by the identity of ungulate species?*

2 Method

2.1 Study areas

I used ungulate browsing survey data collected within the Foma (Fortlöpande miljöanalys) project “Reference areas for ungulate management southern Sweden” 2012-2015 (Edenius 2012b). Surveys were carried out in two areas in southern Sweden (Växjö and Öster Malma).

Öster Malma is situated outside the city of Nyköping in Sörmland province (midpoint coordinate – 58.950778, 17.159450 – WSG84), and distinctive for the Öster Malma area is high densities of ungulate species, partially due to extensive supportive feeding by hunters in the area.

Växjö is situated in Småland province in southern Sweden (midpoint coordinate – 57.084610, 14.812889 – WSG84). During early January 2005 the area was hit hard by the storm Gudrun, which knocked down large areas of forest; according to Fridman et al. (2006) 272 000 hectares were damaged and between 110 000 to 130 000 hectares were so damaged that reforestation was demanded (Wallstedt et al. 2013). Ten years after the storm areas affected by the storm had luxurious regrowth of birch, spruce and other tree species. In contrast, Scots pine has been very sparsely regenerated due to the perceived risk of browsing damages (Bergquist 2009). Many stands could not be immediately treated through salvage logging because of the enormous task to clear all felled logs so many areas were resting for several years before reforestation (Bergquist 2009).

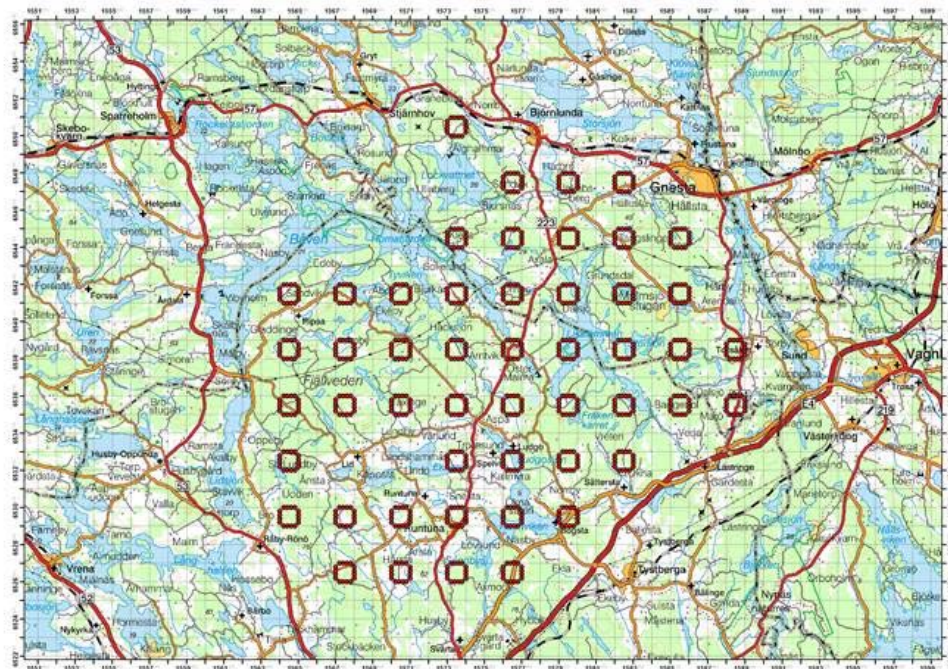


Figure 2, Öster Malma study area and sampling design.

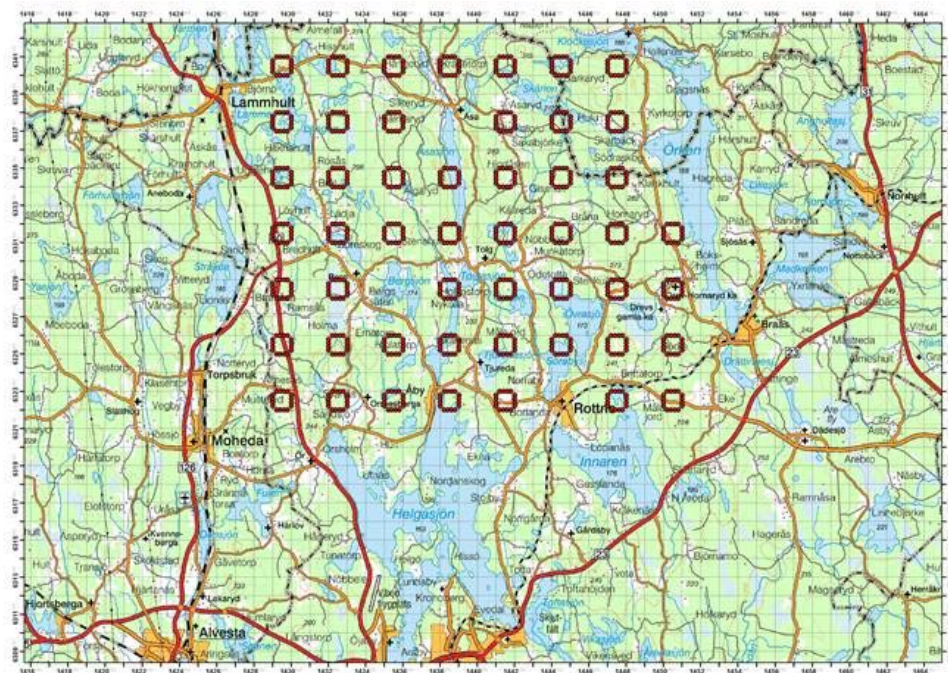


Figure 3, Växjö study area and sampling design.

2.2 Study design

Inventories of pellets and browsing were carried out in 100 m² large sample plots with 16 sample plots clustered within 1 x 1 km tracts, with 50 tracts per study area. The tracts were placed in a regular grid system with 3km distance between tracts. Further description of the method is available in (Edenius 2012).

2.2.1 Fecal pellets surveys

Each fresh pile was counted if it was considered representative and more than half was within the plots. For moose and red deer 20 pellets in a pile were used as a lower limit and 10 pellets in a pile for fallow deer and roe deer. Pellets belonging to roe deer and fallow deer are very hard to differentiate so piles with fewer than 45 pellets were attributed to roe deer while piles with more than 45 pellets were attributed to fallow deer (Eckervall 2007; Pfeffer 2016).

The fecal pellets survey use circular plots with a radius of 5.64 (100m²) in case of moose and red deer. Due to the smaller and therefore harder to detect pellets from roe deer and fallow deer fecal pellet groups of these species were surveyed in circular plots with a radius of 1,78m (10m²).

Fecal pellet survey is a low cost method to monitor ungulate populations (Sutherland 2006) over large areas over time. The method have been partially evaluated with the main focus on moose where it was found that the method offers the best relationship between the moose population and forage utilization considering the cost of inventory (Rönnegård et al. 2008; Hörnell-Willebrand et al. 2010). Whereas pellet count surveys have proved a reliable method for moose population monitoring, the method's applicability in case of other ungulate species is more uncertain. For example, Pfeffer et al. (2017) has suggested that dung counts can underestimate density of roe deer. The output from the method can be used as an index of population size to compare between years and areas and total densities can be calculated. However, uncertainty about defecation rate and age of counted pellet groups limits the accuracy of the method for estimates of absolute density (Table 1).

Density (animals per 1000 hectares) can be calculated through the formula: $(S \cdot K) / (P \cdot D \cdot T)$ where S = Sum of all piles on all visited plots, K = Scaling factor, P = Number of visited plots, D = Defecation rate and T = Deposition time.

The method allows survey of multiple species simultaneously and can be carried out voluntarily by hunters, forest owners and other stakeholders. Unlike aerial inventories, counting pellet groups are not depending on snow which makes it useful in areas where snow is absent or rare (Hörnell-Willebrand 2010).

The counting of past winters pellets is preferably carried out in spring after the snow have melted yet before the pellet groups have been covered by the greening up of vegetation. In my survey the sampling was carried out in April. In order to increase

accuracy of the method, permanent plots can be used where pellets are cleared during fall, in my survey the plots were not cleaned, instead the inventory personnel were instructed to count only fresh piles. Knowledge of site-specific defecation rate were not available but would improve the accuracy of the survey.

Table 1, Assumptions for calculations of total density based on the fecal pellet data in this study.

Species	Assumed defecation rate (piles/day)	Source	Assumed defecation time
Moose	23	Matala et al. (2013)	180 days
Red deer	15	Jarnemo et al. (2010); Mitchell (1984)	180 days
Fallow deer	23	Massei et al. (1998) ; Mayle et al. (1996)	180 days
Roe deer	22	Mitchell et al. (1985)	180 days

2.2.2 Browsing pressure survey

The browsing survey was carried out simultaneously with the fecal pellets surveys within the same 100 m² circular plot areas. Pine (*Pinus sylvestris*), silver birch (*Betula pubescens*), pendular birch (*Betula pendula*), rowan (*Sorbus aucuparia*) and oak (*Quercus robur*) were surveyed.

The definition of browsing pressure was the proportion of last year's shoots browsed during winter. This was surveyed by estimating the number of freshly browsed shoots and the total number of shoots. Browsing pressure was assessed on the tree closest to the center point with a height between 0.3–3.0 meters for each tree species.

2.3 Statistical analysis

Generalized linear mixed models (GLMM) were used to analyze the species-browsing relationship. GLMMs are a mixture between linear mixed models and generalized linear models, and are preferably used for analysis of data that defy normal statistic procedures (Bolker et al. 2009). I transformed all densities to moose equivalents by using a formula that includes female body weight (table 2). After transformation of the ungulate densities into moose equivalents the variables could be utilized together in statistical models. Variables included in the models were; i) number of ungulate species present, ii) total density of the 4 ungulates expressed in moose equivalents, iii) combined ungulate densities in moose equivalents based on feeding strategy, iv) browsing pressure for the 5 different tree species and weighted browsing pressure for all tree species combined. Browsing pressure was used as response variable, whereas species identities were used as fixed variables. Year, area and tract were set as random effects with tract nested within area. A logit link function with binomial distribution was used. Presence of multicollinearity was investigated with the variance inflation factor (VIF),

descriptive statistics were calculated and significance was tested with two sample t-test.

Models were compared based on Acaice information criteria (AIC) which takes into account the ability of the model to fit the data, it is based both on model simplicity and goodness of fit; a lower AIC indicate a better model. I elected to use the cut-off points for ΔAIC from Burnham et al. (2004) Where $\Delta AIC = 10$ is used as final limiting factor for candidate models, model support is rated depending on ΔAIC where $\Delta AIC < 2$ indicate models with very strong support, models with ΔAIC between 2-4 were considered to have strong support, models with ΔAIC between 4-7 were considered to have moderate support, models with ΔAIC between 7-10 were considered to have weak support, finally models with $\Delta AIC > 10$ were considered to have no support (Appendix 2). AIC-weights were also calculated and used for explanatory purposes. Models were created in the statistical program R-studio (R core team 2017) using the package lme4.

Table 2. Assumptions and calculations for transformations to moose equivalents (ME) in order to include the variables in the same models.

Species	Average weight kg	Source	Formula	ME
Moose	330	Belowski(1997);Peterson(1955);Sand et al. (1996);Saether et al. (1993);Saether et al. (1985)	$0.75 * 330^{0.75} = 58.06$	1
Red deer	125	Jarnemo (2001)	$0.75 * 125^{0.75} = 28.03$	$58.06 / 28.03 =$ 2.07
Fallow deer	45	Chapman et al. (1975);mcEligott et al. (2002)	$0.75 * 45^{0.75} = 13.03$	$58.06 / 13.03 =$ 4.45
Roe deer	23	Andersen et al. (1998);Liberg et al. (1995); Pettorelli et al. (2002)	$0.75 * 23^{0.75} = 7.87$	$58.06 / 7.87 =$ 7.37

3 Results

3.1 Main findings

The composition of the four ungulate species at tract scale varied between the areas for the duration of the study-period. Öster Malma (Figure 4) exhibited a significantly higher (two sample t-test – $t(337) = 8.62, p < 0.0005$) richness of ungulate species than Väjö (Figure 5).

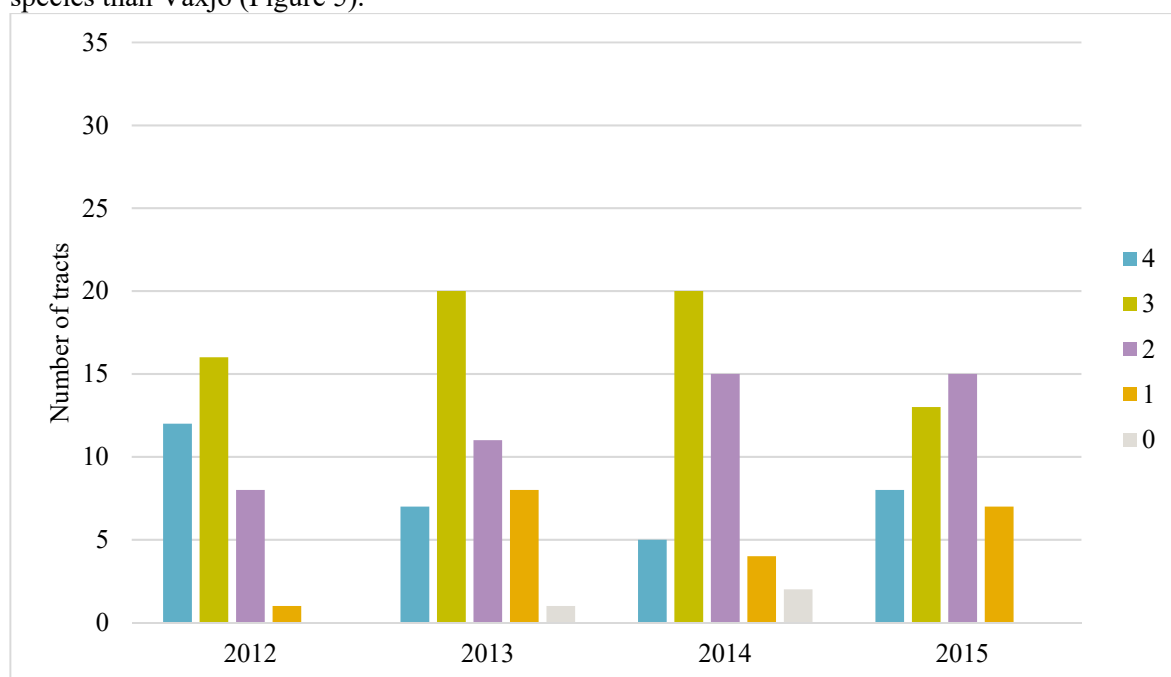


Figure 4. Number of tracts with numbers of different ungulate species recorded for the years 2012-2015 for Öster Malma.

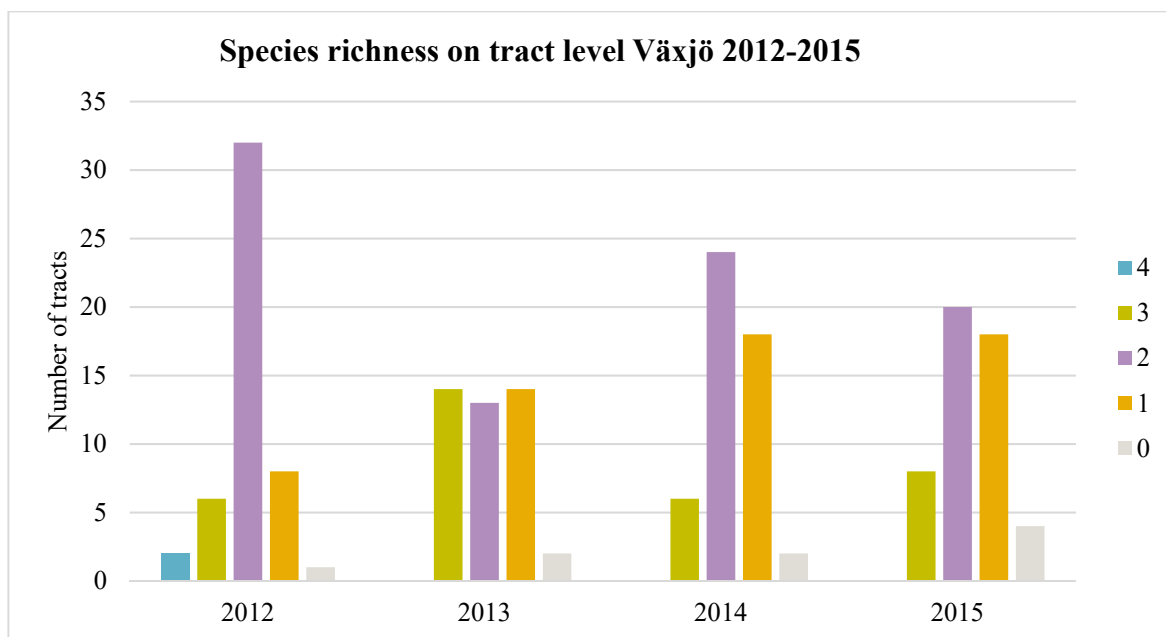


Figure 5. Number of tracts with numbers of different ungulate species recorded for the years 2012-2015 for Väjö.

The main difference for the fecal dropping piles found was the significantly higher presence of red deer (two sample t-test ($t(174) = 7.11$, $p\text{-value} < 0.0005$)) and fallow deer (two sample t-test ($t(182) = 9.30$, $p\text{-value} < 0.0005$)) in the Öster Malma area (Figure 6) compared with the Väjö area (Figure 7) where both species occurs to a much lesser extent.

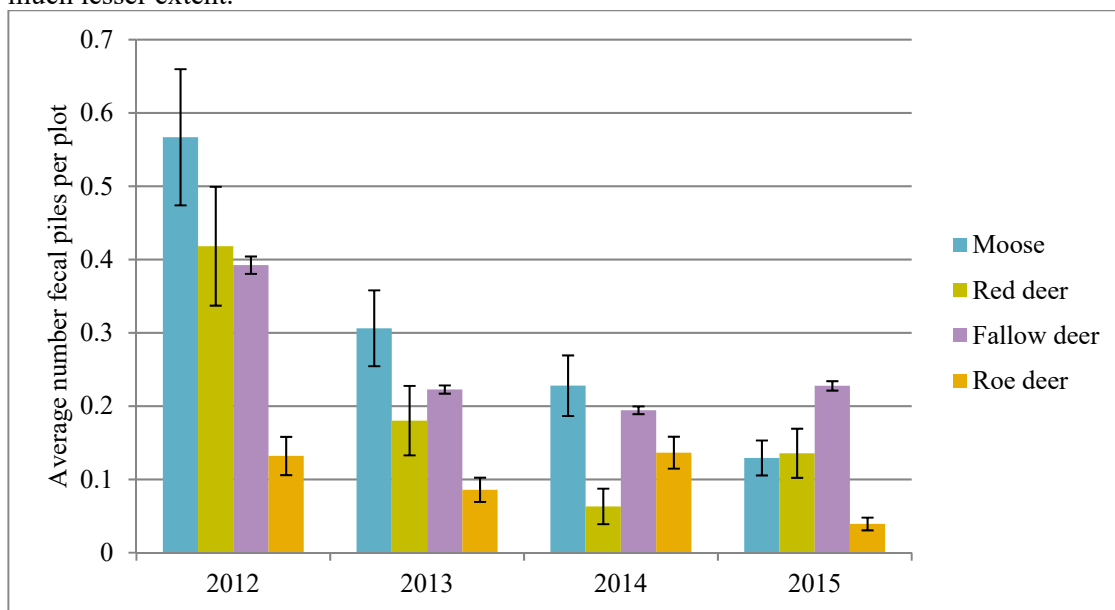


Figure 6. Average number of fresh piles per year and ungulate species on plot level in Öster Malma 2012 – 2015, standard error visualized per bar.

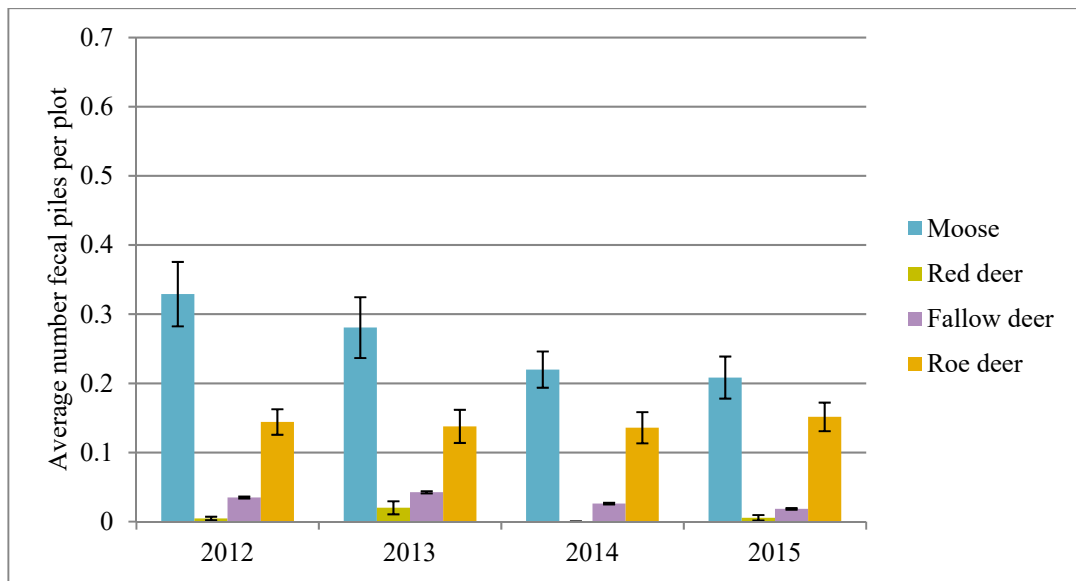


Figure 7. Average number of fresh piles per year and species on plot level in Väjö 2012 – 2015, standard error visualized per bar

The overall weighted browsing pressure for all tree species was significantly higher (two sample t-test ($t(204) = 4.37$, p -value < 0.0005) in the Öster Malma area than the Väjö area; the yearly variation was higher in the Väjö area (Figure 8).

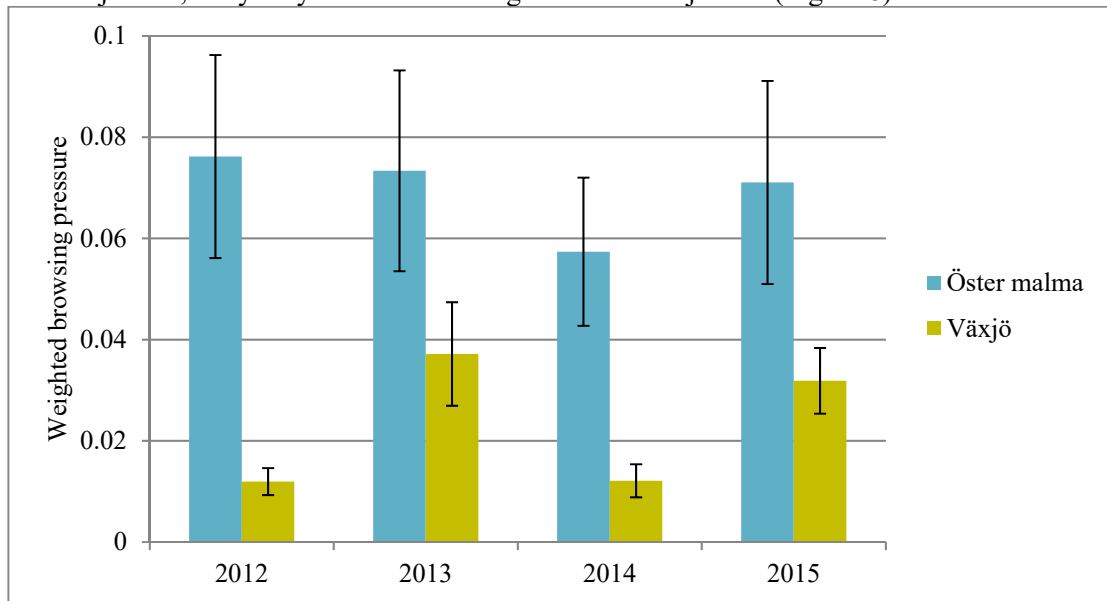


Figure 8. Weighted browsing pressure for all tree species combined, standard error visualized per bar.

In Öster Malma, pine browsing pressure decreased during the study period whereas the deciduous browsing pressure was generally stable with the exception of oak during 2014 (figure 9).

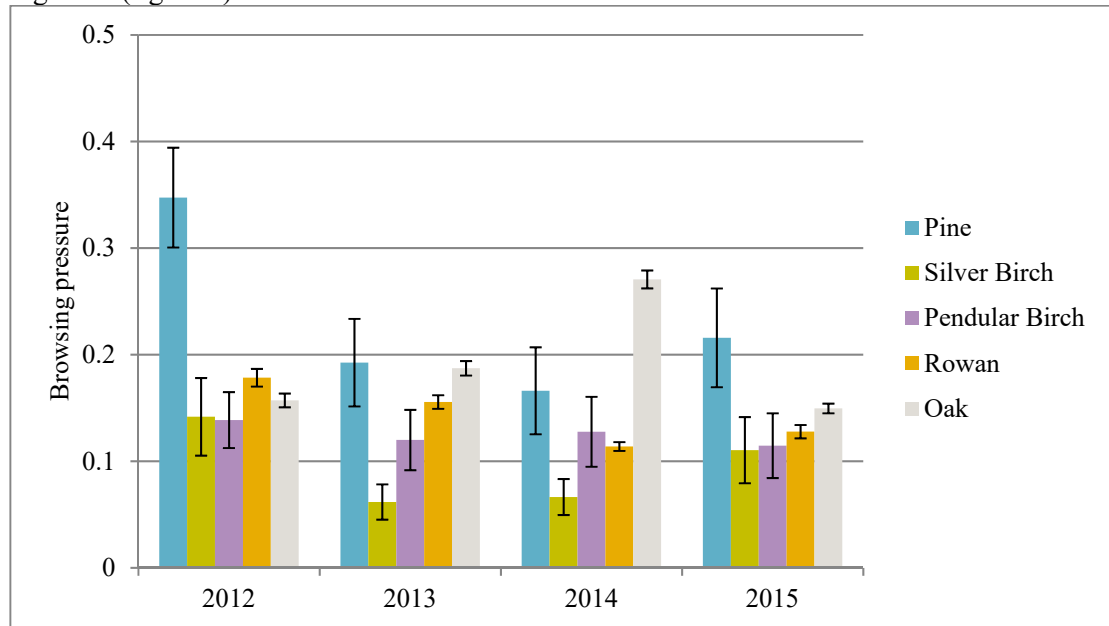


Figure 9. Average browsing pressure for each tree species at tract scale Öster Malma 2012-2015, standard error visualized per bar.

In Växjö, the tree species specific browsing pressure during the study period had a larger variation between species and year than Öster Malma during the same period (figure 10).

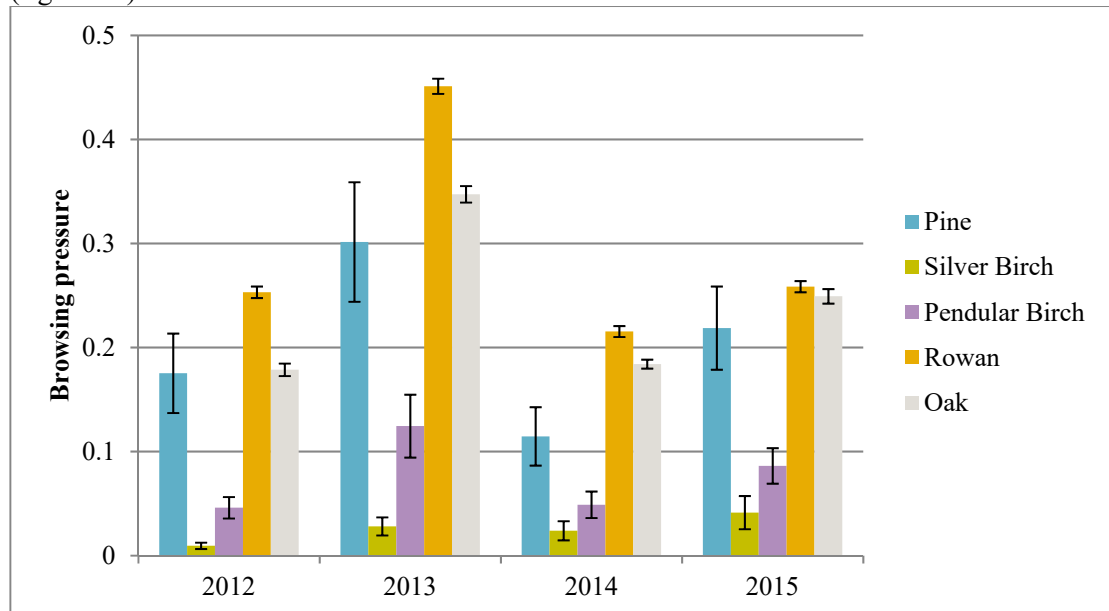


Figure 10. Average browsing pressure for each tree species at tract scale Växjö 2012-2015, standard error visualized per bar.

There was a relatively high density of fallow deer (10.54 – 21.29 units of moose-equivalent per 1000 hectares) in the Öster Malma study-area for the entire study period and a high density of moose in Öster Malma during year 2012 (13.68 animals per 1000 hectares) (Table 3).

Table 3. Average number ungulates per 1000 hectares, transformed into moose equivalents

Total density roe deer	Öster Malma	Växjö
2012	4.52	4.93
2013	2.93	4.71
2014	4.67	4.65
2015	1.34	5.18
Total density Red deer		
2012	7.48	0.08
2013	3.22	0.35
2014	1.12	0.00
2015	2.42	0.09
Total density Fallow deer		
2012	21.29	1.89
2013	12.08	2.30
2014	10.54	1.41
2015	12.35	1.00
Total density Moose		
2012	13.68	7.94
2013	7.39	6.77
2014	5.50	5.31
2015	3.12	5.03

3.2 Statistical analysis

In total 106 GLMM-models were created to explain the browsing data (Appendix 2). Each model was investigated for multicollinearity, no evidence of multicollinearity was found in any of the models. Out of the 106 models I selected 39 models as candidate models as having a higher probability of explaining the data (Appendix 1) Out of the candidate models I selected one or several models considered to be the strongest model (Table 5) or having an equally strong probability to explain the data (Table 4). Support codes - ΔAIC ; 0 – 2 ****, 2-4 ***, 4-7 **, 7-10*.

Table 4. Models with the strongest support according the AIC-criteria, support codes - ΔAIC ; 0-2

All tree species							
Model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	Aic weight
modelv	Richness+Moose+Reddeer	7	4428,9	0	****	1	0,551
modelu	Richness+Totaldensity+Moose+Reddeer	8	4429,3	0,412	****	0,814	0,449
Pine							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelq1	Intermediate+Moose	6	2518,2	0	****	1	0,443
modeln1	Moose+Red+Fallow	7	2520,2	1,975	****	0,373	0,165
Silver Birch							
Model	Variable	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelv2	Moose+Roedeer+Totaldensity	7	2908,5	0	****	1	0,234
modelu2	Roedeer+Totaldensity	6	2908,6	0,066	****	0,968	0,226
modelk2	Moose + Roe + Red + Fallow	8	2909,2	0,645	****	0,724	0,169
modelo2	Moose+Roe+Fallow	7	2910,1	1,555	****	0,460	0,107
modelt2	Roe+Totaldensity+Richness	7	2910,2	1,639	****	0,441	0,103
models2	Moose+Roe+Totaldensity+Richness	8	2910,4	1,846	****	0,397	0,093
Pendular birch							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	Aic-weight
modelu3	Moose+Reddeer+Roedeer+Totaldensity+Richness	9	4987,4	0	****	1	0,693
modelw3	Reddeer+Fallowdeer+Totaldensity+Richness	8	4989,1	1,647	****	0,439	0,304
Rowan							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelg4	Moose	5	1315,3	0	****	1	0,193
modelc4	Total density	5	1316,1	0,799	****	0,671	0,130
modelf4	Concentrate	5	1316,1	0,849	****	0,654	0,126
modelo4	Moose+Totaldensity	6	1316,9	1,569	****	0,456	0,088
modeln4	Moose+Reddeer	6	1317,2	1,906	****	0,386	0,075
modelp4	Moose+Richness	6	1317,3	1,987	****	0,370	0,072
Oak							
model	Variable	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelp5	Richness+Moose+Red	7	1691,6	0	****	1	0,730
modelo5	Totaldensity+Richness+Moose+Red	8	1693,6	1,99	***	0,370	0,270

Table 5. The final GLMM-model fitted to the browsing data.

Response	Model#	Variable	Estimate	Std.error	Pr(> z)
Weighted all browsing pressure	Model-v	(Intercept)	-3.891	0.473	<2e-16***
		Richness	-0.181	0.029	8.69e-10***
		Moose	0.040	0.003	<2e-16***
		Red deer	-0.041	0.005	2.16e-12***
Pine browsing pressure	Model-q1	(Intercept)	-2.294	0.216	<2e-16***
		Intermediate	0.015	0.003	4.84e-06***
		Moose	0.011	0.005	0.0223*
Silver Birch brows- ing pressure	Model-v2	(Intercept)	-4.526	0.468	<2e-16***
		Moose	0.014	0.009	0.144
		Roe deer	-0.102	0.011	<2e-16***
		Total density	0.026	0.006	2.12e-05***
Pendular Birch browsing pressure	Model-u3	(Intercept)	-2.763	0.397	3.17e-12***
		Moose	0.036	0.003	<2e-16***
		Red deer	-0.044	0.006	4.61e-12***
		Roe deer	0.022	0.006	0.0002***
		Total Density	0.008	0.002	9.92e-05***
		Richness	-0.414	0.035	<2e-16***
Rowan browsing pressure	Model-g4	(Intercept)	-1.953	0.456	1.89e-05***
		Moose	0.019	0.008	0.0299*
Oak browsing pres- sure	Model-p5	(Intercept)	-2.037	0.431	2.33e-06***
		Richness	-0.454	0.076	3.31e-09***
		Moose	0.073	0.017	2.24e-05***
		Red deer	-0.059	0.013	2.10e-05***

The combined average weighted browsing pressure for all tree species could best be explained by a model containing *ungulate species richness*, *moose* and *red deer*. For pine I found that including *moose* and *intermediate* grazers (red deer and fallow deer) in my model explained most of the variation in the data. For silver birch I found that most of the variation could be explained by a model containing *moose*, *roe deer* and *total density*. For pendular birch I found that the model that best explains the variation included *moose*, *red deer*, *roe deer*, *total density* and *ungulate species richness*. For rowan I found that the variation could be explained best by only including the variable *moose* in my model. For oak I found that including *ungulate species richness*, *moose* and *red deer* in my model could best explain the variation in the data.

4 Discussion

This study investigated the impact of multi-species ungulate communities on browsing pressure in boreal forests and semi-open landscapes in southern Sweden in order to gain knowledge of factors contributing to browsing pressure with focus on potential interspecific or intraspecific competition where knowledge previously have been limited.

4.1 Is browsing pressure on tree saplings more strongly related to the number of ungulate species than to their combined densities?

The *ungulate species richness*-variable had a negative estimate in all three models where it is present (model-v, model-u3 and model-p5) This goes against my expectation that species richness could be an contributing factor to increasing browsing pressure, on the other hand I found that species richness is still to be considered an important variable in explaining browsing pressure as a negative estimate could mean that a higher interspecific competition might cause a decrease in browsing pressure, this is supported by previous studies that show interspecific competition as an important factor on ungulate condition (Stewart et al. 2005) and resource partitioning (Gordon et al. 1989). The *total density* - variable was included in two models (model-v2 and model-u3) where it has a positive effect on browsing pressure in each one, which is not very surprising given that it is an established fact that browsing pressure increases with increasing ungulate densities on a habitat-specific scale (Bergquist et al. 2002; Månsson 2007; Tremblay et al. 2007).

4.2 To what extent is browsing pressure influenced by the identity of ungulate species?

In four out of six models there are indications that presence of several ungulate species with different feeding strategy will have an impact on browsing pressure. I

found clear evidence in only one model (Model-q1 with pine browsing as response variable) where *intermediate* grazers had a slightly larger positive estimate than *moose*. In six out of six models I found that moose had a relatively large, positive estimate, which is in line with previous studies (Bergquist et al. 2001) that *moose* is responsible for a considerable part of the browsing carried out by ungulates in Sweden.

4.3 Evaluation of the methods used in this study

The models presented in table 5 as the final GLMM-models are considered the strongest, the competing models with $\Delta AIC < 2$ should not be regarded as having exactly the same explanatory power as the model with $\Delta AIC = 0$, but they should be regarded as having a significant possibility to explain the data while not being the strongest model. AIC-weights are defined as the probability that an model is the actually best model to explain the data compared to the next one, in this case, the strongest model (model-v) explaining the total weighted browsing pressure have an AIC-weight of 0.55, that can be regarded as model-v being 5.5 times more likely to explain the data than the second best model.

When modelling reality there are always simplifications and assumptions that might create a misleading result. In this case a number of assumptions that could have a large effect on the final result have been made. Relevant assumptions to be aware of relating to the survey method and basic data preparation are: the defecation rate, the assumed accumulation time and the assumed average weight for ungulate females used to calculate moose equivalents.

All assumptions have been scientifically based as far as possible and to the authors' greatest knowledge. The calculations into moose equivalents were made in order to be able to compare ungulate species of different size, unfortunately, the formula does not correct for size difference, which in this case is the higher energy need per kg body mass that a smaller ungulate need in comparison with a larger one. The defecation rate is assumed to be constant over the entire area and time period, the correct defecation rate is very hard to estimate accurately since it is depending on local conditions, the climate and other factors. Aerial inventories could be combined with pellet inventories to calibrate and improve the method (Rönnegård et al. 2008) but then the original reason of why the method was chosen would be ignored and the profits disregarded.

The choice of GLMM to model the browsing – ungulate presence relationship was made with the structure of the data in mind, to shoehorn data into classical statistical procedures is not recommended and will likely result in pseudo-replication (Bolker et al. 2009). When modelling with GLMM we include random factors which are factors related to the experimental design that might have an effect on the result while not being what we are interested in investigating

4.4 Conclusion

Ungulate species richness, ungulate density and ungulate feeding strategy all have a significant effect on browsing pressure. Hunters and foresters need to hold the moose population on a sustainable level while keeping in mind that there are other factors such as interspecific competition and ungulate species richness which will have a significant effect on browsing pressure. Another challenge is to differentiate between ecological systems with different ungulate species richness depending on site in the country; a moose management system adapted to northern Sweden might not work in southern Sweden where previously described factors might interfere.

The result from my thesis might be valuable when predicting areas where occurrence of multi-species ungulate communities might be a contributing factor to ungulate browsing. The result from my thesis can also be valuable when predicting effects from introducing ungulate species to new areas in Sweden, one example would be evaluation of a possible whitetail deer establishment in Sweden. Whitetail deer is a concentrate selector and is thus partially included in this study by extension.

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Appendix 1 - Candidate models

All tree species							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	Aic weight
modelv	Richness+Moose+Reddeer	7	4428,9	0	****	1	0,551
modelu	Richness+Totaldensity+Moose+Reddeer	8	4429,3	0,41	****	0,814	0,449
Pine							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelq1	Intermediate+Moose	6	2518,2	0	****	1	0,443
modeln1	Moose+Red+Fallow	7	2520,2	1,97	****	0,373	0,165
modelo1	Moose+Fallow	6	2521,2	3,02	***	0,221	0,098
modele1	Intermediate	5	2521,3	3,13	***	0,210	0,093
modelb1	Concentrate + Intermediate	6	2521,4	3,19	***	0,203	0,090
modelc1	Total density	5	2522,8	4,6	**	0,100	0,044
model11	Total density + Richness + Intermediate + Concentrate	7	2523	4,82	**	0,090	0,040
modela1	total density + Richness	6	2524,1	5,88	**	0,053	0,023
modelj1	Fallow	5	2527,3	9,08	*	0,011	0,005
Silver Birch							
Model	Variable	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelv2	Moose+Roedeer+Totaldensity	7	2908,5	0	****	1	0,234
modelu2	Roedeer+Totaldensity	6	2908,6	0,07	****	0,968	0,226
modelk2	Moose + Roe + Red + Fallow	8	2909,2	0,64	****	0,724	0,169
modelo2	Moose+Roe+Fallow	7	2910,1	1,56	****	0,460	0,107
modelt2	Roe+Totaldensity+Richness	7	2910,2	1,64	****	0,441	0,103
models2	Moose+Roe+Totaldensity+Richness	8	2910,4	1,85	****	0,397	0,093
modelq2	Moose+Roe+Red+Fallow+Richness+Totaldensity	9	2911	2,47	***	0,292	0,068
Pendular birch							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	Aic-weight
modelu3	Moose+Reddeer+Roedeer+Totaldensity+Richness	9	4987,4	0	****	1	0,693
modelw3	Reddeer+Fallowdeer+Totaldensity+Richness	8	4989,1	1,65	****	0,439	0,304
Rowan							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelg4	Moose	5	1315,3	0	****	1	0,193
modelc4	Total density	5	1316,1	0,8	****	0,671	0,130
modelf4	Concentrate	5	1316,1	0,85	****	0,654	0,126
modelo4	Moose+Totaldensity	6	1316,9	1,57	****	0,456	0,088
modeln4	Moose+Reddeer	6	1317,2	1,91	****	0,386	0,075
modelp4	Moose+Richness	6	1317,3	1,99	****	0,370	0,072
modela4	total density + Richness	6	1317,8	2,48	***	0,289	0,056
modelb4	Concentrate + Intermediate	6	1317,9	2,57	***	0,277	0,054
models4	Totaldensity+Intermediate+Moose	7	1318,8	3,56	***	0,169	0,033
modelj4	Fallow	5	1318,9	3,61	***	0,165	0,032
modele4	Intermediate	5	1319,2	3,9	***	0,142	0,027
modelh4	Roe	5	1319,2	3,95	***	0,139	0,027
modeld4	Richness	5	1319,3	4,06	**	0,131	0,025
model14	Total density + Richness + Intermediate + Concentrate	7	1319,6	4,29	**	0,117	0,023
modeli4	Red	5	1319,8	4,54	**	0,104	0,020
modelk4	Moose + Roe + Red + Fallow	8	1320,5	5,23	**	0,073	0,014
modelr4	Moose+Concentrate+Roedeer+Reddeer+Richness+Intermediate+Totaldensity	9	1322,1	6,84	**	0,033	0,006
Oak							
model	Variable	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelp5	Richness+Moose+Red	7	1691,6	0	****	1	0,730
modelo5	Totaldensity+Richness+Moose+Red	8	1693,6	1,99	***	0,370	0,270

Appendix 2 - All models

All tree species							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	Aic weight
modelv	Richness+Moose+Reddeer	7	4428,88	0	****	1	5,51E-01
modelu	Richness+Totaldensity+Moose+Reddeer	8	4429,29	0,412	****	8,14E-01	4,49E-01
modelq	Moose+Red	6	4464,08	35,202		2,27E-08	1,25E-08
modelk	Moose + Roe + Red + Fallow	8	4466,76	37,882		5,94E-09	3,28E-09
modeln	Moose + Roe + Richness	7	4473,23	44,35		2,34E-10	1,29E-10
models	Richness+Concentrate+Intermediate	7	4481,15	52,268		4,47E-12	2,46E-12
modelt	Richness+Concentrate	6	4481,88	52,999		3,10E-12	1,71E-12
modelg	Moose	5	4513,16	84,28		5,00E-19	2,76E-19
modelo	Moose+Fallow	6	4514,81	85,927		2,19E-19	1,21E-19
modelp	Moose+Roe	6	4515,16	86,28		1,84E-19	1,01E-19
modelb	Concentrate + Intermediate	6	4538	109,116		2,02E-24	1,11E-24
modelf	Concentrate	5	4545,9	117,015		3,90E-26	2,15E-26
modela	total density + Richness	6	4571,47	142,584		1,09E-31	6,02E-32
modeld	Richness	5	4609,75	180,872		5,30E-40	2,92E-40
modeli	Red	5	4619,56	190,675		3,94E-42	2,17E-42
modelc	Total density	5	4620,62	191,734		2,32E-42	1,28E-42
modele	Intermediate	5	4634,12	205,24		2,71E-45	1,49E-45
modelj	Fallow	5	4639,8	210,917		1,58E-46	8,74E-47
modelh	Roe	5	4640,11	211,224		1,36E-46	7,49E-47
Pine							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelq1	Intermediate+Moose	6	2518,2	0	****	1	4,43E-01
modeln1	Moose+Red+Fallow	7	2520,17	1,975	****	3,73E-01	1,65E-01
modelo1	Moose+Fallow	6	2521,22	3,022	***	2,21E-01	9,77E-02
modele1	Intermediate	5	2521,32	3,126	***	2,10E-01	9,27E-02
modelb1	Concentrate + Intermediate	6	2521,38	3,187	***	2,03E-01	8,99E-02
modelc1	Total density	5	2522,8	4,599	**	1,00E-01	4,44E-02
modell1	Total density + Richness + Intermediate + Concentrate	7	2523,02	4,82	**	8,98E-02	3,97E-02
modela1	total density + Richness	6	2524,08	5,883	**	5,28E-02	2,34E-02
modelj1	Fallow	5	2527,28	9,078	*	1,07E-02	4,73E-03
modelg1	Moose	5	2536,88	18,687		8,75E-05	3,87E-05
modeli1	Red	5	2538,83	20,637		3,30E-05	1,46E-05
modelh1	Roe	5	2541,74	23,547		7,71E-06	3,41E-06
modelf1	Concentrate	5	2542,63	24,436		4,94E-06	2,19E-06
modeld1	Richness	5	2544,44	26,247		2,00E-06	8,84E-07
Silver Birch							
Model	Variable	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelv2	Moose+Roedeer+Totaldensity	7	2908,53	0	****	1	2,34E-01
modelu2	Roedeer+Totaldensity	6	2908,59	0,066	****	9,68E-01	2,26E-01
modelk2	Moose + Roe + Red + Fallow	8	2909,17	0,645	****	7,24E-01	1,69E-01
modelo2	Moose+Roe+Fallow	7	2910,08	1,555	****	4,60E-01	1,07E-01
modelt2	Roe+Totaldensity+Richness	7	2910,17	1,639	****	4,41E-01	1,03E-01
models2	Moose+Roe+Totaldensity+Richness	8	2910,37	1,846	****	3,97E-01	9,28E-02
modelq2	Moose+Roe+Red+Fallow+Richness+Totaldensity	9	2910,99	2,465	***	2,92E-01	6,81E-02
modeln2	Moose+Fallow	6	2979,19	70,659		4,54E-16	1,06E-16
modelh2	Roe	5	2985,45	76,917		1,98E-17	4,64E-18
modelg2	Moose	5	2986,64	78,108		1,09E-17	2,56E-18
modell2	Total density + Richness + Intermediate + Concentrate	7	3001,17	92,638		7,65E-21	1,79E-21
modele2	Intermediate	5	3007,33	98,8		3,51E-22	8,21E-23
modelb2	Concentrate + Intermediate	6	3008,06	99,534		2,43E-22	5,69E-23
modela2	total density + Richness	6	3011,74	103,216		3,86E-23	9,02E-24
modelc2	Total density	5	3016,76	108,227		3,15E-24	7,37E-25
modeli2	Red	5	3020,83	112,299		4,12E-25	9,62E-26
modelp2	Concentrate+Fallowdeer	6	3027,95	119,419		1,17E-26	2,73E-27
modelj2	Fallow	5	3029,77	121,243		4,70E-27	1,10E-27
modelf2	Concentrate	5	3035,52	126,992		2,65E-28	6,20E-29
modeld2	Richness	5	3039,35	130,824		3,91E-29	9,13E-30

Pendular birch							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	Aic-weight
modelh3	Moose+Reddeer+Roedeer+Totaldensity+Richness	9	4987.44		0 ****	1	6,93E-01
modelw3	Reddeer+Fallowdeer+Totaldensity+Richness	8	4989.09	1,647	****	4,39E-01	3,04E-01
modelk3	Moose+Reddeer+Totaldensity+Richness	8	4998.56	11,125		3,84E-03	2,66E-03
modelf3	Moose+Reddeer+Richness	7	5019.46	32,018		1,12E-07	7,73E-08
modelp3	Richness+Concentrate	6	5031,21	43,768		3,13E-10	2,17E-10
modelB3	Total density + Richness + Intermediate + Concentrate	7	5032,53	45,092		1,62E-10	1,12E-10
modelq3	Moose+Reddeer	6	5120,35	132,914		1,37E-29	9,53E-30
modelk3	Moose + Roe + Red + Fallow	8	5123,52	136,078		2,83E-30	1,96E-30
modela3	total density + Richness	6	5161,98	174,54		1,26E-38	8,71E-39
modelg3	Moose	5	5183,72	196,283		2,39E-43	1,65E-43
modelh3	Moose+Fallow	6	5185,62	198,176		9,26E-44	6,42E-44
modelb3	Concentrate + Intermediate	6	5205,6	218,162		4,23E-48	2,93E-48
modelB3	Concentrate	5	5209,78	222,342		5,24E-49	3,63E-49
modeld3	Richness	5	5236,77	249,333		7,21E-55	5,00E-55
modelk3	Total density	5	5314,85	327,414		8,00E-72	5,54E-72
modelB3	Red	5	5317,76	330,325		1,87E-72	1,29E-72
modelk3	Intermediate	5	5333,95	346,507		5,71E-76	3,96E-76
modelh3	Roe	5	5334,98	347,536		3,42E-76	2,37E-76
modelj3	Fallow	5	5338,64	351,201		5,47E-77	3,79E-77
Rowan							
model	Variables	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelg4	Moose	5	1315,29		0 ****	1	1,93E-01
modelk4	Total density	5	1316,08	0,799	****	6,71E-01	1,30E-01
modelf4	Concentrate	5	1316,13	0,849	****	6,54E-01	1,26E-01
modelo4	Moose+Totaldensity	6	1316,85	1,569	****	4,56E-01	8,82E-02
modelh4	Moose+Reddeer	6	1317,19	1,906	****	3,86E-01	7,45E-02
modelp4	Moose+Richness	6	1317,27	1,987	****	3,70E-01	7,16E-02
modela4	total density + Richness	6	1317,77	2,482	***	2,89E-01	5,59E-02
modelb4	Concentrate + Intermediate	6	1317,85	2,568	***	2,77E-01	5,35E-02
models4	Totaldensity+Intermediate+Moose	7	1318,84	3,559	***	1,69E-01	3,26E-02
modelj4	Fallow	5	1318,89	3,608	***	1,65E-01	3,18E-02
modela4	Intermediate	5	1319,19	3,905	***	1,42E-01	2,74E-02
modelh4	Roe	5	1319,24	3,953	***	1,39E-01	2,68E-02
modelk4	Richness	5	1319,35	4,062	**	1,31E-01	2,54E-02
modell4	Total density + Richness + Intermediate + Concentrate	7	1319,57	4,289	**	1,17E-01	2,26E-02
modeli4	Red	5	1319,82	4,536	**	1,04E-01	2,00E-02
modelk4	Moose + Roe + Red + Fallow	8	1320,51	5,229	**	7,32E-02	1,41E-02
modelf4	Moose+Concentrate+Roedeer+Reddeer+Richness+Intermediate+Totaldensity	9	1322,13	6,842	**	3,27E-02	6,32E-03
Oak							
model	Variable	df	AIC	ΔAIC	Support	Relative Likelihood	AIC-weight
modelp5	Richness+Moose+Red	7	1691,57		0 ****	1	7,30E-01
modelo5	Totaldensity+Richness+Moose+Red	8	1693,56	1,99	***	3,70E-01	2,70E-01
modelk5	Richness+Moose+Red	6	1707,41	15,845		3,62E-04	2,65E-04
modelk5	Moose + Roe + Red + Fallow	8	1724	32,43		9,08E-08	6,62E-08
modelB5	Total density + Richness + Intermediate + Concentrate	7	1734,17	42,604		5,61E-10	4,09E-10
modelf5	Moose+Red	6	1737,03	45,461		1,34E-10	9,81E-11
modela5	total density + Richness	6	1739,3	47,732		4,32E-11	3,15E-11
modelg5	Moose	5	1750,73	59,161		1,42E-13	1,04E-13
modeld5	Richness	5	1753,57	62,002		3,44E-14	2,51E-14
models5	Richness+Reddeer	6	1754,47	62,908		2,19E-14	1,60E-14
modelh5	Roe	5	1775,04	83,479		7,46E-19	5,45E-19
modelB5	Concentrate	5	1777,54	85,97		2,15E-19	1,57E-19
modelb5	Concentrate + Intermediate	6	1779,5	87,93		8,06E-20	5,88E-20
modelk5	Total density	5	1780,28	88,718		5,43E-20	3,97E-20
modelj5	Fallow	5	1780,85	89,282		4,10E-20	2,99E-20
modeli5	Red	5	1782,53	90,969		1,76E-20	1,29E-20
modelk5	Intermediate	5	1784,14	92,572		7,91E-21	5,77E-21

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