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Influencing factors on red deer bark stripping on spruce: plant diversity, crop intake and temperature

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Influencing factors on red deer bark stripping on spruce: plant diversity, crop intake and temperature

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Abstract

Red deer (*Cervus elaphus*) is increasing in distribution and population density in several regions of Europe and may cause severe damage in commercial forestry and agriculture. Bark stripping is the main problem in forests, especially on Norway spruce (*Picea abies*). It has been suggested that an imbalance in the nutrient intake, and especially a diet composed of high amounts of easily-digestible macronutrients, such as crops, can lead to an increased urge to consume bark. Feeding on brassicas, for example oil seed rape (*Brassica napus*) might have this effect. My aim with this study is to investigate the relationship between intake of oil seed rape and bark stripping on Norway spruce by red deer during early spring. I did this by a controlled feeding experiment with four groups of captive red deer in southern Sweden. All groups were given spruce logs every week, while only two groups had access to fresh harvested oil seed rape plants. In addition, influence of air temperature and plant diversity was taken into account, and the deers' selectivity of different parts of oil seed rape plants was measured. My results show that red deer bark stripping can be considerable not only during periods of food shortage but also during spring green-up. There was no significant influence of oil seed rape on bark stripping. This was most likely due to overshadowing factors: air temperature was significantly positively related to bark intake, and red deer in enclosures with lowest plant diversity consumed the highest amount of bark. Finally, red deer showed a positive selection towards leaves, rather than stems, of oil seed rape, and this selection increased with the amount of oil seed rape provided (the dose). I conclude that to understand and to mitigate bark stripping by red deer on spruce several interactive effects must be considered, such as crop intake, plant diversity in the habitat and air temperature. Obviously, interactions between agriculture and forestry needs to be further studied, and more knowledge is needed before we can implement suggestions in wildlife management and forestry.

Keywords: Cervus elaphus, bark stripping, *Norway spruce, Picea abies*, forest damage, oil seed rape, *Brassica napus*, deer management, ungulates

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1. Introduction

Ungulates play an important role in forest ecosystems as they maintain heterogeneity and support diversity of flora and fauna in the forest landscape (Virtanen 2002, Apollonio et al. 2017). However, they also have big impacts on forest and agricultural production, something that together with an increase in numbers and spatial distribution throughout Europe and North America, will result in challenges for wildlife management (Milner et al. 2006, Apollonio et al. 2017).

Red deer (*Cervus elaphus*) is an ungulate species that is increasing in distribution and population density in several regions in Europe (Apollonio et al. 2010). Red deer can cause severe damage in commercial forestry and agriculture, foraging and trampling leading to crop loss are the main problems in agricultural fields (Jordbruksverket/SCB. 2015, Apollonio et al. 2017), while bark stripping is the main problem in forests (Gill. 1992, Gerhardt et al. 2013). Bark stripping can cause economic losses through reduced growth, fungal infestation, stem deformation and wood decay (Gill 1992, Verheyden et al. 2006). Red deer are known to eat bark from 21 tree species in Europe (Gill 1992, Verheyden et al. 2006) and Norway spruce (*Picea abies*) is one of the most affected species (Vospernik 2006, Månsson and Jarnemo 2013). Damage generally occurs during winter as a response to a shortage of alternative forage (Gill 1992, Welch et al. 1987, Ueda et al. 2002), however it has also been shown that red deer strip bark during spring and summer (Gill 1992, Ando et al. 2004, Ando et al. 2005). Bark stripping during spring can lead to extensive damage since the bark detaches easier from the stem (Jensen 1968, Gill 1992, Jarnemo and Månsson 2011).

Red deer are usually classified among the intermediate and mixed feeders, with a diet composed of grasses, sedges and woody vegetation (Hoffman 1989, Gebert and Verheyden 2001, Chevalier-Redor et al. 2001, Zweifel-Schielly et al. 2012). Their diet changes with seasons and is affected by seasonal fluctuations of forage quality and availability of food items (Hoffman 1989). Selectivity increases when food availability is higher, usually with a preference for fresh and nutritious plants (Emlen 1966, Pyke 1984, Ceacero et al. 2012, Lande et al. 2014)

Availability and selection of food items play an important role in the selection of habitat types (Langvatn and Hanley 1993, Lande et al. 2014). Furthermore, habitat type per se plays an important role in diet selection, since it influences the availability of food items (Hoffman 1989, Gebert and Verheyden. 2001, Zweifel-Schielly et al. 2012). Ungulate diet selectivity in general, and bark stripping in particular, is thus complex and operates on several spatio-temporal scales. For example, the level of bark stripping damage has been positively related to deer density at the scale of stands (Verheyden et al. 2006, Kiffner et al. 2008) and landscape (Jerina et al. 2008, Ligot et al. 2013). However, several studies have been unable to detect this relationship (Szederjei 1957, Völk 1999, Verheyden et al. 2006, Jarnemo et al. 2014). Furthermore, the effect of deer density on bark damage can be overshadowed by other factors, such as forest and landscape structure (Gill 1992, Völk 1999, Vospernik 2006, Jerina et al. 2008, Jarnemo and Månsson 2011, Jarnemo et al. 2014), tree characteristics (Gill 1992, Jiang and Ueda 2005, Vospernik 2006, Månsson and Jarnemo 2013), alternative forage (Gill 1992, Jarnemo and Månsson 2011,Welch et al. 1987, Völk 1999, Ueda et al. 2002, Nopp-Mayr et al. 2011, Jarnemo et al. 2014) and nutritional balancing (Ando et al. 2004, Saint-Andireux et al. 2009, Miranda et al. 2015).

Studies have shown that stems of Norway spruce, planted in even- aged monocultures with dense crown closure are highly affected by bark stripping, possibly due to the poor light availability, making alternative forage less available on the ground (Reimoser and Gossow 1996, Völk 1999, Verheyden 2006, Vospernik 2006, Jerina et al. 2008, Kiffner et al. 2008, Nopp-Mayr et al. 2011, Jarnemo 2016). The availability of alternative forage (e.g. dwarf bushes and herbs) is an important factor explaining the severity of bark stripping in a stand, as bark stripping levels often are higher when alternative forage is scarce (Welch et al. 1987, Völk 1999, Ueda et al. 2002, Nopp-Mayr et al. 2011, Jarnemo et al. 2014). The idea that deer consume bark in order to alleviate some long-term nutritional deficiency has led to different hypotheses (Gill. 1992, Ando et al. 2003, 2005). However, it has been difficult to prove that this is actually a driving factor. Instead of nutritional deficiencies per se driving the intake of bark by the deer, a growing pool of evidence suggests that nutritional balancing might be an important factor explaining bark stripping (Ando et al. 2004, Miranda et al. 2015, Saint-Andireux et al. 2009). Nutritional balancing is found to explain the food selection in a variety of taxonomic groups (Simpson et al. 2004, Raubenheimer et al. 2005, Robbins et al 2007, Felton et al. 2009, Rothman et al. 2011) and can be described as the altering of food intake to obtain a nutritionally balanced diet with the aim of reaching optimal performance (Westoby 1974, Raubenheimer and Simpson 1997). This can either be done by selecting nutritionally balanced food items or by combining two or more imbalanced food items that complement each other (Westoby 1974, Simpson and Raubenheimer 1997, Felton et al. 2009)

It has been suggested that when ungulates feed on forage rich in easily-digestible macronutrients, for example crops, they need to compensate by increasing their intake of roughage to ensure proper rumen function (Faber 1996, Ando et al. 2004, Saint-Andireux et al. 2009, Felton et al. 2016, Zweifel-Schielly et al. 2012, Miranda et al. 2015). For example, ingestion of too much carbohydrates may lead to a shift in the rumen pH, potentially resulting in ruminal acidosis (Keunen 2002). In a feeding experiment with captive moose, Felton et al. (2016) showed that moose compensated for the imbalance in nutrient intake by increasing their consumption of twigs. This response was not due to deficiencies of nutrients, rather it was a result from the imbalance in their nutrient intake.

Similar findings have been done by Miranda et al. (2015), who found that red deer provided with nutrient rich supplementary feed increase their intake of woody vegetation. Additional support to this on a larger scale has been found by Jarnemo et al. (2014) and Jarnemo and Månsson (2011) who found that damage levels were higher in agricultural landscapes compared to forest landscapes, possibly due to red deer' intake of crops increasing the urge to consume bark.

The process of nutritional balancing and its effects is therefore likely to be of high relevance when trying to develop and improve the management of ungulate species and at the same time maintaining a productive forestry and agriculture. For example, in Sweden, hunter and forest owners sometimes suggest that oil seed rape (*Brassica napus*) may lead to increased bark stripping levels in Norway spruce production stands (Jarnemo 2016). Oil seed rape seems to be attractive to red deer (Jarnemo 2016) and is a nutritious crop with relatively high protein content and high digestibility (Spörndly 2003). It has also been found that brassicas, including oil seed rape, could generate lower pH in the rumen (Barry 2013).

One can therefore assume that a large intake of oil seed rape would affect rumen function leading to a need for compensation and an increased urge for fibre and roughage according to the nutrient balancing hypothesis. Here, I report a study with the aim of investigating the relationship between the intake of oil seed rape and bark stripping on Norway spruce trees by red deer. I did this by conducting a controlled feeding experiment with captive red deer in southern Sweden. I predict that red deer will increase their intake of bark if provided with oil seed rape, and that this is a function of dose. I also predict that when provided with high amounts of oil seed rape, red deer will become more selective, with a preference for the most nutritious and fresh part of the plant. Finally, based on the knowledge about bark being less adhesive to the stem during spring, implying that red deer will be able to detach greater amounts of bark at every occasion, I predict that bark intake will increase with higher temperature, using temperature as a measure of season.

2. Materials and methods

2.1 Ethical considerations

The study was granted an ethical permit by the Swedish board of agriculture. The owner of the land gave permit to conduct the study at this site.

2.2 Study area and study design

The study was carried out between 20 March – 21 May on a private red deer farm in southern Sweden (56°04'26.9''N 13°18'58.0''E). The daily average temperature in the region during March – May ranges between minimum -2.2 and maximum 18.6 degrees (SMHI Klimatdata 2018). In total, 40 red deer were allocated to four enclosures with ten red deer in each enclosure (three adult males, six adult females, and one calf) (figure 1). Enclosure 1, 2, and 4 had a size of 5.0 ha while enclosure 3 had a size of 7.5 ha. Due to a sudden death of one calf in enclosure 1 during the first week, this group only consisted of nine individuals throughout the rest of the experiment.

Each enclosure had ten spruce logs systematically distributed in two groups of five (figure 2 and 3). New logs were harvested at the end of each week and placed in the enclosures every Monday, replacing the old ones that were removed from the enclosures. The logs (length 3 meters) were harvested within the same planted Norway spruce stand and had an age of 25 years. Trees of this particular age was chosen since it has been shown that they are most vulnerable to bark stripping (Sjöström 1961, Ahlén 1965, Lavsund 1968). The logs were placed firmly upright in 1 m deep holes prepared with plastic tubes. Diameter and exact height of each log was measured at the beginning of every week. Height was measured from the ground to the top of the log.

After snow melt in April, the animals had access to natural forage available in the enclosure as well as silage. However, feeding with silage stopped 10th of April. Habitat type in the four enclosures was grassland with occurrence of occasional trees and small areas of water-logged ground in enclosure 3 and 4 (vegetation survey below).

Figure 1. The private red deer farm with placement of the four enclosures

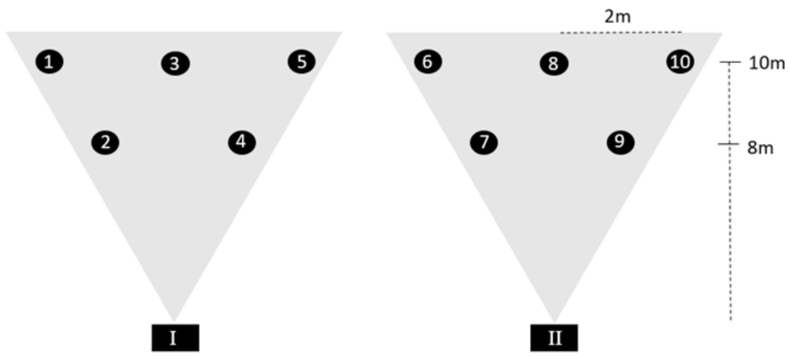

Figure 2. Systematic placement of the ten spruce logs in the enclosures seen from above, indicated with numbers. The reason for this placement was due to camera traps used in another part of the project, indicated by squares labelled I and II

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Figure 3. Placement of one spruce logs in one of the enclosures. On these logs bark has been peeled off, exposing large areas of the wood. Another type of bark stripping is gnawing, where smaller parts of bark is removed (Photo: Anders Jarnemo)

The experiment had two phases, one control phase and one treatment phase.

Phase 1: – control phase; 3 weeks.

During this phase the groups had only access to spruce logs as a complement to the natural forage.

Phase 2: – treatment phase; 3+3 weeks.

During this phase, two of the enclosures (number 2 and 4, hereafter called treatment groups) were provided with fresh oil seed rape plants. The other two groups (number 1 and 3, hereafter called control groups) were control groups and only had access to spruce logs. The control and treatment groups were randomly chosen.

During the first three weeks of phase 2 the treatment groups were given low dose of oil seed rape. I defined low dose as 10% of a red deer's estimated daily feed intake on a dry matter (dm) basis. The normal daily food intake for an average red deer during winter time was estimated to be 2.6 kg dm,based on the assumption that 1.8 red deer consume the same amount of food as 1 moose originating from the concept of animal equivalence (Vallentin, 2001) and that one moose consume 4.7 kg dm during winter (Persson et al. 2000). A 10% dose therefore represented 6 kg of fresh oil seed rape plants per group (600 g wet weight per individual), based on measurements of the oil seed rape plants containing 42% dm. I, together with other members of the team collected, dried and weighed oil seed rape plants to get a continuous measure of the gradually increasing proportion of water in the plants during the study period (% dm changed from 42 to 18 during the three weeks). I adjusted the total wet weight of supplied plants accordingly to make sure that the daily dose approximated 10% on a dm basis, all through that experimental phase.

During the last three weeks of phase 2 the treatment groups were given high dose of oil seed rape. I defined high dose as 70% of a red deer' daily feed intake on a dm basis, which represented 100 kg wet weight per group (10 kg wet weight per individual (at 18 % dm in oil seed rape plants)). To avoid potential complications due to fast shifts in diets (Keunen et al. 2002), the high dose treatment was gradually introduced during the first week until the full dose was reached on day 8. The total wet weight of supplied plants was from then on not increased above 100 kg, despite a continued (but slower) increase in water content, due to logistical reasons. The actual amount consumed biomass, in terms of dm intake by the deer, was calculated based on our measured values of % dm.

2.3. Spruce logs, bark sampling and calculation of bark intake

The proportion of bark consumed on each spruce log was measured every day. The log was divided into 30 cm sections starting at 30 cm above ground. For each 30 cm section the percentage of missing bark was estimated.

To get a reliable estimate of how much bark that was actually eaten I accounted for other types of damage. Bark damage was categorized into mechanical damage (chainsaw during logging), fraying, gnawing and peeling. Bark stripping is used to define both gnawing and peeling (figure 3), i.e. a sum of all bark eaten. Mechanical damage caused by the chainsaw during logging was marked on the new logs when placed in the enclosures, to assure that this damage type was not later measured as damage caused by the animals. To account for fraying damage caused by antlered male red deer I weighed bark pieces that had fallen to the ground. At the end of every week I also removed and weighed bark hanging from the log, this was later subtracted from the amount missing bark of that particular log. If one log was 90% debarked before the end of the week I removed this log and replaced it with a new one.

One log per week was kept and used as a sample log to estimate weight per area unit. From this log I peeled off the bark from an area of 50 x 20 cm that was later dried and weighed (wet weight and dry weight). These samples gave a measurement of weekly dry weight in grams per 1000 cm^2 and could later be used to transform our field measurements in % missing bark of each log to consumed biomass in gram. Biomass consumed was calculated in the following way. First, the total area of the log was calculated by multiplying the circumference with the height of that log. To get an estimate of the area that was actually available for bark stripping by deer, I subtracted the area of mechanical damage (caused by the chain saw) from the total area of that log. The next step was to calculate the bark area per log that was eaten by deer. This was done by multiplying the percentage of bark stripping (measured in the field) with the available area. Dry weight in grams per 1000 cm^2 was converted into dry weight gram/cm^2 and multiplied with the damaged area. Finally, bark that had been peeled from the log but not eaten was subtracted.

2.4 Oil seed rape measurements

Every day I harvested fresh oil seed rape plants, on the same field, with a hedge cutter when plants were small and a clearing saw when plants had grown larger, all according to the already decided feeding plan (appendix 1). The plants were put into bags and weighed. After harvest I placed the plants in two feed troughs in the enclosures of each treatment group. During the high dose phase, one more feed trough was used since there was not room for all the plants in two troughs per group.

Each day I collected and weighed the leftover plants from the previous day, before providing the new plants. The difference in weight between the days was defined as the amount of oil seed rape eaten in gram wet weight.

To account for evaporation due to sun exposure I placed a sample of oil seed rape plants outside the enclosures. The total weight of the pile corresponded to the weight given to the animals. Every day the pile was weighed before it was replaced by a new one. The difference in weight from day 1 to day 2 gave us an estimate of how much water had disappeared from the plants over 24h and was later subtracted from the amount oil seed rape eaten by the groups the corresponding 24h. This calculation did not take into account the fact that the plants could have been eaten before 24 hours had passed.

2.5 Oil seed rape sample

Every day I took a sample of fresh oil seed rape plants during harvest that was later dried and weighed (wet weight and dry weight). All samples were separated into leaf and stem before drying, to achieve data on proportion of biomass for the different parts. Daily data on water content allowed for more exact estimations post-hoc of the groups' intake of oil seed rape in terms of dm. To assess selectivity, samples of leftover oil seed rape plants were collected from each enclosure. These samples were also separated into leaf and stem as well as dried and weighed.

2.6 Air temperature

To test whether temperature influenced bark stripping I obtained air temperature data (° C recorded every hour) from a weather station run by the Swedish Meteorological Service located nearby (Klippan 8 km). Based on those data I calculated the daily mean air temperature per week during the study period.

2.7 Potential confounding factor: plant diversity

While setting up the experiment during the winter I estimated all four enclosures to be homogenous and similar to each other in terms of vegetation cover and diversity. However, to account for any possible difference between enclosures in plant diversity, and the effect of such variation on the deer' food selection, I conducted a vegetation survey at the end of the experiment when the growing season had begun (16 – 20th of May). With the pre-conditions of having different sized enclosures and with the aim of obtaining a good sampling cover in each enclosure, I decided to sample different number of plots in each enclosure.

A grid (100 x 100m) was placed over the enclosures and the nodes were used to decide the number of plots to be surveyed in each enclosure as well as the placement of the 1 x 1m sample plots. Each node in each enclosure was labeled with a number using the grid. Nodes were then randomly selected based on the decided number of plots. The randomly selected nodes were found using a compass and with the help of the grid. If a selected node was on the border of the enclosure, it was used in the survey. 9 plots were distributed in enclosure 1 and 2, 12 plots in enclosure 3 and 8 plots in enclosure 4. In each sample plot, plant species present was identified, and its percentage cover was measured.

2.8 Statistical analysis

To test if there was a difference in bark intake between the groups during the control phase I analyzed the data using a one-way ANOVA. The response variable was log transformed to attain normalized and homogenous residuals (Zuur et al. 2009). Similarly, possible difference in bark intake between the groups during the treatment phase was analyzed using a one-way ANOVA. The ANOVAs were conducted using function aov in stats package in R.3.4.1. I performed a Tukey post-hoc test to check for differences between the groups of red deer using the function ghlt in package multcomp in R.3.4.1.

2.8.1 Effect of oil seed rape

Air temperature was highly correlated with oil seed rape intake (corr. coeff = 0.85, Pearson correlation calculated in R.3.4.1). Furthermore, since oil seed rape intake and dose treatment are similar variables and the fact that dose treatment increased with temperature, the assumption was made that the correlation would be strong between dose treatment and temperature as well. I was therefore restricted to only using oil rape seed intake and dose treatment as explanatory variables in my models.

I used linear mixed effects models (LMEs, function lme in nlme package), enclosure was used as random factor to account for repeated measurements in each enclosure. The transformations square root and log were used to obtain normalized and homogenous residuals (Zuur et al. 2009). Four different LMEs were carried out, all with bark intake (daily average in gram per week) as response variable.

To test whether there was a difference in red deer bark intake (daily average in grams per week) between treatment groups and control groups I used treatment as a factor with two levels (no oil seed rape = control, oil seed rape = treatment) as an explanatory variable. The response variable was log transformed.

To test whether there was a difference in bark intake between the different dose treatments, I used treatment as a factor with three levels (no oil seed rape = control, low dosage of oil seed rape = low, high dosage of oil seed rape = high) as explanatory variable. The response variable was square root transformed.

Furthermore, to test the possible influence of oil seed rape as a quantitative variable, I used the average daily intake in grams consumed per week as explanatory variable. In this model, only the two treatment groups were used. The response variable was log transformed.

Finally, to test influence of air temperature I used average daily temperature ° C per week as explanatory variable. Due to the correlation between oil seed rape intake and temperature I was restricted to only using the control groups for this analysis. To obtain more variation in temperature data I used a greater span of data, including the three first weeks of the study as well. The response variable was log transformed.

2.8.2 Plant diversity

Possible difference in plant diversity between the four enclosures was measured by using Shannon Wiener index, species richness (number of species in each enclosure), and species accumulation curves.

Shannon Wiener index was calculated using diversity function in VEGAN package in R.3.4.1. Since the Shannon Wiener index requires the same number of plots, the extra plots in some enclosures were randomly eliminated. To get one index per group, the average percentage cover of each species per group was used in the calculation. Species richness and species accumulation curves were calculated in Excel 2016. For the latter I used occurrence of species in each plot (present = 1, non-present = 0). For each new plot the number of new species were added, giving the accumulated number of species in each enclosure.

2.8.3 Relative difference in bark intake between weeks

To estimate whether control groups and treatment groups changed their bark intake correspondingly between weeks during the treatment phase, the relative difference in bark intake between weeks was calculated using this equation:

$$\mathrm{W}_b - W_a = \mathrm{diff}_{b-a}$$

$$\mathrm{diff}_{b-a}/\mathrm{W}_a = \mathrm{cf}$$

$$\mathrm{cf} * 100 = \%\ \mathrm{difference}$$

with W_a being average daily bark intake for week a and W_b being average daily bark intake for week b. The change factor (cf) was calculated by dividing the difference in gram bark intake between the two weeks ($\mathrm{diff}_{b\text{-}a}$) with W_a. Finally, to attain the difference in percent, cf was multiplied by 100.

2.8.4 Selectivity

To determine selection between leaves and stem of oil seed rape and asses temporal differences in how the red deer in the treatment groups selected, I had comparable data from the four treatment groups. Based on this a resource selection ratio (Ŵ) was calculated using this equation:

$$\hat{\mathrm{W}} = \frac{0i}{pi}$$

with 0_i being the proportion of used resource *i*, and p_i , being the proportion available resource *i* (Ceacero et al. 2012, Manly et al. 2002). Due to lack of necessary data for some weeks, I was restricted to only use four weeks of data instead of six weeks for this analysis (two for low oil rape seed treatment, and two for high). Since I did not have any data on evaporation for leaves and stem separately, I assumed the evaporation to be the same.

3. Results

3.1 Bark intake during the control phase

There was no significant difference in bark intake between the four groups of red deer during the control phase (ANOVA, p-value = 0.1, F-value = 4.0) (figure 4). This implies that the pre-conditions were the same for control and treatment groups at the start of the experiment.

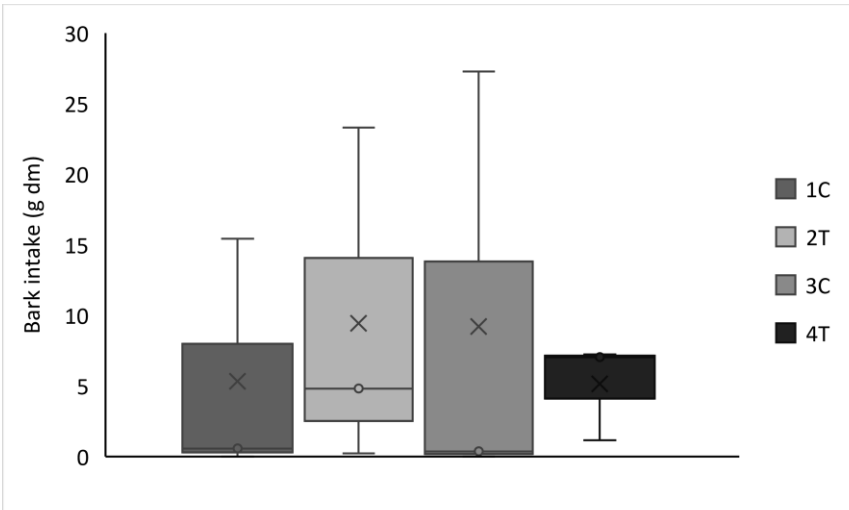

Figure 4. Daily average bark intake per week in the four red deer groups during the control phase. C and T represents whether the group later in the experiment was a treatment group or control group. Median is indicated by the vertical line dividing the box into two parts. Average bark intake is indicated by X in the center of the box. The top end of the box represents the upper quartile, while the lower end of the box represents the lower quartile. The lines (whiskers) above and below the box represents the max and min values in the data set.

3.2 Difference in bark intake between groups during the treatment weeks

There was a significant difference in bark intake between the four groups of red deer during the treatment weeks (ANOVA, p-value = 0.0, F-value = 8.6). Group 1C consumed the greatest amount of bark, while group 3C consumed on average the lowest amount of bark (figure 5). Group 4T and 3C had the lowest variation among days (figure 5). The post hoc test showed a significant difference between group 1 and 3 (p-value = 0,0, z-value = -2,7), none of the other groups were significantly different from each other.

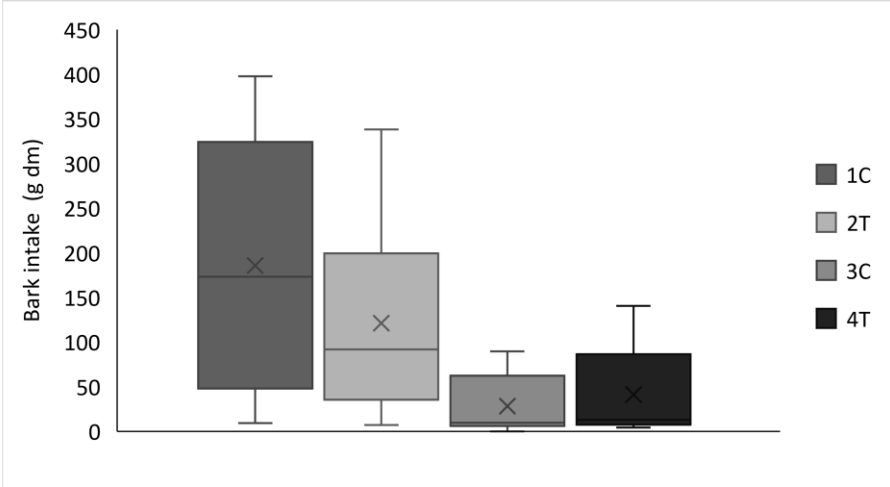

Figure 5. Daily average bark intake per week in the four red deer groups during the treatment phase. C and T represents whether the group was a treatment group or control group. Median is indicated by the vertical line dividing the box into two parts. Average bark intake is indicated by X in the center of the box. The top end of the box represents the upper quartile, while the lower end of the box represents the lower quartile. The lines (whiskers) above and below the box represents the max and min values in the data set.

3.3 Relative difference in bark intake between treatment weeks

There was a relatively large increase in bark intake between the second and third week of low-dose treatment, and this increase was higher in the treatment groups than the control groups (figure 6). During the last weeks of the experiment the relative differences are similar between the treatment and control groups (figure 6).

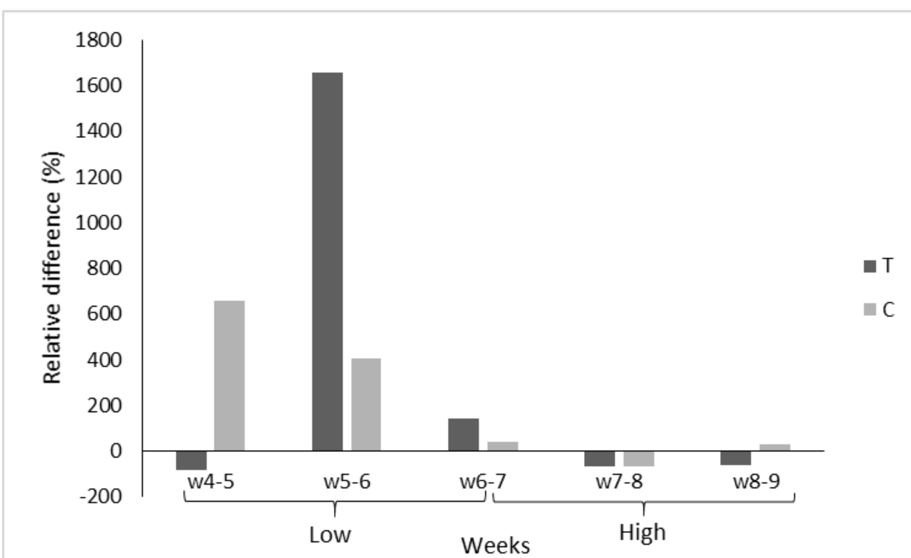

Figure 6. Relative difference in bark intake (daily average per week in g dm) between weeks of the treatment (T) and control (C) groups of red deer. The three different treatment phases are indicated with labels control, low and high on the x-axis

3.4 Bark intake over the entire study period

There was an increase in bark intake for all deer groups starting at the end of April and decreasing in mid-May (figure 7). The peak coincided with the high dose treatment. However, the two control groups also increased their intake during the same period (figure 7).

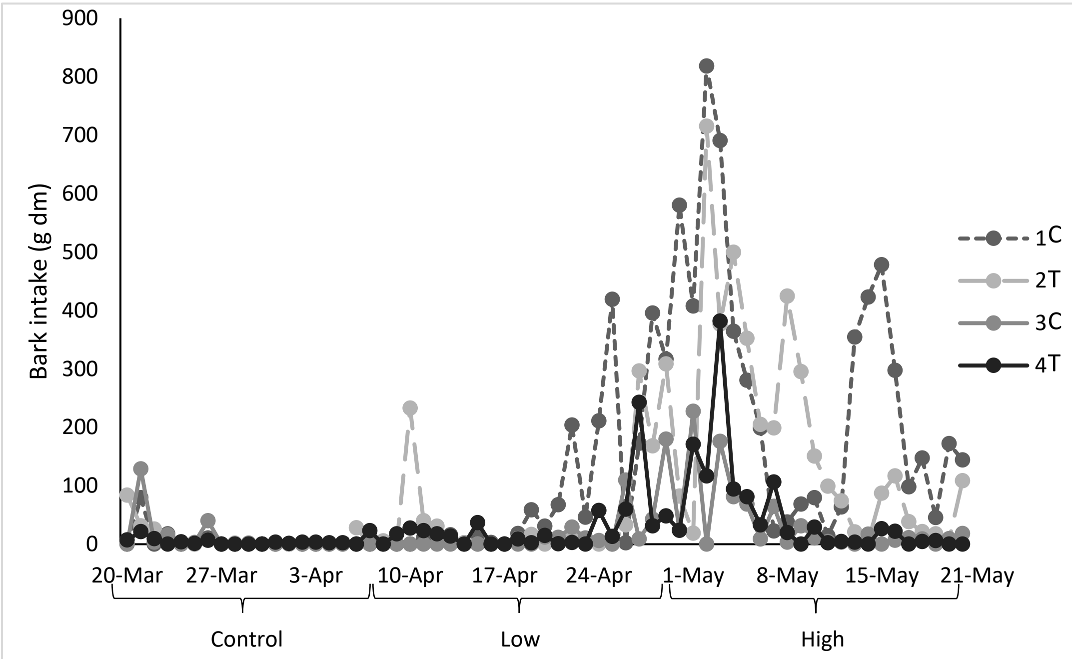

Figure 7. Daily bark intake of the four different red deer groups over time. C and T represents control groups and treatment groups respectively. The different treatment phases are indicated with labels control, low and treatment on the x-axis.

3.5 Influence of oil seed rape on bark intake

3.5.1 Oil seed rape vs. no oil seed rape

I found no significant difference in bark intake between control groups and treatment groups (table 1, figure 8a).

Table 1. *Model parameters from LME for the probability of bark intake against control or treatment.*

	Estimate	SE	t	p
Control	3.7	0.7	5.6	0.0
Treatment	0.0	0.9	0.0	1.0

3.5.2 Effect of dose treatment

I found no significant effect of dose treatment on the bark intake by red deer (table 2, figure 8b).

Table 2. *Model parameters from LME for the probability of bark intake against the three different treatments.*

Treatment	Estimate	SE	t	p
Control	8.3	2.5	3.4	0.0
Low	-2.5	3.8	0.3	0.5
High	1.0	3.8	-0.7	0.8

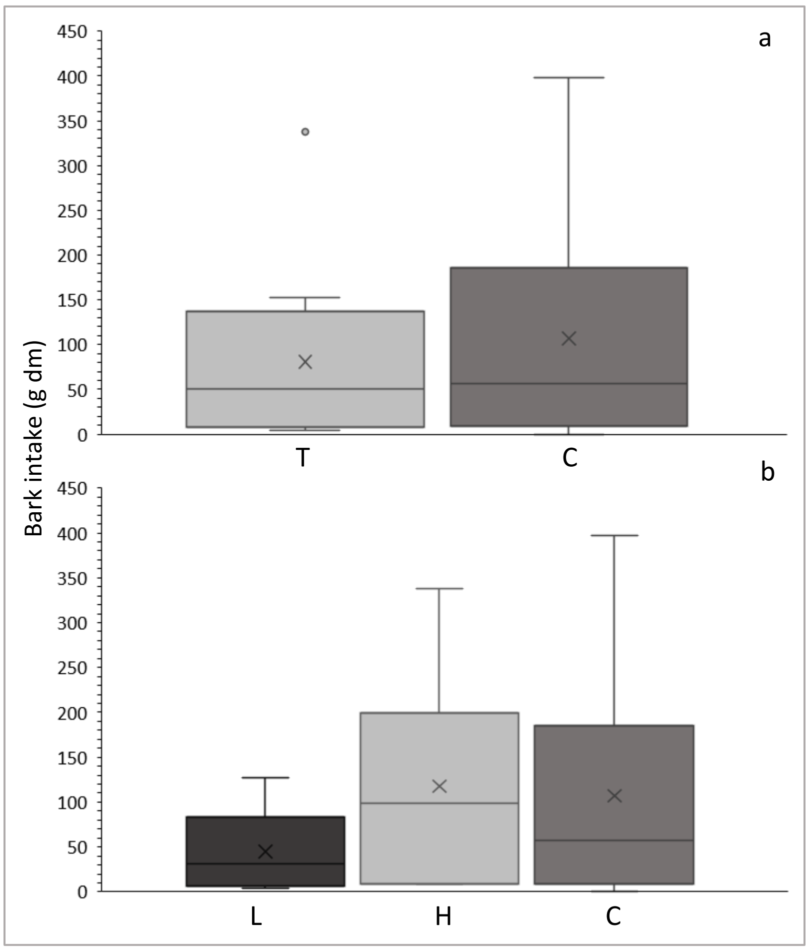

Figure 8ab. Daily average bark intake per week consumed by red deer groups in the experiment. a) bark intake in treatment groups and control groups; b) bark intake in the three different dose treatments used in the experiment, low dose (L), high dose (H) and control (C). Median is indicated by the vertical line dividing the box into two parts. Mean bark intake is indicated by X in the center of the box. The top end of the box represents the upper quartile, while the lower end of the box represents the lower quartile. The lines (whiskers) represents the max and min values in the data set.

3.5.3 Relationship between bark intake and amount of consumed oil seed rape

There was no significant relationship between oil seed rape intake and bark intake, when measuring how much oil seed rape the red deer actually consumed (LME, t-value = 0.27, p-value = 0.8, estimate = 0.0). There is thus no pattern of potential influence by oil seed rape dose in bark intake (figure 9).

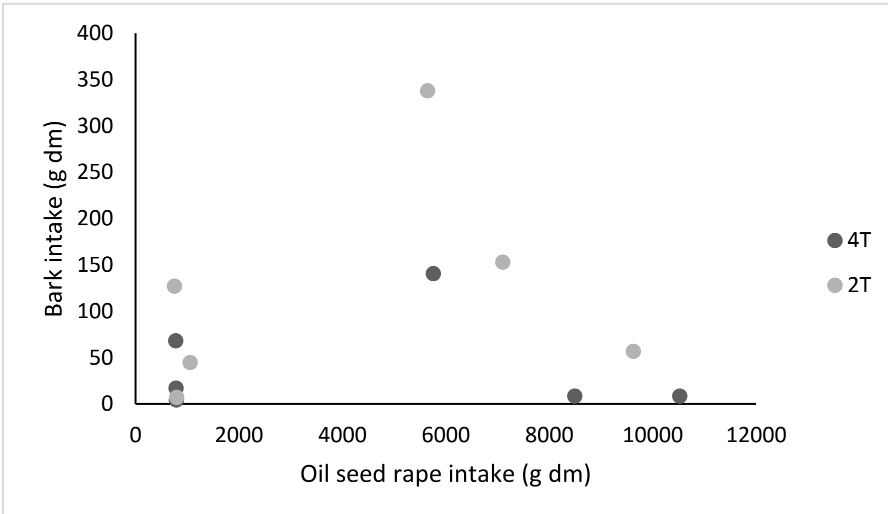

Figure 9. Relationship between daily average bark intake per week, and daily average oil seed rape intake per week in g dm, consumed by red deer in the two treatment groups

3.6 Relationship between air temperature and bark intake

There was a significant positive relationship between temperature and bark intake for the two control groups of red deer over the entire study period (LME, t-value = 2,31, p-value = 0.03, estimate = 0.19). The data indicate a threshold effect around 9C° with an increase in bark intake (figure 10)

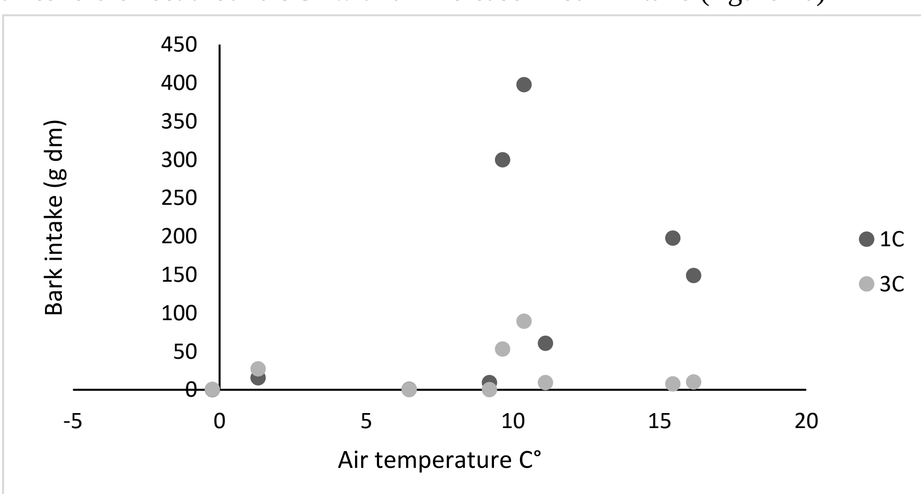

Figure 10. Relationship between daily average bark intake per week in the two control groups of red deer and the daily average air temperature (C°) per week.

3.7 Plant diversity

Plant diversity differed between the four enclosures with 3 and 4 being most diverse, and 1 and 2 being least diverse. Species richness was approximately twice as large in enclosure 3C and 4T as in enclosure 1C and 2T (figure 11a). Enclosure 3 had the highest species richness while enclosure 1 had the lowest (figure 11a). Shannon Wiener diversity index is larger in enclosure 3C (2.56) and 4T (2.59) compared to 1C (1.54) and 2T (1.64) (figure 11b). Species accumulation curves also show that enclosure 3 and 4 are most diverse, while enclosure 1C and 2T are least diverse (figure 11c). This is represented both in terms of steepness and length of the curve (figure 11c). Furthermore, red deer in enclosures with lower diversity, consumed higher amounts bark.

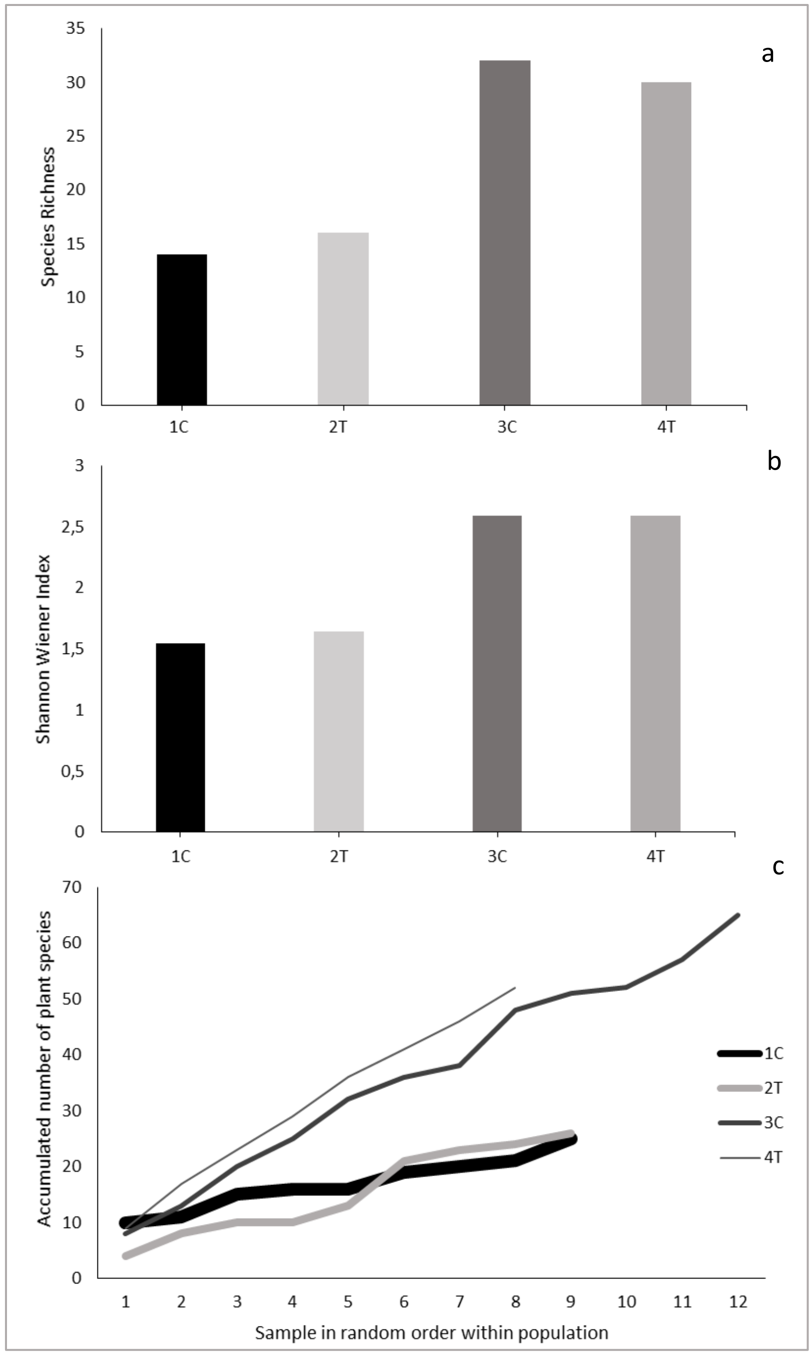

Figure 11abc. Different measures of plant diversity in the four enclosures used in the experiment. Figure a represents species richness in the four enclosures; figure b Shannon Wiener diversity index calculated for the four different enclosures. Finally, figure c represents species accumulation curves of the four different enclosures. Thickness of the line represents bark intake. C and T indicated control groups and treatment groups respectively

3.8 Selection between leaves and stem of oil seed rape

There was a difference in selection ratio between leaves and stem of oil seed rape plants, with a higher selectivity for leaves over time and with increased dose (figure 12).

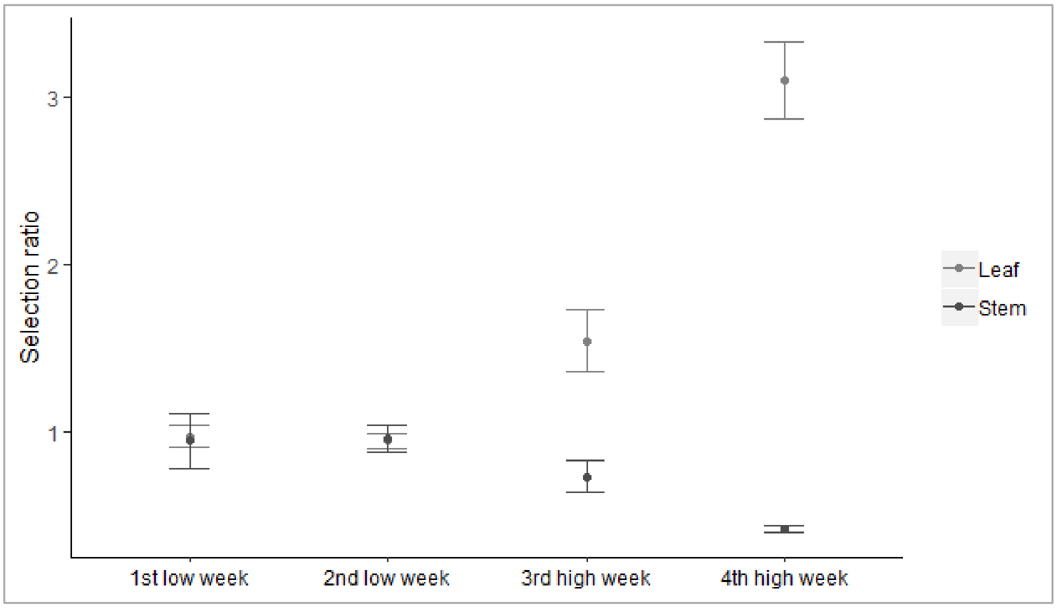

Figure 12. Selection ratio of leaf and stem of oil seed rape plants, over weeks and with increased dose. Dose of oil seed rape given to the red deer and week is represented by the label on the x-axis. Error bars represent SE, being variation among days.

4. Discussion

My results indicate that the red deer bark stripping on Norway spruce is influenced by several factors, and that mainly factors dictated by seasonal changes seems to have a large influence on bark stripping behaviour.

There was no significant influence of oil seed rape on bark stripping, something that contradicts other studies showing that an intake of highly nutritious forage with easily digestible macronutrients will lead to an increased intake of roughage (Faber 1996, Ando et al. 2004, Saint-Andireux et al. 2009, Zweifel-Schielly et al. 2012, Miranda et al. 2015, Felton et al. 2016). The treatment groups increased their bark intake with 163% from low dose weeks to high dose weeks, however, there was no relationship between the actual amount of eaten oil seed rape and bark intake when not taking into account the temporal aspect, being change in bark intake over weeks. I can therefore conclude that factors dictated by seasonal changes most likely had a stronger influence on bark stripping and overshadowed the effect of oil seed rape.

One such factor could have been air temperature. I found a significant positive relationship between bark intake and temperature in the control groups. There was also a sudden increase in bark intake starting at the end of April. These results differ compared to findings from other studies suggesting that bark intake is worse during winter when temperature is low, with the explanation that bark serves the role as shortage food when alternative forage is scarce (Welch et al. 1987, Gill 1992, Ueda et al. 2002). However, my results support other studies showing that intensive bark stripping can occur during spring and summer (Ando et al. 2004, Ando et al. 2005, Jiang et al. 2005). One potential explanation for the relationship between bark intake and temperature is the dehardening process in spruce. During spring, cells responsible for secondary growth in trees starts to expand (Widén and Widén 2018, Evert and Eichhorn, 2012). This expansion stimulates decomposition of surrounding nutrient transporting cells, increasing the availability of nutrients, such as sugar (Widén and Widén 2008). This process decreases the adhesiveness of the bark to the stem, making it possible for red deer to peel off large chunks of bark and extract the inner bark, usually defined as bark peeling. Bark peeling leads to large bare portions of the stem, resulting in very extensive damage (Jensen 1968, Gill 1992). The dehardening process has been shown to start during March to April in southern part of Sweden (during period 1961-1999) (Jönsson et al. 2004) and requires five consecutive days with a mean temperature above five degrees (Cº) to initiate (Jönsson et al. 2004). Something that corresponds well to the sudden outbreak of bark stripping that I found.

Krogell et al. (2012) found that inner and outer bark of Norway spruce differ considerably in chemical composition, with the inner bark containing more carbohydrates and larger amounts of glucose. It has also been found that intensity of bark damage in spring was positively related to the seasonal changes in nutritional quality of bark (Jiang et al. 2005). These findings suggest that the increased bark intake during spring also has to do with the access to inner bark containing preferred nutrients and a change in nutrient composition of bark.

An additional factor influencing bark stripping during spring might be the start of plant phenology, resulting in red deer switching their diet. Something that is strongly influenced by temperature (Evert and Eichorn 2012). This possible influence has been discussed by several authors. Ando et al. (2004) found no seasonal change in physical bark properties but instead suggested that the intense bark stripping during spring and summer had to do with seasonal changes in the content of the main forage. More precisely, they found that the peak in bark stripping during spring coincides with corresponding increased levels of digestible nutrients and crude protein in red deer's main forage. The same pattern has been found by other authors, suggesting that a sudden increase in bark stripping during spring coincides with a change to a more nutritious diet resulting in an increased urge for roughage (Gill 1992, Faber 1996).

Similar findings regarding the effect of have been done by Månsson and Jarnemo (2013) who found that bark peeling was much more common in the study site in southern Sweden, with a dominant habitat type of agricultural land cover, compared to the study site further north with a dominant habitat type mainly covered by forests. Red deer in the southern study site were found to use arable land to a higher extent than red deer in the northern site (Allen et al. 2014). One possible reason for the difference regarding peeling could be the difference in diet composition between the sites, with a diet composed of large amounts of highly nutritious crops in the southern study site, increasing the urge to consume bark. This implies that spruce stands in areas with large amounts of agriculture might be more susceptible to extensive damage during spring than stands in a forest landscape.

It can be concluded that the sudden increase in bark intake during April-May observed in my study might be influenced by several different factors all driven by temperature. Factors such as bark adhesiveness to the stem, differences in nutritional value of bark, and a switch to a more nutritious and digestible diet increasing requirements of roughage. Therefore, together with earlier findings my result implies that there is an active behavior towards consuming bark during spring.

A relationship between diet composition and bark stripping is further indicated by my findings regarding plant diversity. Both species richness, Shannon Wiener index, and the species accumulation curve shows that available plant diversity might be negatively related to bark damage. My results show that bark intake is similar between group 1 and 2 and between group 3 and 4, a pattern that coincides well with similarities in plant diversity. These similarities are not only shown graphically but can be further supported by the fact that there was no significant difference in bark intake between enclosure 1 and 2, nor between enclosure 3 and 4. It was only enclosure 1 and 3 that differed significantly in their bark intake, these two enclosures also had the largest difference in plant diversity. Therefore, I can conclude that plant diversity may be a strong factor explaining bark stripping behavior in our study. However, since we did not measure what plants that were actually consumed in the enclosures, in addition to the provided oil seed rape, one cannot draw any conclusions about red deer diet composition in relation to bark consumption. However, it is reasonable to assume that red deer restricted to an area with very low plant diversity and less ability to compose a mixed diet will most likely have a narrow and unbalanced diet that may result in an increased urge for an additional food source, the bark, based on the nutritional balancing hypothesis (Westoby 1974, Simpson and Raubenheimer 1997, Felton et al. 2009, Felton et al. 2016). Moreover, my results also lend support to findings regarding the importance of availability of alternative forage to prevent bark damage (Jarnemo et al. 2014). These findings are significant since there are signs of decreased diversity and abundance of important forage species in Swedish forests today (Hedwall et al. 2013) and according to my findings this might lead to an increased damage level.

4.1 Caveats

Being restricted to only four groups of red deer, leaving us with only two replicates, most likely had an effect on my results. Even though I cannot say if an increased number of replicates would lead to a stronger influence of oil seed rape, one can conclude that it would give better pre-conditions to detect a possible influence.

Having designed the study in a way that prevented oil seed rape and temperature to correlate with each other would have given me a better opportunity to tell which variable that explained the variation in bark intake the best. This could have been done by alternating the doses simultaneously, so giving high dosage to one group, simultaneously giving low dosage to the other group. This study design was the original design, but due to logistical reasons we could not continue with this design.

Due to snowy weather conditions, the start of the experiment had to be postponed, resulting in the dehardening process starting before the end of the experiment, something that might have had an effect on my results since as mentioned above, the dehardening process seems to have a large influence on bark stripping.

One aspect that possibly overshadowed the influence of oil seed rape was individual behavioral differences and social rank between groups. The social rank and the behavior of dominant hinds has been shown to be important, especially in feeding systems (Ceacero et al. 2012). I observed that behaviour differed between groups. Some groups were led by curios and brave hinds, while other groups were led by cautious hinds. Groups led by curious hinds seemed to have a more courageous approach towards the novel food items, the oil seed rape and the spruce logs, while groups led by suspicious dominant hinds seemed to be more restricted and skeptical**.** Ceacero et al. (2012) found that social rank was positively related to the amount of time spent feeding. Therefore, it is possible that these differences in behavior may have shaped the feeding behavior of the groups in my study and might explain why group 1 ate such a high amount of bark compared to the other groups**.**

I found a difference in plant diversity between the four enclosures, but I was not able to test this statistically due to lack of replicates. Since we conducted one vegetation survey at the end of the study I cannot rule out the possibility that red deer themselves drove species community composition differently in each enclosure. However, based on background knowledge stating that enclosure 1 and 2 were earlier used as fertilized cropland, while enclosure 3 and 4 were used as pastures for cattle, I assume that diversity is most likely driven by difference in former land use rather than red deer herbivory. I believe that this difference in land use may be an important factor driving differences in plant diversity and indirectly bark stripping behavior. I assume that forage on earlier fertilized cropland will most likely be less diverse and possibly also contain high amounts of nutrients due to the fertilization, and thereby increasing the urge to consume bark to reach a balanced diet, while forage on earlier pasture land will most likely be more diverse making red deer able to compose a more mixed and balanced diet.

4.2 Selectivity for leaves of oil seed rape plants

The red deer in the experiment showed a positive selection towards leaves of oil seed rape, Additionally, they showed a stronger selectivity towards leaves with increasing dose of oil seed rape. This is in concordance with other studies suggesting that red deer are selective, and more so with increased amount of forage (Ceacero et al. 2012, Zweifel-Schielly et al. 2012, Emlen 1966, Pyke 1984). According to optimal foraging theory (OFT) and the associated idea of herbivores' food choice being driven by energy maximization, selectivity will increase when animals are offered high abundances of high-quality food, and more so, with a higher selectivity for the food with best quality in terms of nutrients (Emlen 1966, Pyke 1984).

Since analyzing the nutritional content of different parts of the plant was beyond the scope of this study, I cannot conclude whether the red deer in the experiment base their food choice according to OFT. However, there is evidence on leaves being more nutritious than stems from studies on other plants (Ishida et al. 2010 (sweet potatoes (*Ipomoea batatas poir*), Idris et al. 2011(*Ocimum Gratissimum*)), de Lima et al. 2015 (jatropha plants). One can especially notice that leaves tend to have high values of crude protein and carbohydrates (Ishida et al. 2010, Idris et al. 2011). Even though I cannot be certain about the nutritional differences between leaves and stem in oil seed rape, I can assume that the pattern should be quite similar to findings in other plant groups, supporting the hypothesis of OFT. This could indicate that red deer may select the most nutritious part of the plant based on energy maximization.

However, other studies have shown that cervid food choice is not driven by energy maximization (Felton, Wam et al. 2018). More specifically, some studies show evidence of ungulates continuing to eat low-quality food, regardless of given access to high-quality food (Schmitz.1990, Miranda et al.2015, Felton et al. 2016), possibly with the aim of reaching a daily balance of macronutrients. Instead of supporting the OFT those studies support the nutritional balancing hypothesis. The fact that the red deer in my experiment continued to consume bark regardless of the presence of highly nutritious oil seed rape plants lends further support to these findings and it can therefore be concluded that more research is needed to detangle these mechanisms.

An important factor to consider when interpreting my results is that it was not only the dose of oil seed rape that changed with time, so did also plant characteristics. Over time the plant grew larger and the stem got thicker and more rigid. Therefore, the increased selectivity for leaves over time might also have been influenced by changes in plant characteristics, not only by amount given.

My results regarding selectivity are not only important in trying to understand the nutritional ecology of red deer, they might also be important for wildlife management and landowners since it gives an indication of red deer foraging behavior. It is also valuable knowledge that damage on oil seed rape fields might differ depending on the age of the plants. More precise, in older fields the damage may be more directed towards the leaves, while in young fields the entire plant will be eaten.

4.3 Conclusion

Based on results from my study I can conclude that plant diversity and factors driven by temperature interact with each other in a complex manner, influencing bark stripping by red deer**.** Investigating the reasons behind bark stripping is therefore very complicated and involves several different interacting factors, some that are not even touched upon in this study. This is a conclusion that goes in line with other studies, stating the complexity of ungulate damage (Reimoser and Gossow 1996, Reimoser 2003, Nopp-Mayr et al. 2011, Gerhardt et al. 2013).

Importantly, with support also from other earlier findings, I can conclude that bark stripping can be considerable not only during periods of food shortage. This lends further support to the hypothesis that also diet composition, and not only the amount of alternative forage, influences barks stripping.

I can also conclude that plant diversity plays an important role in bark stripping behavior, with an indication that plant diversity is possibly negatively related to bark damage. This indication needs to be further studied and has potential to become an important factor in management's role in decreasing bark damage. It is likely that by increasing the diversity of herbs, grasses and trees in the landscape, damage on spruce by red deer will be reduced.

Finally, I can conclude that regardless of our nonsignificant effect of oil seed rape in the overall model, it is still important to consider the possible effect of crop intake on forest damage. The interactive effects between agriculture and forestry is something that needs to be further studied, and more knowledge is needed before we can implement suggestions in wildlife management and forestry.

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Appendix 1

Feeding plan – oil seed rape

Table 1. *Feeding plan for oil seed rape in a controlled feeding experiment with captive red deer. This feeding plan represents the high dose treatment in the experiment where two groups of red deer á 10 individuals were given 100 kg of oil seed rape respectively (200kg/2). To avoid potential complications due to fast shifts in diet, the high dose treatment was gradually increased during the first week until full dose was reached on day 8*

Day	Total amount of harvested oil seed rape plants (kg)
1	12
2	38
3	64
4	90
5	116
6	142
7	168
8	200

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