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Nutrient balancing or spring flush – What determines spruce bark stripping level by red deer?

Anna Widén [a], Anders Jarnemo [b], Johan Månsson [c], Johan Lilja [d,g], Julien Morel [e], Annika M. Felton [f,*]

[a] Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SLU, SE-901 83 Umeå, Sweden
[b] School of Business, Innovation and Sustainability, Halmstad University, P.O. Box 823, SE-301 18 Halmstad, Sweden
[c] Department of Ecology, Wildlife Ecology Unit, Swedish University of Agricultural Sciences, SLU, Grimsö 152, SE-730 91 Riddarhyttan, Sweden
[d] Biology Education Centre, Uppsala University, P.O. Box 256, SE-751 05 Uppsala, Sweden
[e] Department of Agricultural Research for Northern Sweden, Swedish University of Agricultural Sciences, SLU, SE-901 83 Umeå, Sweden
[f] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 190, SE-234 22 Lomma, Sweden
[g] Länsstyrelsen Uppsala län, SE-751 86 Uppsala, Sweden

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ABSTRACT

The distribution and population density of red deer (*Cervus elaphus*) are increasing in several regions of Europe. The deer may cause severe damage in commercial forestry and agriculture. Bark stripping is the main problem in forests, especially on Norway spruce (*Picea abies*), and is thought to mostly occur during winter when other forage is scarce. It has been suggested that an imbalance in the nutrient intake, and especially a diet including high amounts of easily-digestible macronutrients, such as agricultural crops, can lead to an increased urge to consume bark. Feeding on brassicas, for example rapeseed (*Brassica napus*) might have this effect. The aim with this study was to investigate the relationship between intake of rapeseed and bark stripping on Norway spruce by red deer during early spring. We 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 freshly harvested rapeseed plants. In addition, influence of air temperature and forage nutritional composition was taken into account. Our results show that red deer bark stripping can be considerable not only during winter but also during spring green-up. We found no significant influence of rapeseed on bark stripping performed by the deer. However, at a threshold temperature, deer suddenly started to ingest large amounts of bark biomass, coinciding with a significant change in the bark's concentration of starch. We suggest that the lack of effect of rapeseed feeding can partly be explained by overshadowing effects caused by such seasonal changes of bark characteristics, and partly by the fact that the rapeseed plants in our study contained lower than expected concentrations of easily-digestible macronutrients (apart from protein). We conclude that the risk of damage on spruce can be especially high during certain periods, something that is important to consider when mitigating bark stripping. However, several interactive effects are involved and must be considered in order to more efficiently mitigate damage.

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 (Apollonio et al., 2017; Virtanen et al., 2002). However, they also have negative effects on forest and agricultural production, something that together with an increase in numbers and spatial distribution throughout Europe and North America, result in challenges for wildlife management (Linnell et al., 2020; Valente et al., 2020; Apollonio et al., 2017; Milner et al., 2006).

One challenge in commercial forestry is bark stripping by deer, which can result in severe damage to production trees and lead to economic losses through reduced growth, fungal infestation, stem deformation and wood decay (Gill 1992;Verheyden et al., 2006). One species

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* Corresponding author.

E-mail addresses: anna.widen@slu.se (A. Widén), anders.jarnemo@hh.se (A. Jarnemo), johan.mansson@slu.se (J. Månsson), johan.lilja@lansstyrelsen.se (J. Lilja), julien.morel@slu.se (J. Morel), annika.felton@slu.se (A.M. Felton).

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known for bark stripping is red deer (*Cervus elaphus*) which is increasing in several regions in Europe (Gerhardt et al., 2013; Apollonio et al., 2010). Red deer are known to strip bark from at least 21 tree species in Europe (Gill 1992, Verheyden et al., 2006), and Norway spruce (*Picea abies*) is one of the most affected tree species (Månsson & Jarnemo, 2013; Vospernik, 2006). As expected, the level of bark stripping damage by red deer on production trees has been shown to be positively related to deer density at the scale of stands (Kiffner et al., 2008; Verheyden et al., 2006) and landscape (Ligot et al., 2013; Jerina et al., 2008). However, several studies have been unable to detect this relationship (Jarnemo et al., 2014; Verheyden et al., 2006; Völk, 1999; Szederjei 1957). It appears that the effect of deer density on bark stripping damage can be overshadowed by other factors. For example, the degree to which red deer eat spruce bark vary among seasons at northern latitudes. Due to the associated costs involved for forest owners, it is important to understand which factors influence the animals' behavior during different seasons, to enable managers to act accordingly.

Winter-time bark stripping on spruce by red deer is commonly occurring and may be a response to a shortage of alternative forage (Gill 1992; Ueda et al., 2002; Welch et al., 1987). This relationship is referred to as the food resource hypothesis (Verheyden et al., 2006; Gill 1992). For example, the availability of dwarf shrubs and herbs has been related to relative severity of bark stripping caused during winter (Jarnemo et al., 2014; Nopp-Mayr et al., 2011; Ueda et al., 2002; Völk, 1999; Welch et al., 1987). Studies have shown that stems of Norway spruce, planted in even-aged monocultures with dense crown closure are highly affected by bark stripping (Jerina et al., 2008; Vospernik, 2006; Völk, 1999; Reimoser & Gossow, 1996), likely due to the poor light availability, making alternative forage less available on the ground (Jarnemo 2016; Nopp-Mayr et al., 2011). During harsh winters when forage availability is poor, the animals may also suffer from nutritional deficiencies. The nutritional value hypothesis suggests that deer consume bark in order to alleviate nutritional deficiency (Saint-Andrieux et al., 2009; Ando et al., 2005; Ando et al., 2003; Gill 1992), and therefore provide an additional explanation to bark stripping during winter.

However, bark stripping caused by red deer during spring (Gill 1992; Saint-Andrieux et al., 2009) is less well studied and associated drivers are therefore more uncertain. Bark stripping during spring can lead to extensive damage (Jarnemo & Månsson, 2011; Jensen, 1968), since the bark detaches easier from the stem after the temperature induced dehardening process, when cells responsible for secondary growth expands (Widén & Widén, 2008; Raven et al., 2005). A related increase in bark foraging efficiency may therefore be one factor underlying observed peaks in spring bark stripping. At the same time, free-ranging deer gradually get access to greater volumes of forage plants in the landscape during spring green-up, and many of these plants will be of relatively high nutritional quality. Therefore, instead of food shortage or nutritional deficiencies potentially driving the intake of bark during this season, nutritional balancing may offer an additional explanation.

Nutritional balancing is found to explain the food selection in a variety of taxonomic groups, including insects (Simpson et al., 2004), fish (Raubenheimer et al., 2005), non-ruminant (Rothman et al., 2011; Felton et al., 2009; T. Robbins et al., 2007) and ruminant mammals (Felton et al., 2021). Nutritional balancing can be described as the altering of food intake to obtain a nutritionally balanced diet with the aim of reaching optimal performance (Raubenheimer & Simpson, 1997; Westoby, 1974). This can either be done by selecting nutritionally balanced food items or by combining two or more imbalanced food items that complement each other (Simpson & Raubenheimer, 2012). A greater diversity of available forage species can in some cases improve the animal's ability to compose a balanced diet in this way (Felton et al., 2021; Felton et al., 2020). Ruminants also need to maintain a rumen environment beneficial for their rumen flora, adding another dimension to their quest to obtain a balanced intake. Sudden ingestion of too much sugar or starch may lead to a shift in the rumen pH, potentially resulting in ruminal acidosis (Keunen et al., 2002). Therefore, when ungulates feed on forage rich in such easily-digestible macronutrients, for example crops, they may need to compensate by increasing their intake of structural carbohydrates (hereon "fiber" for simplicity) found in woody material (Felton et al., 2021; Felton et al., 2016; Miranda et al., 2015; Ando et al., 2004). For example, captive red deer provided with nutrient rich supplementary feed all-year round increase their intake of woody vegetation (Miranda et al., 2015), and a similar pattern has been observed in supplemented captive moose during winter (Felton et al., 2016). These experimental results are supported by research carried out on landscape-scale, with free-ranging red deer. Studies have found that levels of deer-caused damage on spruce bark is higher in landscapes dominated by agriculture, compared to forest dominated landscapes, possibly due to red deer' intake of crops resulting in an increased urge to consume bark (Jarnemo et al., 2014; Jarnemo & Månsson, 2011).

Nutritional balancing is therefore likely to be of high relevance when trying to understand bark stripping behavior at any time of the year, and to resolve the challenges related to integrated management of red deer, silviculture and agriculture. Swedish hunters and forest owners sometimes suggest that red deer cause more bark damage in Norway spruce production stands after having spent time on fields with rapeseed (*Brassica napus*) (Jarnemo 2016). Indeed, spruce stands located close to rapeseed fields suffer significantly more bark stripping damage than stands further away, regardless of local deer densities (Jarnemo et al., 2022). Rapeseed 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 rapeseed plants, can generate lower pH in the rumen (Barry, 2013). One can therefore assume that a large intake of rapeseed during spring would affect the rumen flora leading to a need for compensation and an increased urge for complementary food items, according to the nutrient balancing hypothesis.

We tested this hypothesis by conducting a controlled feeding experiment with captive red deer in southern Sweden. We assessed the deer' intake of both bark and rapeseed plants, the nutritional composition of each of these food types, as well as air temperature (may affect the bark structure). We expected rapeseed plants to have a nutritional composition very different from that of bark and other woody forage items, but similar to other energy-dense agricultural crops; and that red deer would therefore increase their intake of bark if provided with rapeseed, depending on the dose of rapeseed plants ingested.

2. Materials and methods

2.1. Study area and study design

The study was carried out 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° (Swedish Meterological and Institute, 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) (Fig. 1a). Enclosure 1, 2, and 4 had a size of 5.0 ha while enclosure 3 had a size of 7.5 ha. Due to the 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 (Fig. 1b and c). Norway spruce logs were harvested at the end of each week and placed in the enclosures every Monday, replacing the old stems that were removed from the enclosures. The logs (3 m long) were harvested within the same planted stand and had an age of 25 years. Trees of this particular age was chosen because they appear to be 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 at the middle of the log 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.

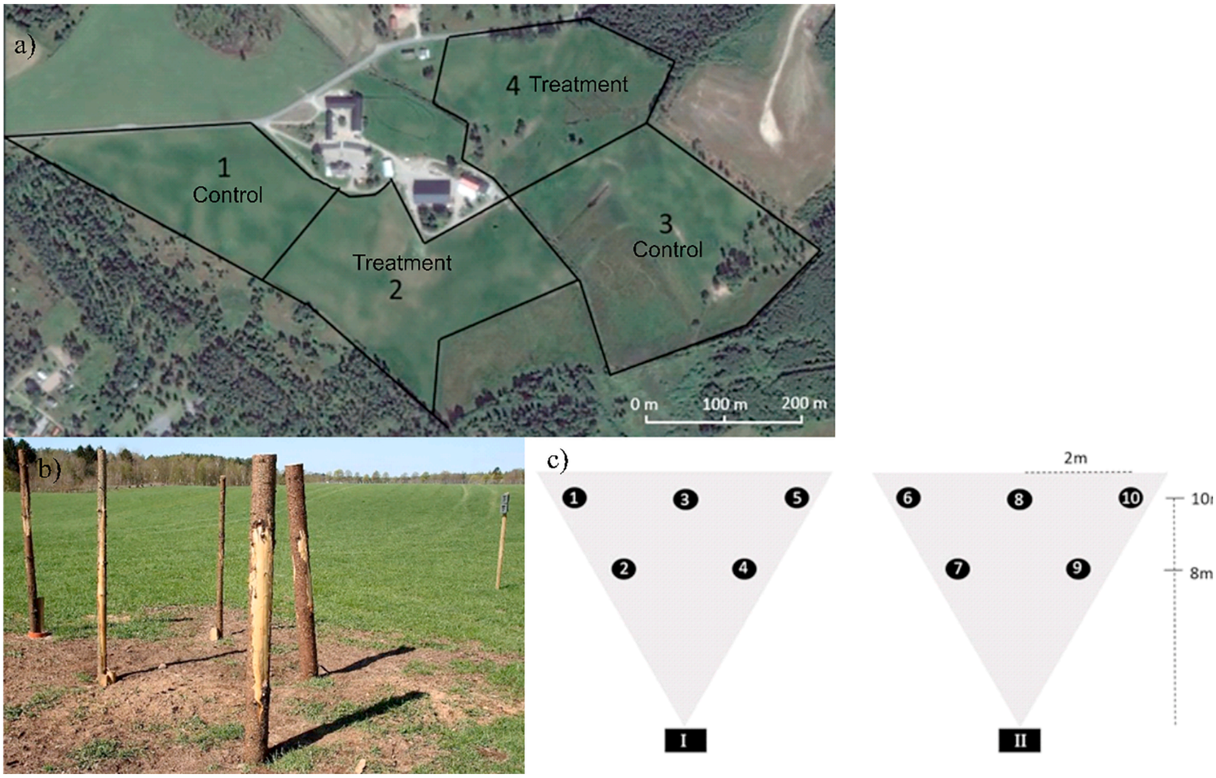

Fig. 1. The red deer farm with placement of the four enclosures used in the study (a); and the systematic placement of ten spruce logs in the enclosures seen from the side (b) and from above (c) indicated with numbered black circles. The reason for this placement was to get free view of all logs from cameras (squares I and II) used in another part of the project. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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). Trees present were too tall to provide foliage to the deer, and we saw no signs of bark consumption on these trees either.

The experiment had two phases, one control phase and one treatment phase. The control phase was 3 weeks in total, while the treatment phase was 3 + 3 weeks long. During the control phase the red deer groups had only access to spruce logs as a complement to the forage growing in enclosures. During the treatment phase, two of the enclosures (number 2 and 4, hereafter called treatment groups) were provided with rapeseed plants harvested the same morning from a nearby field. The other two groups (number 1 and 3, hereafter called control groups) were provided with spruce logs but not rapeseed plants. The control and treatment groups were randomly chosen.

During the first three weeks of the treatment phase the treatment groups were given a low dose of rapeseed. We defined low dose as ten percent 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 one moose originating from the concept of animal equivalence (Vallentine, 2000) and that one moose consumes 4.7 kg dm during winter (Persson et al., 2000). A ten percent dose therefore represented 6 kg of fresh rapeseed plants per group (600 g wet weight per individual), based on measurements of the rapeseed plants containing 42% dm. We collected, dried and weighed rapeseed 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). We adjusted the total wet weight of supplied plants accordingly to make sure that the daily dose approximated ten percent on a dm basis, through that experimental phase.

During the last three weeks of the treatment phase, treatment groups were given high dose of rapeseed. We 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 rapeseed plants). To avoid potential complications due to rapid diet shifts (Keunen et al., 2002), the high dose treatment was gradually introduced during the first week until the full dose was reached on day eight. 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, in terms of dm intake by the deer, was calculated based on our measured values of % dm.

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

We measured the proportion of bark removed from each spruce log every day. The log was divided into 30 cm sections starting at 30 cm above ground. For each 30 cm section we estimated the percentage of missing bark. To get a reliable estimate of how much bark that was actually eaten we accounted for other types of damage. Bark damage was categorized into mechanical damage (chainsaw during logging), fraying, gnawing and peeling. We use the term bark stripping to define both gnawing and peeling, 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. We weighed bark pieces that had fallen to the ground to account for fraying damage caused by antlered male red deer. At the end of every week we also removed and weighed bark hanging from the log, this was later subtracted from the amount of missing bark of that particular log. If one log was 90% debarked before the end of the week, we removed this log and replaced it with a new log.

One harvested log per week was kept outside the enclosures and was used to estimate weight of bark per area unit. From this log we peeled off the bark from an area of 50 × 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 grams. We calculated the biomass consumed in the following way: first, the total area of bark was calculated by multiplying the circumference at the middle of the log with the height of that log. To get an estimate of the area that was actually available for bark stripping by deer, we subtracted the area of mechanical damage (caused by the chain saw) from the total area of that log. We calculated the bark area per log that was eaten by deer by multiplying the percentage of bark stripping (measured in the field) with the available area. Dry weight in g/cm^2 was multiplied with the damaged area. Finally, bark that had been peeled from the log but not eaten was subtracted.

For chemical analysis (see below) we removed bark at the end of each week from a subsample of the spruce logs (average 8 logs/ week (range 6–9); 84 logs in total) that had been inside the four enclosures. Bark was removed using a knife, from an area of 50 × 20 cm, in the same way throughout the experiment (stripping bark off down to the exposed sapwood). Bark samples were immediately frozen and kept separate per log.

2.3. *Rapeseed measurements and sample collection*

Every day during the treatment phase we harvested fresh rapeseed plants from the same field. We used a hedge cutter when plants were small and a clearing saw when plants had grown larger, all according to the already decided feeding plan (Table A1). We weighed the plant material and later distributed it to the red deer groups in feed troughs. We 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 rapeseed eaten in grams wet weight. To account for evaporation due to sun exposure, we placed a sample of rapeseed plants in a feed trough 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 one to day two gave us an estimate of how much water had evaporated from the plants over 24 h and was later subtracted from the amount rapeseed eaten by the groups the corresponding 24 h. This calculation did not take into account the fact that the plants partly had been eaten by treatment groups before the full 24 h had passed. We froze subsamples of harvested rapeseed plants each day. Samples were separated into stems and leaves, and material was pooled so we obtained one leaf and one stem sample for each of the six weeks of the treatment phase (resulting in 6 leaf samples, 6 stem samples).

2.4. *Air temperature*

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

2.5. *Plant diversity*

To account for possible differences in vegetation cover and plant diversity among the four enclosures we conducted a vegetation survey at the end of the experiment (16–20th of May), which corresponded to the beginning of the growing season. With the aim of obtaining a good sampling cover in each enclosure, we adjusted the sampling intensity (number of plots) to the size of each enclosure. The number of sampling plots and the placement of the plots were decided with the help of a grid (100 × 100m). We ended up with nine sampling plots in enclosure 1 and 2, twelve plots in enclosure 3, and eight plots in enclosure 4. The plots were randomly distributed with the help of the nodes of the grid and based on the decided number of plots. In each sample plot, plant species present were identified, and their percentage cover was measured.

2.6. *Chemical analysis*

Samples of rapeseed plants and spruce bark were defrosted, dried at 60 °C and then ground using a hammer mill (KAMAS© Slagy 200B; 1 mm sieve). All bark and rapeseed plant samples were analyzed for total nitrogen, acid-detergent fiber (ADF) and ADF-N (insoluble nitrogen within the ADF fraction) using conventional wet chemistry techniques (Appendix S1 Supplementary methods). Additional wet chemistry analyses were also made on the 12 rape seed plant samples, namely crude fat (hereafter called “lipids”), ash-free neutral-detergent fiber (aNDF), lignin, starch, and water-soluble carbohydrates (WSC) (Appendix S1 Supplementary methods). Using in-vitro digestibility trial noting results at 30, 120 and 240 h, we also obtained an estimation of the proportion of aNDF (on an organic matter basis) that was digestible (aNDFDom). This method involves the use of rumen liquid from dairy cows, which is a rough approximation of what happens in the rumen of wild cervids (Krizsan et al., 2018). We calculated the mean aNDFDom across all three measuring times for use in data analysis.

Due to high costs associated with wet chemistry analyses, and in some cases too small amounts of dry matter per bark sample, we used Near-Infrared Spectroscopy to estimate concentrations of four constituents in bark samples: lipids, aNDF, starch and WSC. Each ground bark sample was thoroughly mixed before taking ca 40 g for scanning. NIRS reflectance spectra were acquired with a hyperspectral camera (Specim SWIR) from 1000 to 2495 nm with 288 bands resulting in hypercubes with a spectral sampling of approximately 5.2 nm. A spectralon white target was used as a reference for converting the hyperspectral images to reflectance factor values. All 84 bark samples were scanned. Of these, 42 bark samples (45% of the whole population of bark samples) that were large enough for wet chemistry were further processed in the lab.

Results from the wet chemistry analyses of the 42 bark samples were used to establish multivariate regressions using NIRS spectra as explanatory variables and laboratory-measured lipids, aNDF, starch and WSC as response variables (see Tigabu & Felton, 2018). Using the “pls” R package (Liland and Mevik, 2021) (R core team. 2013), a leave-one-out cross validation was performed to adjust partial least square regressions. The number of latent variables was manually set as to maximize the performances of the model while reducing the risk of overfitting. Obtained models showed prediction errors of 1.5, 4.9, 3.2, 1.3 and 4.9 % dm, respectively, for lipids, aNDF, aNDFDom, starch and WSC (R^2 = 0.54, 0.75, 0.75, 0.84 and 0.52). The regression lines appeared to be close to the 1:1 line, which suggests that no bias affects the regression models (Table A2). In the following data analyses, we used predicted values for lipids, aNDF, starch and WSC of all bark samples. The data analyses described below include 72 bark samples (Table A3), excluding some of the samples used in modelling due to the exact collection date.

We calculated available protein (AP) as total protein (total N multiplied by 6.25) minus non-digestible protein (ADF-N multiplied by 6.25) (Licitra et al., 1996). Hemicellulose was calculated as aNDF–ADF and cellulose as ADF–lignin. We calculated the energetic value of each food using the following conversion factors (N.R.C 1989): 37.7 kJ/g lipid and 16.7 kJ/g available protein (AP) and total non-structural carbohydrates (TNC = sum of starch and WSC), cellulose and hemicellulose. To adjust for variable levels of digestibility of dietary fibers (cellulose and hemicellulose), we multiplied the estimated kJ of these constituents with the proportion of digestible dietary fibers indicated by in-vitro digestibility trial (aNDFDom).

2.7. Statistical analysis

2.7.1. Differences in nutritional composition among forage items

To test the hypothesis that rapeseed leaf material has a nutritional composition that is different from bark and other woody forage items but similar to other energy-dense agricultural crops, we conducted a Principal Component Analysis (PCA). To take into account rapid nutritional changes in rapeseed leaves that can occur during spring, we used both the mean values for leaves harvested during the first week of the treatment phase, and the mean values for leaves harvested during the last week. In addition to using our own data for rapeseed leaves and spruce bark, we used published data for 12 common tree and shrub forage species: *Pinus sylvestris, Picea abies, Betula pendula, B. pubescens, Sorbus aucuparia, Populus tremula, Salix caprea, Quercus robur, Juniperus communis, Vaccinium vitis-idaea, V. myrtillus,* and *Calluna vulgaris* (data sourced from Felton et al., 2021). We also included published data for agricultural crops that are commonly used as supplementary foods in the study region: whole roots of *Beta vulgaris, Solanum tuberosum* and *Daucus carota,* the peas of *Pisum sativum,* and haycrop (grass) silage with < 25% legume content. Due to limitations in published data, included variables consisted of only three of the nutritional constituents: available protein, NDF, and TNC. For *B. vulgaris*, data on available protein and TNC were found in Spörndly (2003) and data on NDF in (Eriksson et al., 2009) For the remaining four items, we used data in Spörndly (2003).

2.7.2. Difference in bark intake between groups

All further statistical analysis was conducted in in R.3.4.1 (R Core Team 2013). Before analysis we identified a strong correlation between the two numerical variables used in the model; rapeseed intake and air temperature (Pearson correlation coefficient of 0.85). Therefore, both variables could not be included in the same model. Furthermore, our categorical variable dose treatment was similar to the continuous variable rapeseed intake. Because dose treatment increased with temperature, we made the assumption that dose treatment and air temperature would be strongly correlated as well. We therefore had to exclude air temperature as an explanatory variable in all models. In all further analysis, linear mixed effect models (LMEs, function lme in nlme package) (Pinheiro et al. 2013) were used to predict bark intake, expressed as the daily average in gram per week. Enclosure was used as random factor. Response variables were transformed to obtain normalized and homogenous residuals (Zuur et al., 2008).

To test if there was a difference in bark intake between the groups during the control phase we analyzed the data using a one-way ANOVA. The response variable was log-transformed to attain normalized and homogenous residuals (Zuur et al., 2008). 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 (R Core Team 2013). We 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 (Hothorn et al., 2012).

To test whether there was a difference in bark intake between treatment groups and control groups we used treatment as a factor with two levels (no rapeseed = control, rapeseed = 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, we used treatment as a factor with three levels (no rapeseed = control, low dosage of rapeseed = low, high dosage of rapeseed = high) as explanatory variable. The response variable was square root transformed. Furthermore, to test the possible influence of rapeseed as a quantitative variable, we 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. To test influence of air temperature on bark intake we used average daily temperature ° C per week as explanatory variable. Due to the correlation between rapeseed intake and temperature we were restricted to only using the control groups for this analysis. To obtain more variation in temperature data we used a greater span of data, including the three first weeks of the study as well. The response variable was log transformed.

We identified a date at which deer suddenly increased their intake of bark (24th April, see Results). Using ANOVA, we then tested whether there was a difference in the concentration of starch, WSC, available protein, cellulose and hemicellulose in bark samples sourced before (n = 38) and after that date (n = 34).

2.7.3. Difference in plant diversity among enclosures

Possible differences 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. Plant species cover was used as a proxy for plant abundance in the Shannon Wiener Index. Shannon Wiener index was calculated using diversity function in VEGAN package (Oksanen et al., 2013). 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. For the latter we 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.

3. Results

3.1. Average nutritional composition of bark and rape seed plants

The seven constituents measured (available protein, crude fat, starch, WSC, cellulose, hemicellulose and lignin) accounted for 75% and 67% of the total dry matter for bark samples and rapeseed plant samples respectively (rapeseed leaves and stems combined). Compared to stems, rapeseed leaves contained 41% more AP, 473% more starch and 60% more crude fat, while there was 76% and 58% less hemicellulose and cellulose, respectively (Table A3). Fiber digestibility was 20% higher, and total estimated energy content 11% higher, in leaves than in stems. During the treatment phase, deer ingested more leaves than stems from the rapeseed plants than would be predicted from the amounts made available (on average 67%% of available leaf biomass consumed, 31% of stem). This preference for leaves over stems increased during the progression of the experiment, as the plants grew larger and the relative proportion of stem to leaf increased (final two weeks of treatment: on average 80% of available leaf biomass consumed, 19% of stem). For this reason, we here focus on the nutritional data represented by the leaves of rapeseeds.

The nutritional composition of spruce bark resembled those of other woody forage items known to be consumed by free-ranging red deer wintertime (Fig. 2, Table A4). In contrast, the PCA indicates that the nutritional composition of rapeseed leaves was very different from bark and these woody forage items (e.g. mean of 13.1 % aNDF, compared to 37.6 % in bark and 50.4 % in other woody forage items). The composition of rapeseed leaves, particularly during the early growing season, was even more divergent from woody forage items than most of the other agricultural crops included in the comparison (Fig. 2).

It was in particular the protein concentration that made rapeseed leaves differ from other food items (Fig. 2). Our data shows that concentration of AP in rapeseed leaves was 11 times higher than in bark samples (average 20.4 % dm and 1.8 % dm respectively; Table A3). However, the concentration of total non-structural carbohydrates (starch + WSC) was similar: average 29.8 % dm in rapeseed leaves, 30.1 % dm in bark. The concentration of digestible fibers (cellulose + hemicellulose) was 2.5 times higher in bark compared to rapeseed leaves, and there was 5.3 times more indigestible fiber (lignin) in bark than in rapeseed leaves on average. Furthermore, fiber digestibility in bark was only a third of that in rapeseed leaves (Table A3). Concentrations of macronutrients resulted in a 28% difference in estimated total

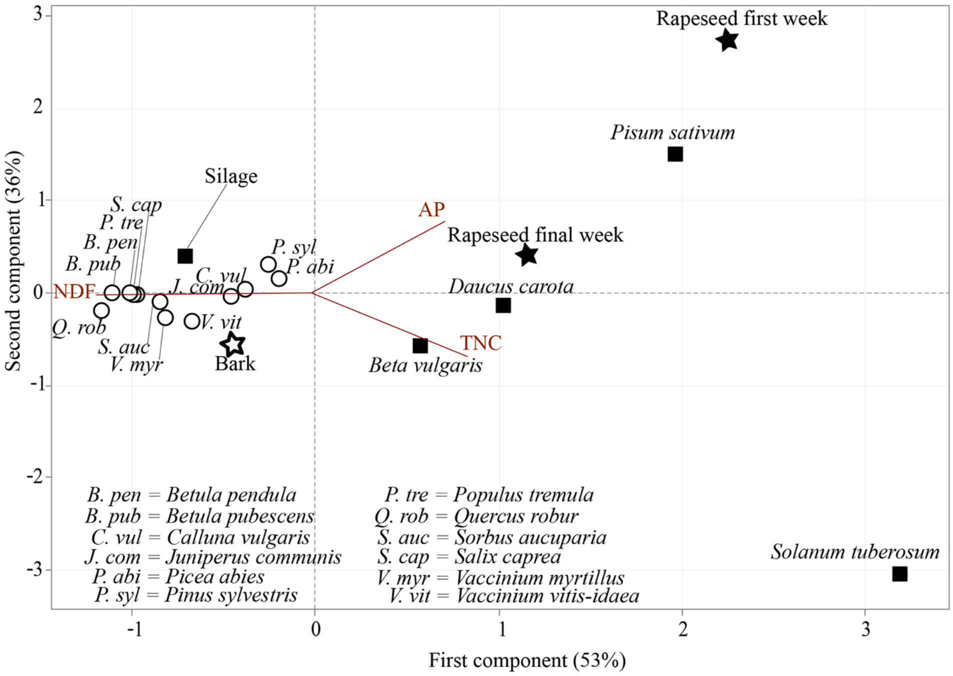

Fig. 2. Bi-plot showing result from Principal Component Analysis of the nutritional composition (available protein, aNDF, and TNC) of spruce bark (hollow star; average for the whole experiment), rape seed leaves (filled stars; harvested during the first and final week of the experiment), five other agricultural crops (squares; whole roots of *Beta vulgaris, Solanum tuberosum* and *Daucus carota,* the peas of *Pisum sativum,* and haycrop (grass) silage with < 25% legume content; data sourced from Spörndly (2003) and Eriksson et al. (2009)), and winter dormant twigs from 12 woody forage items (circles; shrubs and trees within browsing height; data sourced from Felton et al 2021). The first two components together explained 89% of the variation. The first principal component (x-axis) depicts variation in aNDF with increasing values to the left, as indicated by solid loading line (red). The second principal component (y-axis) depicts variation in available protein (AP, increasing values upwards) and TNC (increasing values downwards). Note that bark is clustered together with other woody forage items, while rapeseed leaves have very high protein concentrations even in relation to other agricultural crops. Eigenvectors for PC1 and PC2 are shown in Table A4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mean energy content: average 1118 kJ/ 100 g dm of rapeseed leaves, compared to 872 kJ/ 100 g dm of bark. However, uncertainty is associated with this estimate, partly due to estimates of crude fat (also with regards to digestibility, see Methods). There was a surprisingly high concentration of crude fats in the bark samples (mean 6.0 % dm (2.3 SD), range 2.6–12.9 % dm). It is likely that this value includes non-digestible fats (e.g. waxes) in addition to digestible fats. Therefore, the calculation of total energy content (where 100% digestibility of crude fat was assumed, lacking other information), likely overestimates energy contributed by fat in the bark samples.

3.2. *Bark intake during the entire study period and pre-conditions*

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 = 4.01) (Fig. 3a). This implies that the pre-conditions were the same for control and treatment groups at the start of the experiment.

Pre-conditions in terms of plant diversity differed between the four enclosures with 3 and 4 being most diverse, and 1 and 2 being least diverse. This is represented in all the metrics we used, i.e species richness, Shannon wiener index and species accumulation curve (Fig. A2).

There was a significant difference in bark intake between the four groups of red deer during the treatment weeks (ANOVA, p-value = <0.001, F-value = 8.59). Group 1C consumed the greatest amount of bark, while group 3C consumed on average the lowest amount of bark (Fig. 3b). Group 4T and 3C had the lowest variation among days (Fig. 3b). The post-hoc test showed a significant difference between group 1 and 3 (p-value = <0.001, z-value = −2,72), none of the other groups were significantly different from each other.

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 (Fig. 4). During

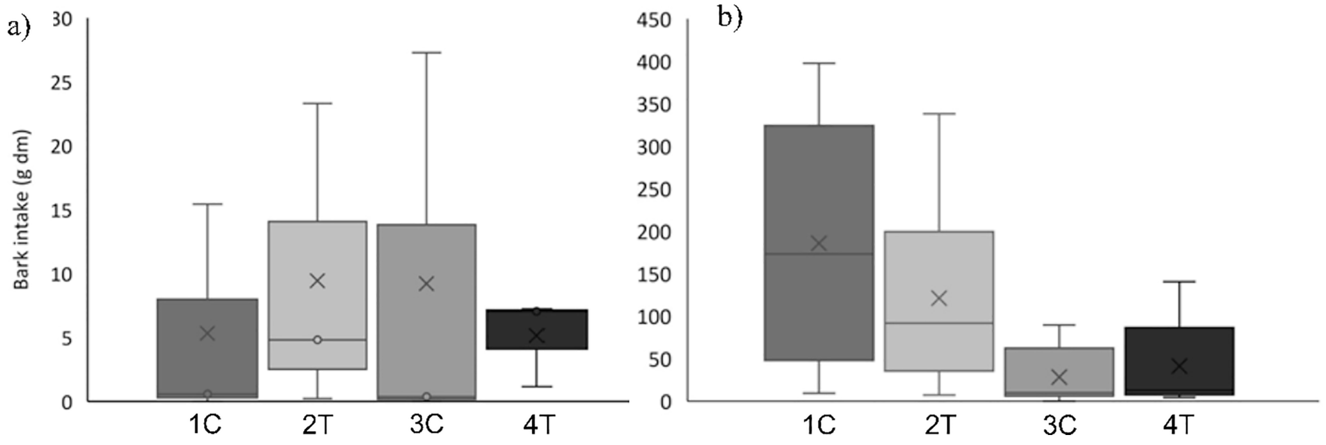

Fig. 3. Boxplots of daily average bark intake per week in the four red deer groups (1–4) where two groups were provided with rapeseed (T) and two were kept as control groups (C) during the control (a) and treatment (b) phase. Median is indicated by the horizontal line dividing the box into two parts. 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.

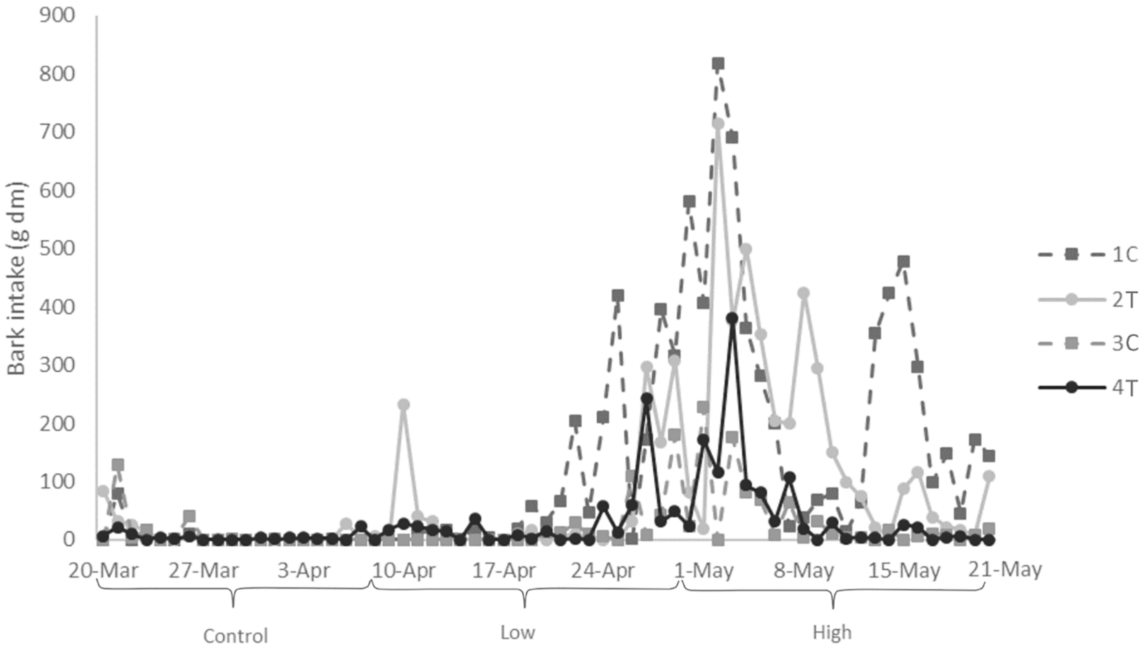

Fig. 4. Daily bark intake of the four different red deer groups (1–4) where two groups were provided with rapeseed (T) and two were kept as control groups (C) during three different treatment phases (control, low and high).

the last weeks of the experiment the relative differences were similar between the treatment and control groups (Fig. 4).

There was an increase in bark intake for all deer groups starting on the 25th of April and decreasing in mid-May (Fig. 4). The peak coincided with the high dose treatment. However, the two control groups also increased their intake during the same period (Fig. 4).

3.3. Influence of rapeseed and temperature on bark intake

We found no significant difference in bark intake between control groups and treatment groups ($p = 0.997$, t-value $= 0.004$, estimate $= 0.004$), nor was there any significant effect of dose treatment on bark intake (low dose: p-value $= 0.516$, t-value $= -0.661$, estimate $= -2.504$; high dose: p-value $= 0.797$, t-value $= 0.261$, estimate $= 0.987$). Furthermore, there was no significant relationship between rapeseed intake and bark intake, when measuring how much rapeseed the red deer actually consumed (LME, t-value $= 0.272$, p-value $= 0.791$, estimate $= 0.00$). There was thus no pattern suggesting that the rapeseed dose affects the bark intake. There was a significant positive relationship between temperature and bark intake for the two control groups over the entire study period (LME, t-value $= 0.080$, p-value $= 0.035$, estimate $= 0.186$). Treatment groups could not be included in this analysis due to the correlation between rapeseed intake and temperature. The data indicate a threshold effect around 9 °C with an increase in bark intake (Fig. 5).

3.4. Bark nutritional composition in relation to deer bark intake pattern

The nutritional composition of spruce bark fluctuated as the spring progressed (Fig. 6). There was significantly less starch (% dm) in the spruce bark samples sourced before compared to after the date when red deer suddenly started to ingest large amounts of bark (before mean 3.0 % dm (SD 2.0), after 5.5 % dm (SD 2.3), equivalent to an 82% increase; ANOVA: $F = 22.81$, $p < 0.001$). There were no significant differences in spruce bark samples before and after that date regarding concentrations of available protein ($F = 0.02$, $p = 0.894$), WSC ($F = 0.12$, $p = 0.726$), hemicellulose ($F = 0.02$, $p = 0.894$), cellulose ($F = 0.09$, $p = 0.761$), lignin ($F = 0.19$, $p = 0.665$), or crude fat ($F = 1.82$, $p = 0.181$). Bark was

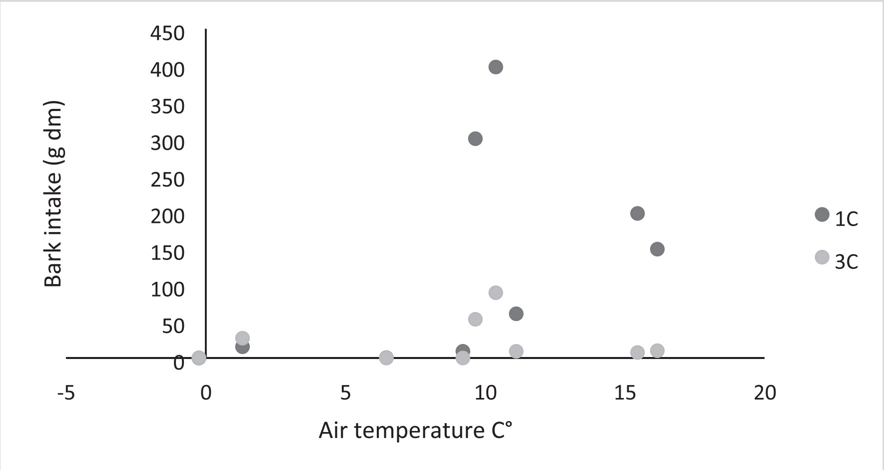

Fig. 5. Relationship between daily average bark intake per week in the two control groups of red deer and the daily average air temperature (C°) per week.

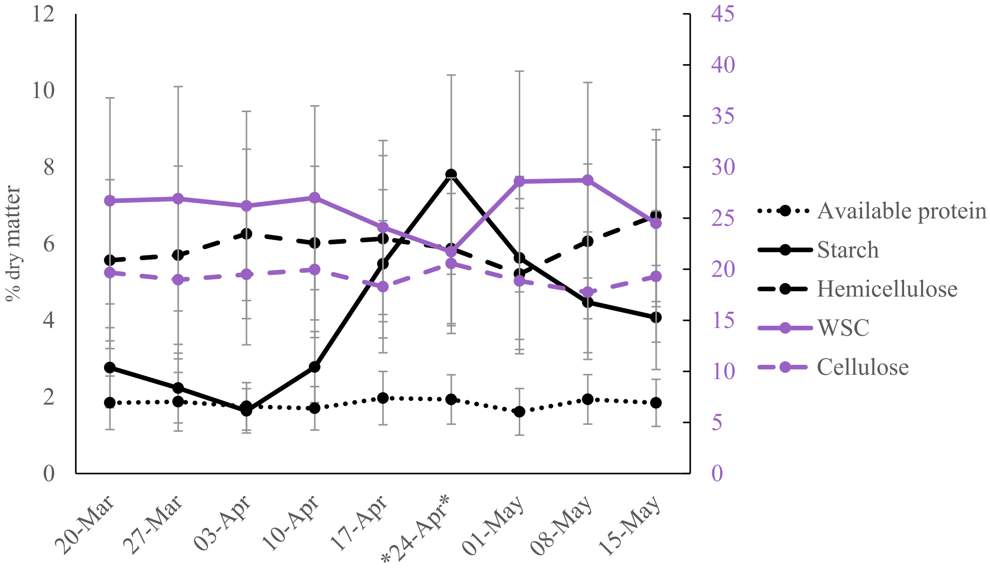

Fig. 6. Mean concentrations (% of total dry matter on both y-axes) of starch (y1, solid black line), available protein (y1, dotted black), hemicellulose (y1, dashed black), cellulose (y2, dashed grey) and WSC (y2, solid grey) per week in spruce bark during the progression of the experiment. Dates on the x-axis represent the first day of each week, and stars indicate when the deer suddenly started to eat large volumes of spruce bark (Fig. 4). Error bars show 1 SE of the weekly mean (7–9 spruce stems were sampled per week).

estimated to contain 868 kJ/100 g dm before, and 877 kJ/100 g dm after that date (assuming that 100% of crude fat was digestible), and this difference was not significant (F = 0.12, p = 0.735).

4. Discussion

The results from our experiment show that red deer bark stripping can be considerable not only during winter but also during spring green-up. At a certain threshold temperature, deer suddenly started to strip large amounts of bark biomass from the spruce stems, coinciding with a significant change in the bark's relative concentration of starch. We did not, however, find support for our hypothesis that a large intake of rapeseed would lead to an increased intake of bark, as there was no significant difference in bark intake between deer fed rapeseed plants (treatment groups) and control groups.

Our data revealed that although leaves from the rapeseed plants used in our spring-time experiment contained 10 times as much available protein than bark, and therefore stand out in comparison with other forage items (Fig. 2), the difference in sugar and starch concentrations was not as great as expected (only 1.3% difference in TNC between rapeseed leaves and bark samples in average). At the same time, however, concentrations of digestible and indigestible fibers were 2.5 and 5 times higher in bark than in rapeseed leaves. This means that although bark contributed with more fibers to the deer' diet during the treatment phase, the relatively low TNC concentration in rapeseed plants (compared to bark) may not have induced as great a need to compensate with additional fiber as expected. This finding can be one explanation to why we did not find any evident pattern of compensatory feeding in our experiment. We did observe a 163% increase in bark intake by the two treatment groups, between low dose and high dose weeks. However, other factors changed during the experiment that may have affected bark intake.

One such factor could have been air temperature. We found a significant positive relationship between bark intake and air temperature in the control groups. There was a sudden increase in bark intake starting at the end of April, when air temperature reached ca 9° C. Other studies have suggested that bark intake by red deer during winter is higher when temperature is low (or snow cover is deep), and that bark mostly serves as shortage food when alternative forage is scarce (Ueda et al., 2002; Welch et al., 1987; Gill 1992). For example, a study in Germany showed that bark intake by red deer increased with cumulating snow depth (Kiffner et al 2008). However, our results support other studies showing that intensive bark stripping can occur during spring and summer (Saint-Andrieux et al., 2009; Ando et al., 2005; Jiang et al., 2005; Ando et al., 2004). One potential explanation for the positive relationship between bark intake and air temperature is the de-hardening process in spruce.

During spring, cell division in the cambium is initiated. Cells responsible for secondary growth in trees start to expand, and the newly formed cells have thin cell walls that easily break (Widén & Widén, 2008; Raven et al., 2005). 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. Furthermore, de-hardening stimulates decomposition of surrounding nutrient transporting cells, increasing the availability of nutrients (Widén & Widén, 2008). The de-hardening process is driven by temperature, and requires five consecutive days with a mean temperature above five degrees (C°) to initiate (Jönsson et al., 2004). In southern parts of Sweden, the process has been suggested to start during March to April (assessed during period 1961–1999 by Jönsson et al., 2004). As this corresponds well to the sudden increase in bark stripping that we observed within both control and treatment enclosures, and as we found no relationship between bark intake and dose of rapeseed plants, we suggest that factors dictated by seasonal changes had a stronger influence on bark stripping than any nutritional imbalance that may have been caused by the deer' intake of rapeseed plants.

At the same time as it became easier for red deer to remove larger and deeper sections of bark, the nutritional composition of the bark also changed (Fig. 6). In fact, there was almost twice as much starch in the bark we sampled after the deer suddenly increased their bark intake, compared to before (average 5.5% of dm "after" vs 3.0% "before", with a peak at 7.8% the last week of April). Even more dramatic increases in starch concentration during green-up (May) have been observed in the phloem of mature spruce trees in Finland (Jyske et al., 2015). Changes in the concentrations of other nutritional parameters did not differ significantly between the two groups of bark samples in our study. The net amount of energy provided by the bark we sampled was not very different before compared to after the date in question. Further research is needed to understand whether the deer actually responded to the increase in starch concentration *per se*, or if this merely coincided with an overall increase in efficiency of obtaining bark biomass. The deer ingested relatively more inner bark compared to outer bark after the end of April (deeper wounds). We, however, sampled the spruce bark in a consistent manner throughout the experiment (down to the exposed sapwood). It is therefore possible that the temporal change in nutrition of bark was even greater than our data suggest, as the inner bark of

Norway spruce contains more non-structural carbohydrates than outer bark (Krogell et al., 2012). Also note that our chemical analyses of spruce bark were of samples taken from harvested stems. Bark material from living trees may be slightly different.

Yet another factor that appears to possibly have influenced the degree of bark intake by deer in our study was difference in plant diversity between the enclosures. As snow melted during the spring it became apparent that all enclosures were not similar in terms of diversity of plants available for deer to browse upon. Interestingly, it seems like all metrics we used for plant diversity in enclosures negatively relates to bark damage (Fig. A2), regardless of experimental treatment. However, we were not able to test this possible relationship statistically. It was only group 1 and 3 that differed significantly in their bark intake, and these two enclosures also had the largest difference in plant diversity. Although we lack observational data regarding which herbs and grasses the deer consumed within their respective enclosure, it is reasonable to assume that deer restricted to an area with very low plant diversity had a narrower diet than those with access to a more species-rich habitat. With access to different types of forage items, animals are better able to compose a mixed diet and achieve a balanced diet (Felton et al., 2016; Felton et al., 2009; Westoby, 1974). It is likely that the deer in our study that inhabited the most species-poor paddocks experienced an increased urge for an additional food source – the bark – regardless of whether they were fed rapeseed plants or not.

Some caveats are associated with our study. Being restricted to only four groups of red deer, located at the same farm, places limits on statistical strength and on the applicability of our results to other systems. Future experiments should try to replicate our findings. While doing so, we suggest conducting the experiment during parts of the winter when temperatures are more stable and snow covers the ground, to avoid temperature-induced factors and differences in habitat quality to mask a possible effect of crop intake on bark stripping by the deer.

In conclusion, our findings confirm the complexity involved when trying to understand drivers of ungulate damage on the natural resources upon which humans depend (Gerhardt et al., 2013; Nopp-Mayr et al., 2011; Reimoser, 2003; Reimoser & Gossow, 1996). Our results indicate that bark stripping by red deer during spring is influenced by temperature-induced changes to the spruce trees, and that the resulting changes in both quantity and quality of the available bark under our experimental conditions might have overshadowed potential compensatory effects from ingesting a nutritionally divergent crop. However, the direct effect of crop intake on damage may be greater during other parts of the year and under other circumstances (e.g. crop types with even more divergent nutritional composition), and we therefore suggest that more knowledge is needed about interactive effects between agriculture and forestry to confidently deliver recommendations to wildlife management and forestry.

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.

CRediT authorship contribution statement

Anna Widén: Methodology, Formal analysis, Investigation, Writing – original draft. **Anders Jarnemo:** Conceptualization, Project administration, Funding acquisition, Supervision, Methodology, Investigation, Writing – review & editing. **Johan Månsson:** Conceptualization, Supervision, Methodology, Formal analysis, Writing – review & editing. **Johan Lilja:** Investigation, Writing – review & editing. **Julien Morel:** Investigation, Formal analysis, Data curation, Writing – review & editing. **Annika M. Felton:** Conceptualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120414.

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