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RESEARCH ARTICLE

The proximity of rapeseed fields influences levels of forest damage by red deer

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ABSTRACT

1. Deer can show transitional use between agricultural fields and forests for foraging and shelter. Such transitional use may affect forest damage as nutrient balancing theory suggests that if deer ingest large amounts of nutrient-rich food, complementary browse, such as bark, may be required to balance the diet.
2. We investigated the relationship between the level of red deer *Cervus elaphus* bark-stripping damage in 68 Norway spruce *Picea abies* stands and the presence of rapeseed *Brassica napus* fields – an energy-rich crop preferred by red deer – in the surroundings, hypothesizing that damage increases with decreasing distance to rapeseed fields. We also considered other potentially influencing factors, such as supplemental feeding, alternative forage availability, and deer use of spruce stands as indexed by a pellet group count.
3. Spruce stands closer to rapeseed had a significantly higher proportion of damaged stems. The increased level of bark-stripping damage was not explained by a higher stand use of deer closer to rapeseed fields, indicating that deer increase their consumption of bark in order to balance their diet. Similarly, spruce stands closer to supplemental feeding stations had significantly higher damage levels.
4. In line with earlier findings, damage levels were negatively related to the amount of available browse in the forest. This emphasizes the importance of alternative forage for reducing the damage risk in forest plantations.
5. Our study shows that the availability of fields with nutrient-rich food, such as rapeseed, as well as supplemental feeding needs to be considered when predicting the level of forest damage. With a high availability of nutrient-rich food in the vicinity of forest stands, a higher damage level can be expected and counteractions could be taken such as increased disturbance, harvest or changed choice of both crop and supplemental feed types. These actions may also be combined with a push–pull strategy where the deer are steered to disturbance-free zones insensitive to damage and with alternative forage. The importance of alternative forage availability on

damage levels highlights the necessity for managers to actively promote tree and shrub forage within and around their production stands.

KEYWORDS
bark stripping, *Cervus elaphus*, game management, landscape ecology, Norway spruce, nutritional balancing, timber production, ungulate damage

1 | INTRODUCTION

Wildlife in human-dominated landscapes is largely dependent on man-made habitats such as agricultural fields and forest plantations for foraging and shelter, resulting in conflicts due to damage to human livelihoods (König et al., 2020; Linnell et al., 2020; Valente et al., 2020). Free-ranging herbivores, such as deer (Cervidae, Ungulata) may cause damage to crops and trees by feeding, resting and trampling, often resulting in economic losses (Conover, 1997; Doney & Packer, 1998; Gill, 1992b; Reimoser & Putman, 2011). In forest plantations, damage levels are influenced by population densities but also by weather conditions and landscape features such as forage availability and habitat composition (Gill, 1992a; Putman et al., 2011; Reimoser & Gossow, 1996; Spake et al., 2020). Damage mitigation is therefore a complex challenge, for which knowledge about the relative influence of different driving factors is needed in order to find appropriate management tools (Doney & Packer, 1998; Kuijper, 2011; Reimoser, 2003; Spake et al., 2020).

Bark stripping by red deer (*Cervus elaphus*) is one example of a complex management challenge where several factors seem to influence damage levels (Gill, 1992a; Gerhardt et al., 2013; Verheyden et al., 2006). The magnitude of bark-stripping damage can be positively related to deer population density at different spatial scales (Candaele et al., 2021; Jerina et al., 2008; Kiffner et al., 2008; Ligot et al., 2013), but there are inconsistencies in this relationship (Gill, 1992a; Jarnemo et al., 2014; Verheyden et al., 2006). A weak relationship between red deer density and damage level is likely due to other factors overshadowing the importance of density (Jarnemo et al., 2014; Reimoser & Putman, 2011; Völk, 1999).

The availability of natural forage in the field and shrub layers can affect the level of bark stripping within forest plantations (Jarnemo et al., 2014; Reimoser & Gossow, 1996). This suggests that deer increase their intake of bark when other more palatable and nutritious food resources are scarce (Gill, 1992a; Ueckermann, 1956; Verheyden et al., 2006). Many plants are potentially palatable for red deer as they are intermediate feeders, meaning that they are able to switch between browsing on woody items and grazing on herbaceous vegetation (Clauss et al., 2010; Hofmann, 1989). Moreover, the level of bark stripping can also be positively related to the proportion of agricultural land in the surrounding landscape (Jarnemo et al., 2014), suggesting that landscape structure and/or land use may be important additional factors that should be considered for an increased understanding of deer damage patterns (Kuijper, 2011; Putman et al., 2011; Takarabe & Iijima, 2020; Spake et al., 2020).

In mixed forest–agricultural landscapes, red deer tend to adopt an activity pattern characterized by feeding in the open during the night and seeking shelter and food in the forest during the day (Allen et al., 2014; Georgii, 1981; Pepin et al., 2009). At night, deer commonly feed on various agricultural fields (Lande et al., 2014; Månsson et al., 2021; Zweifel-Schielly et al., 2012) and it is possible that bark-stripping rates in mixed landscapes can be related to the intake of certain crops. Potential drivers behind such a relationship may include nutritional deficiencies or imbalances (Gill, 1992a). While the evidence is scarce regarding a clear relationship between bark nutrient concentration and bark-stripping levels, there are studies suggesting that the animals' nutritional state can affect bark stripping, for example through mineral imbalance (Ando et al., 2004) or imbalance between protein and carbohydrates (macronutrients) in their overall diets (Faber, 1996; Felton et al., 2016; Miranda et al., 2015; Saint-Andrieux et al., 2009; White, 2019).

Red deer often select plants of high nutritional value but also include tannin- and fibre-rich food items in their diet (Felton et al., 2017; Gebert & Verheyden-Tixier, 2001; Zweifel-Schielly et al., 2009, 2012). According to the nutrient balancing hypothesis (Simpson & Raubenheimer, 2012), red deer ingesting a large amount of food items rich in non-structural carbohydrates such as sugars and starches (e.g. crops growing on fields) might require nutritionally complementary material from trees, such as bark, to reach a balanced diet (Felton et al., 2017). Because red deer are ruminants, such complementary intake of bark could also provide some of the roughage (structural carbohydrates) which ruminants require to ensure proper rumen functioning (Faber, 1996; Felton et al., 2016; Van de Veen, 1973). Rapid fermentation, caused by large intakes of non-structural carbohydrates, can lead to low rumen pH which reduces microbial efficiency (Sniffen et al., 1992) and fibre digestion (Pitt et al., 1996). In fact, ruminal acidosis can occur if a ruminant's carbohydrate intake is shifted too far towards starch and sugars. This in turn can have negative implications for digestion, milk production, overall condition and may even cause death (Keunen et al., 2002; M.V.M., 2005). Deer do not only obtain crops rich in non-structural carbohydrates on agricultural fields but may also be supplied such crops, for example root vegetables, at feeding stations by managers. Supplementary feeding of deer is a common practice both in Europe and in North America (Putman & Staines, 2004) and has been shown to both mitigate damage in production forests and increase damage levels (Gundersen et al., 2004; Masuko et al., 2011; Mathisen et al., 2014; Milner et al., 2014; Rajský et al., 2008).

Rapeseed (*Brassica napus ssp. napus*) is an energy-rich crop that wild red deer appear to prefer to eat (Ahlén, 1965; Månsson et al., 2021) and that may affect their nutrient balance and in turn forest damage levels. Rapeseed contains high concentrations of macronutrients (Spörndly, 2003). For example, leaves of rapeseed plants eaten by deer in the spring have approximately 11 times higher protein concentrations and five times lower indigestible fibre (lignin) concentrations than spruce bark (A. Widén, unpublished data, collected 2018). Feeding on brassicas has accordingly been found to generate lower pH in the forestomach of ruminants (Barry, 2013). Among managers in Sweden, it is suggested that autumn-sown rapeseed, which is available for red deer throughout the winter and spring, can induce higher bark-stripping rates in adjacent Norway spruce (*Picea abies*) stands. Both production of spruce timber and rapeseed crops are common in regions of Sweden where red deer occur today. Our study was conducted in a mixed forest–agricultural landscape, where high bark-stripping levels have been observed since the early 1900s (Ahlén, 1965; Ekman, 1990; Månsson & Jarnemo, 2013). Earlier studies (Allen et al., 2014; Månsson et al., 2021) have confirmed that red deer in the area display a transitional use between agricultural fields and forests for foraging and shelter. The main aim of our study was to investigate whether bark stripping is influenced by the distance between rapeseed fields and production forests. We hypothesized that bark-stripping damage increases with decreasing distance to rapeseed fields. To control for other factors that have previously been shown to impact bark stripping, we also included supplemental feeding, availability of alternative forage and deer stand use.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is in the county of Skåne in southernmost Sweden (N55°4 E13°40, nemoral zone, Figure 1). It is a mainly flat lowland area with small altitudinal variations (elevation ranging from 25 to 160 m above sea level). The climate is mild with a mean temperature of −1°C in January and 16° C in July. Annual snow cover averages 25 days. Annual precipitation averages 700–800 mm with a monthly minimum in February–March with 30 mm and most precipitation in July and August with 60–70 mm per month (Swedish Meteorological and Hydrological Institute, data retrieved 15 April 2020).

The landscape is highly affected by human land use and dominated by modern agriculture and managed forests. In Skåne county, the ratio of agricultural land to productive forest land is 1.5, and the average forest timber productivity index is 11.1 m^3 ha^{-1} $year^{-1}$. The productive forest area consists of 10% Scots pine (*Pinus sylvestris*), 36% Norway spruce, 2% mixed conifer, 6% mixed conifer/broadleaved and 40% broadleaved tree species (Nilsson et al., 2016). The common agricultural practice is crop rotation and the dominant crops are cereals (48% of arable land), ley (22%), rapeseed (11%), sugar beets (7%), potatoes (2%), leguminous plants (2%) and maize (1%) (Jordbruksverket, 2017).

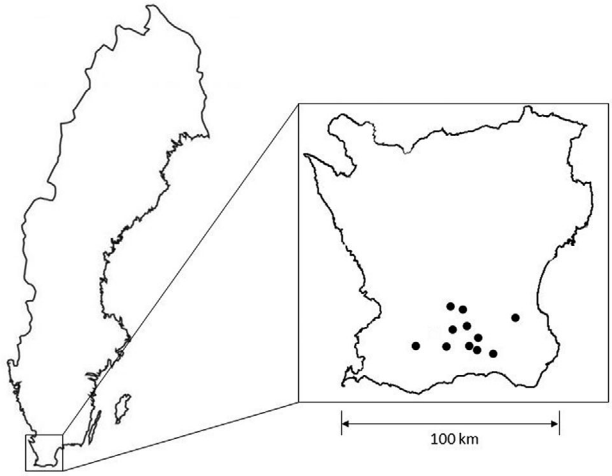

FIGURE 1 Study area: map of Sweden with the southernmost county Skåne. The 11 estates where data was collected are marked with black dots

The red deer population in the study area represents a part of a free-ranging remnant population of the original nominate red deer subspecies *C. elaphus elaphus* (Ahlén, 1965; Jarnemo et al., 2017; Höglund et al., 2013). The deer population is managed through regulated annual hunting within a designated management area of 2600 km^2 where the goal is to maintain a pre-harvest population size of 3000 deer (Jarnemo & Carlsson, 2014). A licensed harvest is allowed from the second Monday in October to 31 January, that is outside the rut (Jarnemo, 2008, 2011). During the 10-year period preceding the study, the total reported harvest has increased from 287 (season 2006/2007) to 801 deer for the season 2016/2017 (data from the County Administration of Skåne). Roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and wild boar (*Sus* scrofa) are common in the study area, whereas moose (*Alces alces*) is rare. Large predators such as wolf (*Canis lupus*) and lynx (*Lynx lynx*) only make rare, occasional visits and should not have any impact on red deer behaviour.

Bark-stripping damage on Norway spruce has been described as a problem in the study area since the 1890s (Ekman, 1990; Lavsund, 1968a). Surveys in the 1960s showed damage levels of 50–100% on Norway spruce in the study area (Hellichius, 1964; Lavsund, 1968b; Sjöström, 1961), and during this decade the total red deer population was estimated to increase from 150 to 300 (Ahlén, 1965). Bark stripping can make the tree vulnerable to fungal infestation leading to rotted wood. Other effects can be discoloration and stem deformation. The tree generally does not die from the damage, but the weakened stem can be more susceptible to storm breakage (Gill, 1992b; Krisans et al., 2020; Putman and Moore, 1998; Vasiliauska & Stenlid, 1998; Vasiliauska, 2001).

2.2 | Collection of field data

2.2.1 | Level of damage in spruce stands

Data were collected during April–May 2017 in 11 different estates in the study area (Figure 1). No license was needed for the fieldwork, but the estates permitted data collection and cooperated by supplying background data on spruce stands, rapeseed fields and supplemental feeding. The period for data collection was chosen so that the majority of the season's bark stripping was done, but after snowmelt and before spring green-up in forest habitats, to be able to perform a pellet group count and a forage survey. Bark-stripping rates were measured in 68 planted stands of Norway spruce with a minimum size of 1 ha. We chose the age class 20–40 years to encompass the age interval in which the majority of the damage in the area occurs (Ahlén, 1965; Sjöström, 1961) and to be able to compare our results with previous studies (Jarnemo et al., 2014; Månsson & Jarnemo, 2013). In another study in the same region, Felton and Nilsson (2018) did not find any relationship between spruce stand age and damage level in stands. We selected, a priori, stands in forestry plans with a minimum of 80% spruce. However, all stands were planted in even-aged monocultures where cleaning of deciduous species had occurred at younger stages, resulting in a spruce proportion generally close to 100%. In each stand, 10 circular 100 m^2 survey plots were systematically and evenly distributed (with a random starting point) (see Månsson and Jarnemo, 2013, for details). Occurrence of fresh bark-stripping damage (i.e. wounds from the preceding winter) was noted for the 10 spruce stems closest to the plot centre (i.e. 100 spruce stems per stand). We classified damage to be fresh by the colour of the bite surface and resins. The bright colour of wounds from the latest season differs markedly from the darker older wounds and combined with the fact that the bark tissue around fresh damage is conserved (by dormancy during the preceding winter), fresh wounds are easily distinguished from old bites from previous years. Red deer can either take small bites of the bark ("gnaw") or peel off large sections of the bark ("peel"). We included both types of bark damage in our inventory. Bark stripping on Norway spruce by moose and fallow deer seems comparatively rare in Sweden (despite much higher population numbers than for red deer; Liberg et al., 2010). Bark stripping by these two species can be distinguished from red deer by the height of the wounds and the width of tooth marks (Lavsund, 1980; Mayle, 1999). We did not observe bark stripping where moose or fallow deer could be suspected to be the culprit species.

2.2.2 | Forage availability

An index of relative forage availability was measured by estimating the percentage of living vegetation cover of woody browse projected onto the horizontal plane in 20 m^2 subplots within targeted stands (the same 10 plots per stand as for the damage survey) and in the surrounding landscape in plots distributed along 500 m transects, one in each of the cardinal directions from the targeted stand (plots distributed at 0, 100, 200, 300, 400 and 500 m from the stand edge (0 m) making a total of 24 transect plots per stand) (Hörnberg, 2001; Jarnemo et al., 2014; Månsson et al., 2012). We have earlier shown that the forage index provided by this design relates to the bark-stripping level within targeted stands (Jarnemo et al., 2014). The forage index consisted of the sum of the cover of shrub species like bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), heather (*Calluna vulgaris*), bramble (*Rubus fruticosus*) and raspberry (*Rubus idaeus*) as well as of aspen (*Populus tremula*), ash (*Fraxinus excelsior*), birch (*Betula spp.*), oak (*Quercus robur*), rowan (*Sorbus aucuparia*), willows (*Salix* spp.), juniper (*Juniperus communis*), Scots pine (*Pinus sylvestris*) and Norway spruce trees not higher than 3 m. The 3-m height was chosen to encompass the preferred red deer browsing range roughly equal to their shoulder height (Renaud et al., 2003) but also taking into account that red deer can browse standing on their hind legs, that large-antlered males standing on their hind legs can use their antlers to break off and drag down branches to the ground and that snow cover may help the deer to reach higher.

2.2.3 | Pellet group survey

The number of red deer pellet groups was counted within targeted spruce stands and in the surrounding landscape to provide indices of relative deer stand usage and overall abundance, respectively (Mayle et al., 1999; Jarnemo et al., 2014). Pellet groups were surveyed in 100 m^2 circular plots within the stands (the same plots as for the damage and forage survey) and in the transect plots used for the forage survey described above. Only fresh (from preceding winter) pellet groups were counted. Pellet groups were aged by colour and position in relation to litter and old vegetation (Månsson et al., 2011; Månsson and Jarnemo, 2013).

2.2.4 | Rapeseed fields and supplemental feeding stations

Information regarding the locations of rapeseed fields, supplemental feeding stations as well as the type of feed was provided by landowners, game managers and hunters. Several types of feed were used (sugar beets (*Beta vulgaris*), carrots (*Daucus carota)*, potatoes (*Solanum tuberosum*), maize (*Zea mays*), various types of silage and grains) and were often used simultaneously at the feeding stations. These types of crops have much higher proportions of non-structural carbohydrates than woody forage (Felton et al., 2017). For example, the concentration of sugar is ca. 65% in sugar beets and 60% in carrots (Spörndly, 2003), compared to 5–16% non-structural carbohydrates in woody forage often eaten by deer winter time (browse from dwarf shrubs and twigs of conifer and broadleaved trees; Felton et al., 2021). The amount of feed, or share of the different feeds, was not quantified. However, sugar beets were most likely the dominant feed (see Section 4). Supplemental feeding is generally conducted from October to February. We measured the distance from the rapeseed fields and feeding stations to the spruce stands by using QGIS.

2.3 | Statistical analysis

All analyses were carried out in R (version 4.0.0). We used generalized mixed-effects models (GLMMs, function glmer in lme4 package; Bates et al., 2015) with binomial distribution to model bark-stripping damage. The response variable was the proportion of spruce trees with fresh red deer damage at the stand level. Explanatory variables were the distance from the spruce stand to the closest rapeseed field, the proportion of ground covered by forage in stands (average of 10 plots) and along transects (average of the 24 transect plots surrounding the spruce stand), number of fresh red deer pellet groups in the stand (average for the 10 plots) and along transects (average for the 24 transect plots) and distance to closest supplementary feeding station (regardless of feed type). The interaction between distance to rapeseed and pellet groups in stands was tested, based on the hypothesis that the degree of the effect of stand use by deer on spruce damage may be dependent on the distance to rapeseed fields. The study area (estate) was added as random effect ($n = 11$). The sample size did not allow for more interaction terms to be included in the model, and we prioritized the one that was most central to our core research question.

The number of plots surveyed along transects was sometimes reduced as plots could be placed in water, built areas, roads or cultivated soils. With a maximum of 6 plots per transect and 24 plots per stand, on average 18 ± 0.5 (standard error [SE]) plots surrounding the fields were surveyed, hence, on average 4.5 plots per transect. Stands with less than 10 sample plots along transects were excluded from the analysis. In total, seven stands were excluded from the analysis because of this. The average number of stands per estate was 7 ± 1.01 (SE) with a minimum of 2 and a maximum of 12. The minimum and maximum distances from stands to rapeseed fields were 0 and 4.1 km, respectively. The minimum and maximum distance from stands to supplementary feeding stations were 0 and 2.1 km, respectively. The maximum distance between spruce stands was 7.46 km and the minimum distance was 0.2 km (Table S1 in the Supporting Information),

We first tested multicollinearity among potential explanatory variables (Pearson's $r \geq +0.7$ or ≤ -0.7) but found no evidence for it. We adopted a stepwise deletion approach and verified the removal of variables with likelihood ratio tests (function lrtest in package lmtest). To further investigate whether the red deer stand usage was related to the distance to rapeseed fields or feed stations, we investigated the relationship between the number of red deer pellet groups on stand level and the distance to rapeseed fields and feeding stations using a GLMM with the Poisson distribution and study area as the random effect. All models were checked for basic assumptions of normality and heterogeneity of residuals using the Dharma package in R (Hartig, 2016).

3 | RESULTS

On average, 87% of the total 7400 surveyed trees had been damaged (old and fresh damage) by red deer. In an average spruce stand, 18% of trees showed fresh damage from the latest winter-spring season but damage levels varied between 0% and 73% among stands. Most of the freshly damaged trees had damage of the gnawing type (17%), whereas 1% had the peeling type.

The final model to predict the proportion of freshly damaged trees at the stand level, provided by the stepwise approach, contained distance to the rapeseed field, forage availability in spruce stands, number of fresh red deer pellet groups in spruce stands and along transects, distance to the supplementary feeding station and the interaction between distance to rapeseed field and number of pellet groups in the stand (Table 1). Thus, the only variable removed from the full model was forage availability along transects.

The probability of fresh damage decreased with increasing distance to rapeseed fields, a higher proportion of forage in stands and increasing distance to supplementary feeding stations (Table 2 and Figure 2), while damage probability instead increased with a higher number of red deer pellet groups in stand and along transects (Table 2 and Figure 2). The interaction effect reveals that the proportion of damaged trees increased with a higher rate closer to the rapeseed field given the number of pellet groups in the stands (Table 2 and Figure 3). The marginal R^2 value for the model was 0.196, and the conditional R^2 value was 0.296.

The number of pellet groups found in the spruce stands was not significantly influenced by distance to rapeseed fields (estimate (SE): −0.019 (0.12); z-value: −0.16; p-value: 0.8) nor by distance to feeding station (0.15 (0.08); z-value: 1.78; p-value: 0.07). The marginal R^2 value was 0.016, and the conditional R^2 value was 0.064.

4 | DISCUSSION

We found significant relationships between the damage levels in Norway spruce stands and distance to both rapeseed fields and supplementary feeding stations. The proportion of trees damaged by bark stripping was higher in stands close to rapeseed fields as well as in stands close to supplementary feeding stations. Our study, therefore, shows that when evaluating the risk for bark-stripping damage, crop availability in the surrounding agricultural matrix needs to be considered. Furthermore, our findings suggest that the pattern observed is likely due to nutritional drivers, rather than due to increased deer use of spruce stands close to these sources of crops.

We found that on average 18% of the surveyed trees per stand had been damaged by red deer the preceding winter and that 87% of all trees inventoried had been damaged including old damage. These damage levels are almost identical to a previous study in the same region (17% and 88%, respectively; Månsson & Jarnemo, 2013). Damage levels were negatively related to the amount of forage, which is in line with earlier findings (Jarnemo et al., 2014), highlighting the

TABLE 1 Descriptive values from explanatory variables used in the model

	Mean (SE)	Minimum	Maximum
Distance to rapeseed fields (km)	1.29 (0.12)	0	4.10
Distance to feeding station (km)	0.48 (0.11)	0	7.00
Forage availability in spruce stands (proportion cover)	0.01 (0.00)	0	0.09
Number of red deer pellet groups in spruce stands	1.14 (0.12)	0	6.90
Number of red deer pellet groups along transects	0.38 (0.04)	0	1.27

TABLE 2 Model parameter estimates with standard error (SE) and significance level from the final GLMM for the probability of fresh damage as a function of the six most important explanatory variables

	Estimate (SE)	*z*-value	*p*-value
Intercept	−1.58 (0.188)	−8.38	≤0.001
Distance to rapeseed field (km)	−0.65 (0.08)	−7.67	≤0.001
Forage availability in spruce stands	−0.24 (0.04)	−5.76	≤0.001
Number of red deer pellet groups in spruce stands	0.64 (0.06)	10.33	≤0.001
Number of red deer pellet groups along transects	0.17 (0.04)	4.05	≤0.001
Distance to feeding station (km)	−0.17 (0.05)	−3.20	0.001
Distance to rapeseed pellets in stands	−0.11 (0.05)	−2.43	0.015

mitigating effect that alternative forage can have on damage risk in the forest stands.

The increased risk of bark stripping in the vicinity of rapeseed fields can be explained by two different mechanisms (or a combination of the two): (1) rapeseed is a preferable food item and attracts deer resulting in a higher deer use of spruce plantations close to rapeseed fields, and (2) the intake of rapeseed increases the urge for deer to balance their diet, and bark satisfies this need (Felton et al., 2016, 2017). An earlier study has revealed that red deer in the area spend a disproportionately high amount of time in rapeseed fields compared to their availability, both during winter and summer (Månsson et al., 2021). However, if rapeseed attracted deer to spruce stands in the near surroundings, we should expect that the number of counted pellet groups in the spruce stands increased with decreasing distance to rapeseed. Although we, in accordance with Jarnemo et al. (2014), found a positive relationship between the number of pellet groups in stands and damage level (Figure 2), there was no significant relationship between distance to rapeseed and the number of pellet groups in spruce stands. Instead, the significant interaction effect in the model explaining variation in spruce damage implies that the effect of the number of pellet groups on the damage level is even more pronounced (a steeper slope in the relationship) in stands close to rapeseed fields than further away. Moreover, a spruce stand with a low number of pellet groups (= low use) but close to a rapeseed field has a higher proportion of damaged stems compared to a field with a high number of pellet groups (= high use) but far away from a rapeseed field. That we did not find the expected higher deer use of spruce plantations close to rapeseed fields might reflect that the deer take into account other factors than the distance to feeding patches when selecting daytime resting place. We do know that the red deer in the area display a pattern of seeking shelter in dense forests during the daytime and use open habitats for nocturnal feeding (Allen et al., 2014), but we have not investigated how landscape structure, habitat composition or anthropogenic disturbances affect their selection of daytime resting places in the study area.

We found that spruce stands closer to feeding stations had higher damage levels, while the relationship between the number of pellet groups and distance to feeding stations was non-significant. High levels of damage in forests near supplemental feeding sites have been associated with a higher deer use of such stands than in stands further away from feeding stations (Gossow, 1988; Jerina et al., 2008; Nahlik, 1995), or with an increased need for the bark to balance the diet (Nahlik, 1995; Ueckermann, 1983). However, supplemental feeding can also reduce bark stripping by deer (Borowski et al., 2019; Ueckermann, 1983), and certain types of feed, for example beet pulp or mixed silage, seem to counteract the urge to consume bark (Ueckermann et al., 1977; Masuko et al., 2011; Pheiffer & Hartfiel, 1984; Rajský et al., 2008), which adds further complexity to this issue. Supplemental feeding is generally conducted from October to February and is frequent in the study area. Most of the spruce stands were situated less than 1 km from the nearest feeding station; a distance well within the normal day range of local red deer, for which the average daily area utilized is 2.5 km^2 while feeding and 1.3 km^2 while resting (Allen et al., 2014). Despite this relative lack of variation regarding the distance between spruce stands and feeding stations, we found a clear relationship between damage levels and distance to feeding stations.

Neither in the case of rapeseed fields nor in the case of supplementary feeding stations the pattern of high damage levels in nearby spruce stands could be explained by an elevated stand use of red deer (i.e. an increase in counted pellet groups). Instead, our results may lend

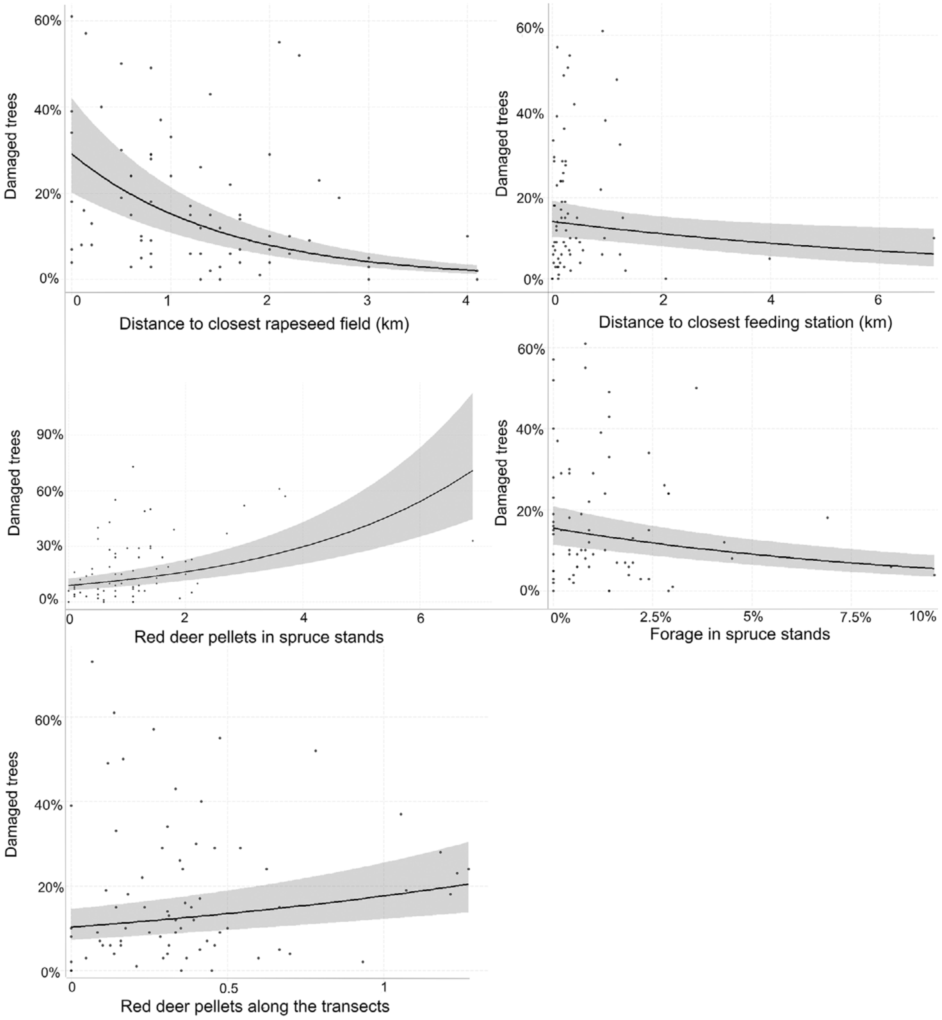

FIGURE 2 Model prediction plots with observed values showing the relationship between the proportion of damaged spruce trees in stands and (a) the distance from the stand to the closest rapeseed field, (b) the distance from the stand to the closest feeding station, (c) the number of pellet groups in spruce stands, (d) available forage in stands and (e) the number of pellet groups along transects (the grey-shaded area shows 95% confidence interval). Plots were created by setting all other variables in the model constant, and continuous variables were set to their mean value

support to the nutritional balancing hypothesis (Simpson & Raubenheimer, 2012). Although our study cannot provide evidence of the actual food selection of individual red deer, we suggest that the animals may have combined intakes of crops with intakes of bark from nearby stands to obtain a more nutritionally balanced diet. Such complementary feeding was observed in captive red deer, with intake of concentrates (pellets) by the deer led to increased browsing of plant species that offered nutritional compositions complementary to the supplement (Miranda et al., 2015). Similarly, captive moose have been found to significantly increase their intake of tree browse when restricted to a pellet diet with high concentrations of either protein or non-structural carbohydrates (Felton et al., 2016). In the above-mentioned studies of captive cervids, the nutritional composition of supplements was very different from the food items that these animals would eat in the wild. In our study, the free-ranging red deer faced similar contrasts. A collection of rapeseed plants from a field in the county of Skåne during spring showed that the leaves of rapeseed plants contained 11 times more protein and 10 times less hemicellulose than spruce bark (A. M. Felton, unpublished data). Similarly, several types of supplemental feed commonly used in our study area (e.g. the root vegetables sugar beets, carrots and potatoes) have been cultivated for enhanced nutrient content and have nutritional compositions very different from browse (Felton et al., 2021). While other feeds were also used in our study area (silage, maize and grains), the most common feed was root vegetables and especially sugar beets (A. M. Felton, unpublished data). Sugar beets have on average seven times higher concentrations of non-structural carbohydrates than the tree and shrub browse does in wintertime, while the proportion of structural carbohydrates (neutral detergent fibre) is only a third of that in the browse (Felton et al., 2021). Due to these contrasts between these agricultural crops and the natural winter forage, the deer are likely to seek out complementary food items, as predicted by the nutrient balancing hypothesis (Simpson & Raubenheimer, 2012), with bark damage as the potential outcome.

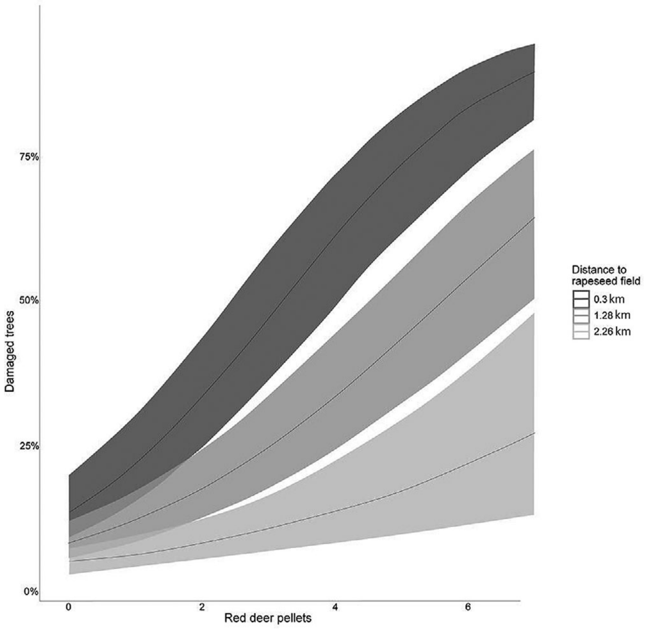

FIGURE 3 Model prediction plot showing the significant interaction effect of the number of pellet groups in spruce stands and the distance to rapeseed field on the proportion of damaged spruce trees. The mean value of distance to rapeseed field (1.28 km) as well as one standard deviation below (0.30 km) and above (2.26 km) mean value is used to illustrate the interaction. Note that the proportion of damaged trees will increase with increasing number of pellet groups more strongly when the stand is closer to a rapeseed field

Our study shows that when forest owners and managers in the mixed forest–agricultural landscape of the study area and region evaluate the risk of bark damage to their conifer production stands caused by deer, the landscape matrix needs to be considered. By carefully assessing the landscape matrix, relevant countermeasures can be planned. For example, in those years when rapeseed fields are established in the vicinity of spruce stands, a higher risk of damage should be expected. A possible counteraction may be to actively create disturbances in the vulnerable stands during winter and spring, such as visits by people or dogs, as red deer tend to avoid such disturbances (Chassagneux et al., 2020; Jarnemo & Wikenros, 2014; Sunde et al., 2009; Sibbald et al., 2011) and possibly combined with creating disturbance-free zones with alternative forage in a 'push–pull' strategy (Cook et al., 2007; Jarnemo et al., 2014). One example of a suitable disturbance-free habitat type could be wetlands with tree and bush vegetation, a habitat type selected by red deer in the study area (Månsson et al. 2021). Another alternative may be provided by short-rotation coppice (bioenergy crops such as willow) that offer both cover and food for deer (Bergström & Guillet, 2002). Red deer in the study area have shown an extensive use of short-rotation coppice (Månsson et al., 2021), and this is a type of habitat that can be created with relatively short notice in order to provide an alternative daytime cover to damage sensitive forest stands. Regarding supplemental feeding stations, our study indicates that managers should avoid types of feed that appear to induce deer to eat bark (e.g. root vegetables and similar crops rich in sugar or starch), and perhaps replace them with feeds that can act as a substitute for bark and thus might reduce bark stripping (Borowski et al., 2019; Masuko et al., 2011; Rajský et al., 2008). Rajský et al. (2008) recommend a combination of hay with maize silage, grass silage or pelleted feed containing biomass of forest woody plants. Masuko et al. (2011) found that beet pulp reduced bark stripping by sika deer (*Cervus nippon*). In addition, it seems wise to avoid placing feeding stations close to damage-sensitive forest plantations. Furthermore, this study confirms the importance of alternative forage availability when evaluating the risk of bark stripping and we, therefore, highlight the necessity for managers to actively promote tree and shrub forage within and around their production stands.

In summary, our results suggest that the red deer in our study area ate more bark in spruce stands closer to rapeseed fields or supplemental feeding stations, possibly to compensate for the macro-nutritional imbalance and that this pattern was more pronounced in stands lacking vegetation offering alternative forage. This is in line with studies on deer damage, in general suggesting that deer and forestry interact in a varied and complex way and do so under the impact of several different factors, for example landscape structure, climate and human disturbance (Gill, 1992a; Gerhardt et al., 2013; Spake et al., 2020). Deer affect forestry by damaging trees, and forestry affects deer and other ungulates by changing tree composition and the age structure of the forest landscape (Reimoser & Gossow, 1996; Völk, 1999; Wam et al., 2016), with repercussions on the availability of forage and shelter (Borkowski & Ukalski, 2012; Felton et al., 2020; Petersson et al., 2019). The influence of agricultural crops on deer bark-stripping behaviour and associated damage to valuable trees that we have presented in this study add to this complex web of interactions. Among several authors (e.g. Gerhardt et al., 2013; Kuijper, 2011; Nopp-Mayr et al., 2011; Reimoser & Gossow, 1996; Reimoser, 2003; Völk, 1999), there is a consensus that the problem with bark stripping and other browsing damage cannot be solved solely through deer management (e.g. increased harvest), but rather requires integration of deer management, forestry practices and sources of human disturbance such as outdoor recreation, hunting and distance to roads and settlements. Our study suggests that also agriculture should be a part of that integration.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Anders Jarnemo, Johan Månsson and Annika M. Felton conceived the idea and designed the study. Anders Jarnemo and Anna Widén collected the field data. Anna Widén made the first analysis of the data, but all authors participated in this work. Anders Jarnemo led the writing of the manuscript, but all authors made contributions to drafts and approved the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fj6q573xg (Jarnemo et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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