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ORIGINAL PAPER

Efficient application of a browsing repellent: Can associational effects within and between plants be exploited?

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Abstract

Browsing can reduce forest productivity, particularly when the apical shoots of trees are damaged. Repellents are used widely to reduce browsing, but application is costly. To improve efficiency, it may be possible to take advantage of associational plant refuge effects, requiring repellents to be applied only to some trees or parts of trees, or reapplied less frequently. Using captive moose (*Alces alces*) and constructed stands of Scots pine (*Pinus sylvestris*), we tested for potential refuges by applying a commercial repellent (HaTe2) to all, alternate or none of the apical shoots, or all of the previous-year apical shoots. We also tested for potential refuges under field conditions, applying the repellent to all, alternate or none of the apical pine shoots in forest stands. Captive moose (two individuals in a 2.1-ha enclosure, ~ 95 individuals km^{-2}) browsed 100% of trees, but were significantly less likely to browse apical shoots treated with repellent. Associational refuge was ineffective both within and between trees. In the field (0.84 moose km^{-2}), only 1.3% of trees sustained browsing damage. Applying the repellent to the apical shoots of pines had no direct repellent effect nor any within-plant associational effects. Trees with treated apical shoots provided some protection for untreated neighbouring trees, but this was not biologically meaningful given the low percentage of trees browsed overall. Here, a simple captive experiment was not predictive of the browsing response observed in the field, demonstrating the need to test repellent application strategies in situ.

Keywords Foraging decision · Forestry · Herbivore · Multi-use management · Pine · Ungulate

Introduction

Large herbivores can influence the composition and structure of forests by browsing trees, with reduced growth and increased mortality ultimately resulting in lower rates of tree recruitment (Husheer et al. 2003; Long et al. 2007). This can be ecologically and economically costly because it can alter habitat and food availability for other biota, hamper forest restoration projects and reduce timber value in harvested forests (Conover 1997; Pedersen et al. 2007; Putman and Moore 1998). Recent increases in the population sizes of several species of mammalian herbivores in forested ecosystems have thus been met with calls for management intervention (Côté et al. 2004; Di Stefano 2004; Menkhorst 2008). In many situations, direct reduction in population numbers by culling is not desirable, particularly where the aim is to manage forests for multiple uses, such as coupling timber production with ecosystem services, maintenance of biodiversity, recreation and hunting (Milner et al. 2013). One alternative for reducing damage by abundant mammalian

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herbivores is to apply browsing repellents to trees. However, using repellents in forests can be costly because it usually involves on-ground application to individual trees, and requires re-application as trees produce new unprotected shoots and the repellent is worn down by the elements. To reduce these costs, it may be possible to lower the spatial and temporal frequency with which the repellent is applied by taking advantage of how herbivores make foraging decisions at multiple scales, from parts of individual trees to forest stands.

Browsing repellents can be considered as a form of artificial plant defence. While classical defence theories assume that a plant is protected from herbivory only by its own chemical or physical defences, several empirical studies indicate that herbivore attack and consumption rates are also dependent on the defence traits of neighbouring plants (Atsatt and O'Dowd 1976; Milchunas and Noy-Meir 2002; Tahvanainen and Root 1972). Associational plant effects determine the probability of browsing by mammals at multiple scales (Bergvall et al. 2008; Herfindal et al. 2015; Stutz et al. 2015). Undefended plants may receive protection from their defended neighbours if the latter cause herbivores to avoid the plant patch (associational refuge via the repellent plant mechanism; Atsatt and O'Dowd 1976), but if herbivores choose between plants within a patch, undefended plants can be browsed preferentially from amongst their defended neighbours (associational susceptibility via the neighbour contrast mechanism; Bergvall et al. 2006). These concepts can be extended to contrasts in the defence characteristics of different parts within a single plant (Bergvall and Leimar 2017). Within- and between-plant contrasts in defence may be created when applying repellents.

Contrasts created by applying repellents are of interest because they can affect the fate of plants or plant parts at the edges of treated areas (Palmer et al. 2003), and they could also be exploited to reduce repellent application frequency in both space and time. Our objective was to test whether within- and between-plant contrasts created by repellent application could be used to manipulate browsing patterns. We conducted two experiments during a Scandinavian winter to quantify the browsing of Scots pine (*Pinus sylvestris*) by moose (*Alces alces*) in response to applications of a commercial repellent (HaTe2). In this region, a large part of the moose diet is comprised of Scots pine, peaking in winter when the preferred deciduous trees have lost their leaves (Hörnberg 2001b; Shipley et al. 1998; Wam and Hjeljord 2010). Browsing of pine causes economic losses from reduced wood quality, lower-density stands, slower vertical growth and extended stand rotation (Gill 1992; Kullberg and Bergström 2001). Although some pines continue to grow in an acceptable manner despite some defoliation (Honkanen et al. 1994), a severe problem arises when ungulates browse the apical shoot as this causes branching and is detrimental to saw timber value (Bergqvist et al. 2001; Hörnberg 2001a; Wallgren et al. 2013). The idea that associational effects could be exploited to use repellents efficiently is supported by existing evidence that pine browsing by moose is influenced by plant neighbourhoods. For example, applying an extract of birch bark (*Betula* spp.) to alternate Scots pine seedlings resulted in associational refuge from captive moose for untreated seedlings planted at standard forestry spacing (Stutz et al. 2017a). In addition, browsing of pine by moose was affected by associations with alternative browse species at multiple scales in forests of southern Norway (Herfindal et al. 2015). Understanding how repellents function in this system is therefore of both basic and applied ecological value.

In Experiment 1, we tested neighbourhood effects within and between pine trees exposed to captive moose. Specifically, we asked whether (a) applying repellent only to the apical shoot had any protective effect on lateral shoots, (b) applying repellent on the previous-year apical shoot could protect the current apical shoot and (c) moose foraging behaviour could explain within-plant patterns of browsing damage. To test for between-plant associational effects, we also determined whether pines with treated apical shoots provided refuge for untreated neighbours. In addition to reducing the amount of repellent needed, applying repellent to only every second tree would require substantially less time than treating all trees; in a pilot study, Pedersen and Bjørke (unpublished data) found that alternate application of HaTe2 took a mean of 41% less time than applying the repellent to all trees in pine forest stands. In Experiment 2, we tested the repellent in the field by applying it to apical shoots of pines in regenerating forest stands exposed to browsing by free-ranging moose. We expected that the probability of browsing would be related to both individual defence and defence of neighbours and that this pattern would be consistent with Experiment 1. Together, our experiments test theoretical repellent function at multiple scales, including potential behavioural mechanisms, and quantify outcomes for trees exposed to mammalian herbivores in the wild.

Materials and methods

The repellent

HaTe2 is a commercial repellent manufactured by Fluegel GmbH, Germany, and distributed in Sweden by Gyllebo plantskydd. The product is a black viscous substance marketed as a physical repellent. Ethanol, balsam resin and black pigment constitute more than 99% of the ingredients. HaTe2 forms a tough and sticky black film on shoots; it is not soluble in water and is therefore suitable for applying in wet weather or at temperatures below freezing. It is recommended for use on dormant plants only. We chose this product because it allowed us to test mechanisms of repellence in winter, when trees in Scandinavia are dormant, exposed to snow and rain, and under the highest pressure from large herbivores. Both experiments were conducted during the winter 2015/2016.

Experiment 1: Captive test

In Experiment 1, we tested how the pattern of repellent application, both within the plant and amongst neighbouring plants, affected the level of protection from herbivory. We quantified the browsing response of two captive female moose held in a 2.1-ha enclosure at the Norwegian Moose Centre (Inland Norway University of Applied Sciences, Hedmark, Norway). No permit was required under the Norwegian Food Safety Authority. Animals were fed pellets daily, and we supplied branches or small trees of willow (*Salix* spp.), downy birch and silver birch, Scots pine and rowan every second day. There were trees growing inside the enclosure but these were out of browsing reach for the moose.

In order to approximate the presentation of trees in a pine production forest, we built four wooden racks, each fitting five trees in a row with 1 m between trees. The racks were placed parallel to each other at 5-m intervals, forming a four-by-five grid of pines. The tree spacing was sufficient that moose needed to move to select between trees and that both animals could move between racks simultaneously. It also represents the tree spacing that moose could encounter in a plantation forest (see Experiment 2). The moose were presented with the racks 9 days before the experiment started, and the racks were filled with pine trees 2 days before the experiment started. The moose quickly became habituated to the racks and fed from them during their normal feeding bouts from the first day that trees were presented. Browsing pressure within this enclosure could best be described as extreme and would not be found under natural conditions over large areas. However, this system provides an opportunity for an experimental set-up and an ‘extreme test’ of the browsing repellent.

We collected pines that were cut during thinning in a different forest stand fenced to exclude moose (as per Pedersen and Bakmann 2015). The pines were approximately 2.0–3.5 m tall and 6–9 years old. For each trial, 20 pines were cut to a length of 2.0 m (± 0.1 m) to create a uniform height and placed upright in the four racks. We used HaTe2 to test the effect of repellent application on browsing of pines. We applied the repellent to the apical shoots of pines using a pressurized spray bottle. Approximately 5–10 cm of the apical shoots were sprayed varying from 1.8 to 4.4 mg wet weight based on 10 test sprays.

The experiment tested four repellent application strategies, with HaTe2 applied to: (1) all current apical shoots, (2) alternating current apical shoots, (3) all previous-year apical shoots and (4) none of the pines. The purpose of application strategy (3) was to simulate a stand where repellent was applied to apical shoots in the previous year but was not reapplied. In reality, the concentration of repellent on the previous-year apical shoot would have reduced through exposure to the elements; this is a limitation of the treatment, but it is relevant to test whether repellent effects are altered when the location of the defended part within the plant changes. Each trial consisted of one repellent strategy applied to 20 trees that were available for moose to browse for approximately 23 h. We tested each of the four repellent strategies once per week for 5 weeks (i.e. five temporal blocks) in February and March 2016, yielding a total of 20 trials using 400 trees. The order of repellent strategies was randomized within the temporal blocks. For each of the pines in the trial, we estimated the percentage of new shoots browsed (i.e. tips of branches which represent growth from the previous season, measured by the same person throughout the trial), whether the apical shoot was browsed, or broken, or if there was any bark damage. None of the apical shoots were broken and no bark damage was found.

We monitored 15 of the 20 trials using motion-triggered infra-red cameras (WingCam II TL, HobbyKing, Hong Kong) to examine how moose browsed individual trees. Cameras were placed on the fence poles of the moose enclosure at approximately 5 m height. Two cameras were used to cover the whole experimental set-up and ensure good quality footage. In 429 min of footage, we recorded 242 complete browsing events on individual trees where a moose either newly entered the tree racks or changed from one tree to another. Some recordings started when the moose had already taken the first bite and these were excluded from our analyses. For each event, we classified the height at which the moose initiated browsing as either (a) below or (b) at and above the lowest level of the back of the moose, behind the withers but in front of the loins (~ 1.7 m).

Statistical analyses

We performed all statistical analyses using the ‘lme4’ package (Bates et al. 2015) in R version 3.2.2 (R Core Team 2016).

We tested the effect of the repellent application strategy on whether moose browsed apical shoots or not (binary variable, 1/0). We constructed a hierarchical contrast matrix for the class variable (repellent application strategy) to test for differences between and within groups. We separated the trees in the alternate repellent strategy into treated and untreated trees, such that repellent application strategy became a class factor with five levels (none, alternative untreated, alternative treated, all, previous). First, we compared the browsing probability of apical shoots that had repellent applied (‘All’ and treated in ‘Alternate’) to those that did not (‘Previous year’, ‘None’ and untreated in ‘Alternate’); next, we compared treating the previous-year apical shoot against not treating any part of the tree (‘Previous year’ vs. ‘None’ and untreated in ‘Alternate’). To test for associational effects, we also contrasted the probability of apical shoot browsing between untreated trees when they had untreated compared to treated neighbours (‘None’ vs. untreated in ‘Alternate’) and treated seedlings when they had untreated compared to treated neighbours (treated in ‘Alternate’ vs. ‘All’). Since trees in alternate repellent strategies were split into two groups, we used weighting to balance the class contrasts and checked for orthogonality by examining the cross-products matrix for the model. In addition to the repellent application strategy, we included the proportion of lateral shoots browsed as a fixed effect and trial as a random effect. To test whether the browsing response to the different repellent strategies changed with exposure, we also included the interaction between the application strategy and block as a fixed effect. We used a GLMM specifying a binomial response distribution with logit link function, and the BOBYQA algorithm to fit the model. To test whether the repellent application strategy had any effect on the proportion of lateral shoots eaten, we used a LMM with block and trial as random effects. We logit-transformed proportions (constrained to 0.025–0.975) and used Q–Q plots to confirm that the distribution of errors was approximately normal.

To understand whether the initiation of feeding had a role in treatment effects, we then tested the frequency with which moose initiated feeding (a) below or (b) at and above the lowest level of the back of the moose. We first created an interaction factor combining feeding height (below and above) with the four treatments, resulting in a factor with eight levels. To test for differences in the number of events in each category of the interaction factor, we fitted a GLMM specifying a Poisson response distribution and log link function. We included block and trial as random effects and used BOBYQA to solve the model. We then constructed a contrast matrix to test our specific hypotheses of interest: any overall differences in initiating feeding above or below the back and any differences within each individual treatment. Post hoc multiple comparisons were adjusted using the single-step method in ‘multcomp’ (Hothorn et al. 2008).

Experiment 2: Field test

In Experiment 2, we tested whether the effects of repellent application strategy held true in the wild. We used young pine stands exposed to wild ungulates at Grimsö Wildlife Research Station (Swedish University of Agricultural Sciences, Riddarhyttan, Sweden) which is a part of the Swedish Infrastructure for Ecosystem Science (SITES) network. The area covers 130 km^2 in south-central Sweden (59°40′N, 15°25′E) and mainly consists of intensively managed Scandinavian boreal forest (Sveaskog), dominated by Norway spruce (*Picea abies*) and Scots pine. Temperatures range from −20 °C in winter up to 25 °C in summer, with an annual precipitation average of 670 mm. An inventory carried out by helicopter over the winter in 2013–2014 estimated moose density at 0.66 animals km^{-2} over the entire Research Station or 0.70 animals km^{-2} of solid land only (excluding lakes and mires).

We compared winter browsing when repellent was applied to the apical shoots of (1) all, (2) alternate and (3) no pines. We selected nine forest stands of similar ages (6–12 years since regeneration) and divided each forest stand into three areas for applying the experimental treatments. We selected 100 adjacent pine trees for each treatment (height range 0.35–2.20 m), which covered areas from 56 to 255 m^2. Trees were marked and treated in December 2015 and key variables quantified: tree height, distance to the nearest tree and any herbivore damage to apical shoots, branches and bark. Personnel at Grimsö Wildlife Research Station provided moose density estimates and tree species compositions for the forest stands in 2015, collected as part of routine monitoring (Petter Kjellander, unpublished data). The mean estimated moose density across all the stands used in this study was 0.84 animals km^{-2} (SE 0.06, range 0.70–1.16), slightly higher than the mean for the whole research area. The mean tree species composition of the stands was 64% pine (SE 7, range 30–90), 18% spruce (SE 7, range 0–50) and 19% birch and aspen (SE 7, range 0–50).

Herbivore damage was again quantified in March 2016 after approximately 3 months of exposure to wild ungulates. Of 2700 trees marked in December, we excluded 11 trees from our analyses because they had died, were accidently marked twice or could not be relocated in March (due to snow cover or tag loss). We monitored presence of ungulates in plots using motion-triggered infra-red cameras (ScoutGuard SG550 V). Since there were more plots than cameras, we systematically recorded subsets of plots for two or three blocks of 9–35 days between 12 December 2015 and 28 March 2016 (see supplementary material).

Statistical analyses

We considered only new browsing damage that occurred over the winter by comparing the browsing damage to apical shoots, branches and bark recorded in December 2015 to that recorded in March 2016. First, we used a GLMM testing the probability of browsing damage to apical shoots as a function of repellent application strategy, tree height, distance to the nearest tree, pine density, pine as a proportion of total trees, previous browsing damage and moose density. We tested four levels of repellent application strategy: none, all, alternate (treated) and alternate (untreated). We constructed an orthogonal, hierarchical contrast matrix for our planned comparisons between and within groups. To test overall repellent function, we first compared all untreated trees ('None' and untreated in 'Alternate') to all treated trees ('All' and treated in 'Alternate'). We then tested for associational plant effects by comparing browsing probability of apical shoots on untreated trees with untreated and treated neighbours ('None' vs. untreated in 'Alternate'), and treated trees with untreated and treated neighbours (treated in 'Alternate' vs. 'All'). Forest stand was included as a random effect. We specified a binomial response distribution with logit link function, and the BOBYQA algorithm to solve the model. As few trees experienced any new damage over the winter, we then combined damage scores across shoots, branches and bark, creating a single binomial variable for any new browsing damage to each tree (1 = damaged, 0 = not damaged). We then tested for effects on this response variable using the same procedure described for damage to apical shoots. Due to the low number of trees damaged, we used the 'boot' package (Canty and Ripley 2017) to construct means, and bias-corrected and accelerated (BCa) bootstrap intervals.

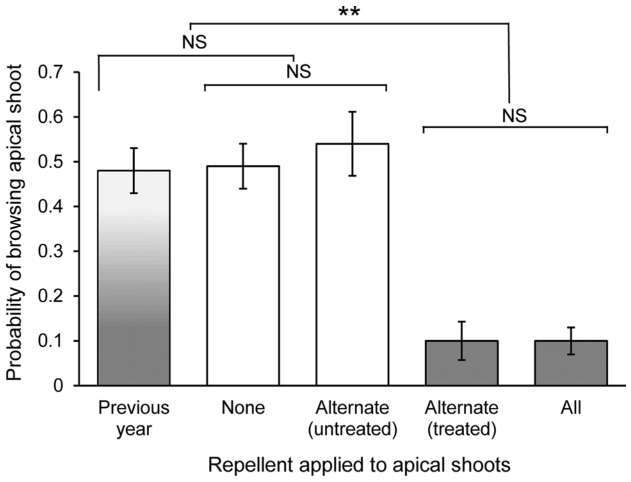

Fig. 1 The probability of captive moose browsing Scots pine trees presented in four strategies of HaTe2 repellent application: none, all apical shoots, alternate apical shoots, all previous-year apical shoots. Treated and untreated trees are presented separately for the alternate pattern. Bars indicate arithmetic mean ± SE; untreated trees are in white and treated trees are in grey. Horizontal brackets show hierarchical planned comparisons tested in GLMM; $^{**}P < 0.01$, *NS* = not significant ($P > 0.05$)

Results

Experiment 1: Captive test

Moose were less likely to damage current apical shoots of pines when these were treated with HaTe2 repellent (Table 1, Fig. 1). Applying the repellent to the previous-year apical shoot did not significantly alter the probability of browsing the current apical shoot compared to completely untreated pines. There were also no differences in the probabilities of browsing untreated apical shoots between 'Alternate' and 'None' repellent application strategies, or treated apical shoots between 'Alternate' and 'All' repellent application strategies. The proportion of lateral shoots damaged was a significant positive predictor of apical shoot damage (Table 1). The probability of browsing did not vary significantly between blocks for any treatment where the repellent

Table 1 Test of fixed effects on probability of Scots pine apical shoots being browsed by captive moose (1 = browsed, 0 = not browsed)

Fixed effect	$\beta \pm$ SE	*Z*	*P*
(Intercept)	−30.42 ± 5.02		
Current apical shoot treated versus not treated	0.78 ± 0.26	2.94	**0.003**
Untreated versus previous apical shoot treated	−0.65 ± 0.40	−1.64	0.100
Untreated: 'None' versus 'Alternate'	1.21 ± 0.81	1.49	0.137
Treated: 'All' versus 'Alternate'	0.16 ± 1.24	0.13	0.900
Proportion of lateral shoots damaged	33.30 ± 5.35	6.23	**< 0.0001**
'None' × Block number	−1.35 ± 0.51	−2.62	**0.009**
Untreated in 'Alternate' × Block number	−0.34 ± 0.47	−0.72	0.474
Treated in 'Alternate' × Block number	0.17 ± 0.92	0.19	0.852
'Every' × Block number	0.06 ± 0.69	0.08	0.933
'Previous' × Block number	−0.50 ± 0.38	−1.31	0.190

The repellent HaTe2 was applied to none, alternate or all current apical shoots, or all previous-year apical shoots, of 20 pine trees per trial. The model fitted was a GLMM specifying a binomial response distribution, with planned contrasts for the repellent treatments and trial included as a random effect. Interactions between treatments and blocks represent temporal patterns in browsing probability, with each treatment having been tested once per block of four trials. *P* values in bold represent statistically significant differences ($\alpha = 0.05$)

was applied, but decreased over blocks of trials where none was applied (Table 1). The repellent application strategy had no effect on the proportion of lateral shoots damaged ($\chi^2_4 = 5.87$, $P = 0.21$).

Moose more often initiated feeding from pines with their heads held below rather than at or above the level of the spine (Table 2). In general, moose started to eat from a lower part of the pine and thereafter moved up towards the apical shoot. This pattern was consistent across repellent application strategies (Table 2).

Experiment 2: Field test

In a total of 1627 days of camera monitoring over all 27 plots, we recorded one or two individual moose on nine occasions (5 at control and 4 at treatment plots) and one individual roe deer (*Capreolus capreolus*) on two occasions (1 control, 1 treatment), across five forest stands. The overall level of ungulate browsing damage was low, with only 11 trees experiencing apical shoot damage and a total of 34 trees receiving any damage of the 2689 trees marked.

The repellent application pattern had no significant effect on browsing of apical shoots (Table 3, Fig. 2a). Apical shoots were more likely to be browsed on trees that had previous browsing damage at the beginning of the winter and that suffered new browsing damage to lateral branches or bark gnaw during the winter (Table 3).

Similarly, the probability of a tree incurring any browsing damage (to the apical shoots, branches or bark) did not differ significantly between untreated and treated trees overall (Table 3, Fig. 2b). However, untreated trees were less likely to be browsed in ‘Alternate’ repellent application plots than those in ‘None’ plots (Fig. 2b). The difference in browsing probability of treated trees between ‘Alternate’ and ‘All’ repellent plots was not significant (Table 3). Pine trees were more likely to be browsed if they were taller and where they occurred in plots of lower pine densities; these effects were not confounded (low correlation between tree height and

Table 2 The number of times captive moose initiated feeding on Scots pines at a height below or at and above the lowest level of the animal’s back (~ 1.7 m), both overall and in the four different treatments

Treatment	No. of trials	Duration (min)	Feeding initiated		$\beta \pm$ SE	Z	P
			< 1.7 m	≥ 1.7 m			
All treatments	15	429	206	36	7.43 ± 0.80	9.29	**< 0.0001**
None	4	137	63	17	1.31 ± 0.27	4.84	**< 0.0001**
Alternate	4	135	59	8	2.00 ± 0.37	5.36	**< 0.0001**
All	3	89	48	7	1.93 ± 0.40	4.81	**< 0.0001**
Previous	4	69	36	4	2.20 ± 0.52	4.25	**0.0001**

The total number and duration of films are also shown. Statistical tests of post hoc comparisons were derived from a log-linear model (GLMM specifying Poisson response distribution) with trial as a random effect. *P* values were adjusted for multiple comparisons (single-step method; Hothorn et al. 2008); those in bold represent statistical significant differences (α = 0.05)

Table 3 Test of fixed effects on probability of Scots pines being browsed by wild ungulates (1 = browsed, 0 = not browsed)

Fixed effect	Damage to apical shoots only			Any damage		
	$\beta \pm$ SE	Z	P	$\beta \pm$ SE	Z	P
(Intercept)	1.56 ± 34.60			3.28 ± 6.24		
Untreated versus treated	0.13 ± 0.67	0.19	0.851	− 0.14 ± 0.20	− 0.72	0.469
Untreated: ‘None’ versus ‘Alternate’	− 0.35 ± 0.76	− 0.46	0.644	− 0.51 ± 0.22	− 2.25	**0.024**
Treated: ‘All’ versus ‘Alternate’	− 0.65 ± 1.22	− 0.53	0.596	0.50 ± 0.28	− 1.82	0.069
Height (m)	0.29 ± 0.86	0.34	0.734	1.45 ± 0.42	3.43	**0.001**
Nearest tree (m)	0.05 ± 0.82	0.06	0.949	− 0.09 ± 0.44	− 0.22	0.828
Pine density (m^{-2})	− 4.27 ± 4.02	− 1.06	0.288	− 2.40 ± 0.93	− 2.57	**0.010**
Pine as proportion of total trees	− 1.48 ± 12.59	− 0.12	0.907	0.43 ± 3.12	0.14	0.891
Moose density (km^{-2})	− 13.40 ± 43.66	− 0.31	0.759	− 10.82 ± 7.27	− 1.49	0.137
Pre-trial browsing damage	1.69 ± 0.79	2.14	**0.032**	− 0.27 ± 0.60	− 0.45	0.650
New damage to lateral shoots/bark	2.63 ± 1.00	2.63	**0.009**			

The repellent HaTe2 was applied to none, alternate or all current apical shoots in three plots of 100 pines across nine forest stands. The model fitted was a GLMM specifying a binomial response distribution, with planned contrasts for repellent treatments and forest stand as a random effect. Any damage represents damage to apical shoots, branches or bark. *P* values in bold represent statistically significant differences (α = 0.05)

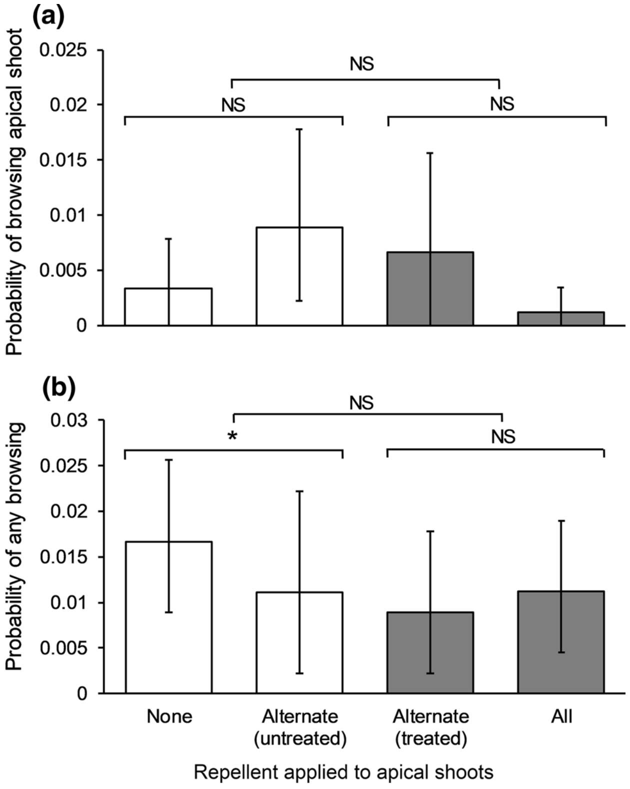

Fig. 2 The probability of any browsing damage to Scots pine **a** apical shoots only and **b** apical shoots, branches or bark, as a function of repellent (HaTe2) application strategy: none applied, applied to alternate trees (untreated and treated trees shown separately) and applied to all trees. Trees were located at Grimsö Research Station, Sweden, and subject to browsing by wild ungulates (moose and roe deer). Bars indicate bootstrap means with bias-corrected and accelerated (BCa) bootstrap intervals (95% confidence); untreated trees are in white and treated trees are in grey. Horizontal brackets show hierarchical planned comparisons tested in GLMM; $*P<0.05$, NS = not significant ($P>0.05$)

pine density, $r^2=0.090$). The distance to the nearest tree was between 0.05 and 4.65 m (mean ± SE = 0.57 ± 0.01 m) but was not a significant predictor of browsing probability.

Discussion

We demonstrated different direct and associational effects of repellent application in captive and field experiments of moose–pine interactions. Captive moose avoided the apical shoots of young pines treated with the commercial repellent, HaTe2, but we found no evidence of associational refuge within or between plants. In contrast, applying the repellent to apical shoots in a pine production forest did not have any biologically or economically meaningful effect on damage by wild ungulates, but treated trees did provide a statistically significant associational refuge for untreated neighbouring trees. Notably, the overall browsing level in these stands was very low despite being exposed to moose densities approximating the mean in Swedish forest stands.

In Experiment 1, we tested the between- and within-plant associational effects of applying repellent to pine apical shoots exposed to captive moose. The repellent protected the apical shoots from browsing, but there was no effect of enhanced protection from neighbours. The apical shoots of pines were eaten as a function of their own defence only. Although moose are the largest ungulates in Scandinavian forests, they show the lowest foraging rate amongst many ungulates and are very selective between trees (Shipley et al. 1994). The moose in the enclosure represent an extreme density of moose (equivalent to 95 individuals km^{-2}), with 10 young pine trees available per moose per day. Thus, an extreme browsing pressure was expected.

There was no evidence of within-plant associational effects: where repellent was applied to the previous-year apical shoots, the current apical shoots were equally vulnerable to moose herbivory compared to completely untreated pines. This suggests that there is a need to reapply repellent after each growing season to maintain protection from browsers. In areas of high forest productivity, apical shoot length could be more than 0.5 m, while in low productivity areas shoot length could be less than 5 cm. Thus, how fast pines grow out of browsing height will determine the economic feasibility of this method and it would most likely differ greatly depending on forest productivity.

The apical shoot had a higher probability of sustaining damage as lateral shoot damage increased, and we suggest that this is the result of moose foraging behaviour at the individual tree level. Moose initiated most feeding bouts on pines at a height below the lowest part of the back (~ 170 cm), within the bite range of 20–280 cm (mean = 122 cm) previously reported for moose (Nichols et al. 2015), and progressed up towards the apical shoot. Protecting apical shoots did not result in refuge for lateral shoots. By the time moose typically encountered the repellent on apical shoots of 2-m-high pines, they had already browsed untreated lateral shoots. Meanwhile, the moose were able to find and browse the untreated apical shoots when repellent had been applied to the previous-year apical shoot. This is in contrast to red deer (*Cervus elaphus*) browsing on 1-m aspen branches, where feeding generally started from the top: when tannin was applied to tops of branches, bottom parts were protected, while adding tannin to bottom parts of branches did not protect tops (Bergvall and Leimar 2017). This pattern was observed despite the forage available per red deer being lower in quantity and more highly preferred by cervids than that presented to the moose in the present study. Tree height and the height at which herbivores initiate feeding are therefore likely to be critical factors determining the outcome of repellent application.

In Experiment 2, we tested between-plant associational effects of repellent application in the field. The level of browsing was lower than we expected given that the mean moose density in the stands studied (0.84 animals km^{-2}) was comparable to the national mean as estimated in 1991–1992 (0.77 animals km^{-2}; Hörnberg 2001a), and within the range estimated in forest stands across Sweden in the winter of 1998–1999 (0.5–1.2 animals km^{-2}; Bergqvist et al. 2001), and across several counties in south-central Sweden during the winter of 2000–2001 (0.6–0.9 animals km^{-2}; Bergqvist et al. 2014). Ungulates in this study browsed only 0.4% of the apical shoots and damaged 1.3% of pine trees in total, lower than in other areas with similar moose densities (7.6% of apical shoots and 10% of pines with any damage; Bergqvist et al. 2001; 4% of pines with any damage; Bergqvist et al. 2014). But even at these very low browsing levels, protection from the repellent was not complete. In this realistic forestry set-up, we found that repellent treatments had no obvious effect on browsing damage, with some of the very few occurrences of browsing occurring on trees treated with repellent. Applying HaTe2 repellent to apical shoots had no direct effect on apical shoot browsing by wild moose. We suggest that this may have resulted from inexperience with the repellent; the low levels of browsing overall indicate that there would have been little opportunity for individuals to learn the cues associated with the repellent, in contrast to the captive moose that had only 20 trees to choose from per day in a small area.

There was some evidence of associational refuge in the field based on total tree damage: untreated pines were less likely to incur any browsing damage when they had treated rather than untreated neighbours (i.e. in ‘Alternate’ compared to ‘None’ repellent application strategies). We interpret this result with caution given the low number of trees browsed and that the overall effect of applying repellent was not significant. However, given that we used a hierarchical planned comparison to analyse the effects of repellent application strategy on browsing probability, it is reasonable to obtain significant differences at lower levels in the hierarchy that are not apparent at a higher level (i.e. the comparison of treated and untreated trees across all repellent application strategies). The evidence for associational refuge in the absence of direct repellence in the field (Experiment 2) contrasts with the browsing pattern in captivity (Experiment 1) where we found direct repellence but no associational effects. There are several possible explanations for this given the differences between the captive and field experiments on both sides of the plant–herbivore interaction. The opportunity for choice could be particularly important: captive moose could choose only within a stand whereas wild moose could choose both within and between plots and stands. It is therefore likely that the captive individuals invested more foraging effort per stand, facilitating selectivity between trees. In contrast, the protection of untreated trees by treated neighbours in the wild suggests that moose were not selective between individual trees in the field but rather at the level of patches of trees. This may be why very high levels of browsing pressure appear to cause associational refuges to break down (Stutz et al. 2015); while we found some evidence for refuge at very low levels of browsing pressure in the field (1.3% of pines damaged), we found no support for refuge at extremely high levels of browsing pressure in captivity (100% of pines damaged). Nonetheless, the browsing pressure in the captive experiment was not high enough for direct repellent effects to break down and result in indiscriminate browsing of repellent-treated plants. Meanwhile, the lack of an overall repellent effect in the field experiment may be related to greater motivation (i.e. hunger) in wild moose, leading them to prioritize food quantity over quality to achieve their required intake of nutrients (Banks et al. 1999; Stutz et al. 2017b).

Our finding that pre-trial browsing damage led to greater probability of apical shoot browsing is consistent with findings from other ungulate foraging studies. Both moose (Bergqvist et al. 2014) and fallow deer (*Dama dama* L.; Moore et al. 2000) have been shown to preferentially browse trees with a history of browsing damage in production forests. This could be the result of preference for particular trees based on nutritional or structural characteristics, or their location along paths through the forest that are used repeatedly. As in Experiment 2, apical shoot browsing coincided with damage to other parts of pines, and we suggest this is related to the way moose initiate browsing on trees. Our experiment included pine trees between 0.2 and 2 m in height, and we found that moose were more likely to browse trees at the higher end of this range; similarly, Nichols et al. (2015) reported a mean browsing height of approximately 1.6 m in mixed forests. Pine trees were less likely to be damaged at higher pine densities, consistent with the findings of Wallgren et al. (2013) and Bergqvist et al. (2014). Our findings support the authors’ suggestion that creating stands with high pine densities could reduce damage.

Our study demonstrated some possible mechanisms of browser deterrence when a commercial repellent was applied in different within- and between-plant patterns, and highlighted the need to use multiple approaches for understanding context-dependent browsing outcomes of repellent application strategies. The use of repellents to protect plants from mammalian herbivores is widespread (Andelt et al. 1992; Nolte 1998; Santilli et al. 2004; Wagner and Nolte 2001), but the cost of application is a major limitation. Our research shows that the browsing patterns observed in captive studies do not necessarily scale up to applications in forests, but they do allow observations of fine-scale behaviours that can explain within-plant browsing patterns. To use repellents efficiently will require an approach tailored to specific herbivore densities, tree species compositions and forest developmental stages. Choosing effective repellent application patterns is likely to become increasingly important as the forestry industry adopts management for multiple values and recognizes the important role of non-timber values in sustainable forest management, including ecological, aesthetic and recreation values (Gamfeldt et al. 2013; Mattsson 1990; Nordlund and Westin 2011).

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Data accessibility All data will be made available on the Mendeley Data repository.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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