

Neighbouring plants and perception of predation risk modulate winter browsing by white-tailed deer (*Odocoileus virginianus*)

E. Champagne, L. Perroud, A. Dumont, J.-P. Tremblay, and S.D. Côté

Abstract: The presence of neighbouring plants and predation risk can affect trophic interactions between plants and herbivores. We hypothesized that the relative preference for neighbouring species would determine winter herbivory and that predation risk would modulate browsing pressure. We tested these hypotheses using feeding trials in two regions with high white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) densities: Outaouais and Anticosti Island (Quebec, Canada). In each, we selected a species of interest and compared browsing rates and time spent foraging with neighbours relatively preferred or avoided. In a subexperiment, we included coyote (*Canis latrans* Say, 1823) urine to test for threat-sensitive foraging and interactions with neighbour effects. In Outaouais, time spent foraging on the focal species was reduced by the presence of potentially avoided neighbours and deer reduced browsing with increased perceived predation risk. On Anticosti, browsing rates on the focal species increased with avoided neighbours, with no effect of the predator urine. Anticosti deer have been in a predator-free environment for more than 120 years, likely reducing antipredator behaviours. This study demonstrates both neighbour effects and threat-sensitive foraging, phenomena that could interact and thus would benefit from being studied together to better represent trophic interactions in natural environments.

Key words: vigilance, associational resistance, associational effects, white-tailed deer, *Odocoileus virginianus*.

Résumé : La présence de plantes compagnes et d'un risque de prédation peut avoir une incidence sur les interactions trophiques entre plantes et herbivores. Nous avons postulé que la préférence relative pour des espèces compagnes déterminerait le comportement herbivore hivernal et que le risque de prédation modulerait le broutement. Nous avons testé ces hypothèses par des tests d'alimentation dans deux régions caractérisées par de fortes densités de cerfs de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) : l'Outaouais et l'île d'Anticosti (Québec, Canada). Dans chacune de ces régions, nous avons sélectionné une espèce d'intérêt et comparé les fréquences de broutement et le temps passé à l'approvisionnement à ceux de plantes compagnes préférées ou évitées. Dans le cadre d'une sous-expérience, nous avons inclus de l'urine de coyote (*Canis latrans* Say, 1823) pour vérifier si l'approvisionnement et les interactions avec les espèces compagnes étaient sensibles au risque de prédation perçu. En Outaouais, la présence d'espèces compagnes potentiellement évitées réduisait le temps passé à brouter l'espèce d'intérêt, et un plus grand risque de prédation perçu entraînait une réduction du broutement par les cerfs. Dans l'île d'Anticosti, le broutement de l'espèce d'intérêt augmentait en présence d'espèces compagnes évitées, sans effet de l'urine de prédateur. Les cerfs de l'île d'Anticosti évoluent dans un milieu exempt de prédateurs depuis plus de 120 ans, ce qui a vraisemblablement diminué leurs comportements antiprédateur. L'étude démontre des effets d'espèces compagnes et le fait que l'approvisionnement est sensible au risque de prédation perçu, des phénomènes qui pourraient interagir et devraient donc être étudiés ensemble pour en arriver à une meilleure représentation des interactions trophiques en milieux naturels. [Traduit par la Rédaction]

Mots-clés : vigilance, résistance associative, effets associatifs, cerf de Virginie, *Odocoileus virginianus*.

Introduction

Wild herbivores make foraging decisions in complex and multi-specific environments and often show preferences for different plant species based on their morphological (Vivås et al. 1991; Côté et al. 2004) and chemical characteristics (Pyke et al. 1977). Environments with high complexity, however, can lead herbivores to make suboptimal choices in species selection (Wang et al. 2010).

Presence of other plant species can influence foraging and increase (associational susceptibility) or decrease (associational defence) herbivory on a plant (see reviews by Barbosa et al. 2009, Underwood et al. 2014, and Champagne et al. 2016). Associational effects can result from the resistance traits of the neighbour (Barbosa et al. 2009); they can also occur when there is a contrast in preference between neighbouring plants (Bergvall et al. 2006; Bee et al. 2009). For example, pademelon (*Thylogale billardierii* (Desmarest, 1822)) in

Received 7 March 2017. Accepted 3 July 2017.

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Tasmania illustrate two neighbour contrast effects: pademelon consumed less shining gum (*Eucalyptus nitens* (H. Deane & Maiden) Maiden) when it was accompanied by more palatable vegetation like grasses (genus *Poa* L.) and oats (*Avena sativa* L.) (neighbour contrast defence) than when it grew in association with avoided white lupins (*Lupinus albus* L.) (neighbour contrast susceptibility; Miller et al. 2007).

Predation risk can also influence foraging behaviour of herbivores. An increase in the perceived risk of predation can increase the time spent by animals in antipredatory activities (Brown et al. 1999), at the expense of foraging time (Lima and Bednekoff 1999). Herbivores can also minimize predation risk by reducing time spent in high-risk areas; however, doing so can result in the use of suboptimal habitats (Brown 1988; Hernández and Laundré 2005). These changes in herbivore behaviour could also influence indirect interactions between neighbouring plants. When foraging in high-risk areas, herbivores may consume high-quality resources predominantly to maximize their intake during a short-time period (Brown and Kotler 2004), thereby decreasing herbivory on relatively less-preferred plant species. Predation risk can also reduce the overall intake of plants, without any impact on plant selection; collared pikas (*Ochotona collaris* (Nelson, 1893)) reduced their forage intake but did not modify their selection of plants under increased risk (Morrison et al. 2004).

Our objective was to determine whether neighbouring plant species and predation risk interact to modify species used as winter forage, namely balsam fir (*Abies balsamea* (L.) Mill.) and white pine (*Pinus strobus* L.), by white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)). We hypothesized that a change in the relative preference for the focal species versus the neighbouring species would modify herbivory level on the focal species and that browsing pressure would be modulated by predation risk. We predicted that increased perception of predation risk would reduce browsing of all plants because of reduced foraging time regardless of vegetation associations. We also predicted that this reduction in foraging time would increase selection for high-quality forage and reduce browsing of relatively less-preferred neighbours, and thus, increase neighbour contrast defence for focal species with relatively preferred neighbours. To test our hypotheses, we performed feeding trials in natural environments with wild white-tailed deer in two contrasting regions at high deer density, one with the presence of natural predators (mainly coyote (*Canis latrans* Say, 1823) and grey wolves (*Canis lupus* L., 1758)) and another without predators.

Materials and methods

Study areas

We performed feeding experiments in two independent study areas, located in Quebec, Canada.

Outaouais

In 2014, the experiment was near Shawville (45°36'N, 76°29'W; Outaouais; Fig. 1a), from 13 January to 5 February. White-tailed deer densities are high in the wintering areas (18 ± 2 deer/km² (mean ± SD) in 2006; Ministère des Forêts, de la Faune et des Parcs, unpublished data) and deer are predated by grey wolves and coyotes. The experiment took place in the sugar maple (*Acer saccharum* Marshall) – bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) bioclimatic domain (Saucier et al. 2009). During the experiment, the nearby Charteris station recorded a mean January temperature of -12.9 °C, with 15 cm of snow (Environment Canada 2016a). In the region, snow depth reached 61 cm at the end of the experiment (Ministère des Forêts, de la Faune et des Parcs, personal communication).

Anticosti Island

In 2015, we repeated the same feeding experiment on Anticosti Island (7943 km²) in the Gulf of St. Lawrence (49°28'N, 63°00'W; Anticosti; Fig. 1a), from 16 January to 15 February. Deer density on

the island can reach >20 deer/km² locally (Rochette and Gingras 2007) and no natural predators are present. The forest is part of the eastern balsam fir – paper birch (*Betula papyrifera* Marshall) bioclimatic subdomain (Saucier et al. 2009). Heavy deer browsing, however, has been preventing fir regeneration and induced white spruce (*Picea glauca* (Moench) Voss) dominated stands (Potvin et al. 2003; Tremblay et al. 2006). In 2015, January mean temperature was -12.3 °C with total precipitation of 71 mm (Environment Canada 2016b), of which approximately one-third was snow (Environment Canada 1982); snow depth reached 70 cm on 11 February (Ministère des Forêts, de la Faune et des Parcs, personal communication).

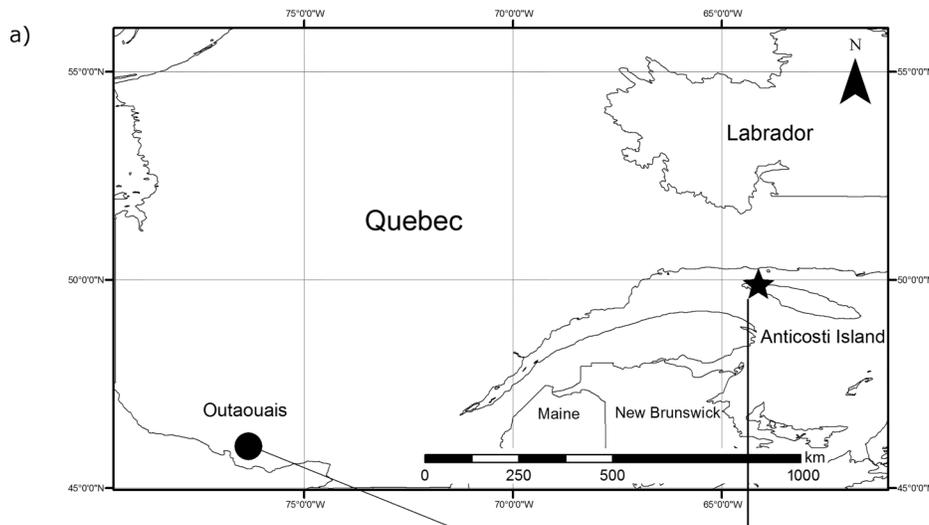
Experimental design

We selected a focal species and two neighbour species, one of relatively higher preference level (hereafter preferred species) and one of lower preference level (hereafter the avoided species), in each area. In Outaouais, white pine (focal species) is an evergreen once highly exploited by the forest industry and now is less abundant in the region (Doyon and Bouillon 2003). This species is not considered a preferred resource by deer but is negatively impacted by deer browsing in wintering areas (Goudreault 2007). We selected white pine because aside from its commercial uses, it is a long-lived species that can provide shelter for deer (Hébert et al. 2013). Based on expert knowledge (A. Dumont), we selected mountain maple (*Acer spicatum* Lam.) as the preferred species and American beech (*Fagus grandifolia* Ehrh.) as the avoided species. On Anticosti Island, we selected balsam fir as the focal species because this is the most important resource for deer in winter in terms of both cover and forage (Lefort et al. 2007), and one of the main management objectives on the island is to increase fir abundance (Beaupré et al. 2004). We chose paper birch as the preferred species, a deciduous tree heavily browsed by deer whenever they are found, and white spruce as the avoided species. White spruce is rarely browsed by deer when other browse is available (Sauvé and Côté 2007), but as deer on the island are limited in browse of high quality, it represents around 20% of deer winter diet (Lefort et al. 2007).

We divided the feeding experiment in three subexperiments, each designed to test one subobjective: (1) confirm deer preference for the selected species; (2) test for associational effects between focal and neighbouring plants; (3) test for predation risk effects and interactions with associational effects. We implemented the experiments in stations consisting of two plots of three branches each (Fig. 1). Plots were 2 m apart, without alternative resources in between. In the preference experiment, we offered two plant species per station, one species per plot (Fig. 1b). In the associational effect experiment, we placed a branch of the focal species at the top of the triangular plot, neighbored by two branches of another species. With this placement, neighbouring species were closer to the deer trail than the focal species. In this experiment, three species arrangements were possible (Fig. 1b) as in Rautio et al. (2008): (1) avoided neighbourhood, where all neighbouring branches were the avoided species; (2) preferred neighbourhood, where all neighbouring branches were the preferred species; (3) mixed neighbourhood, where one plot offered the avoided species and the other plot offered the preferred species. In the third experiment (predation risk), we used the same species arrangements as in the associational effect experiment, but half (Outaouais) or one-third (Anticosti) of the stations included a predation risk treatment. Experiments were repeated temporally (between 7 and 12 days) and spatially (multiple stations, at least 200 m between stations, 6–15 stations in a day); each repetition is named a trial. We randomized distribution of the species arrangements but made sure that no station would present the same species arrangement more than 2 days in a row.

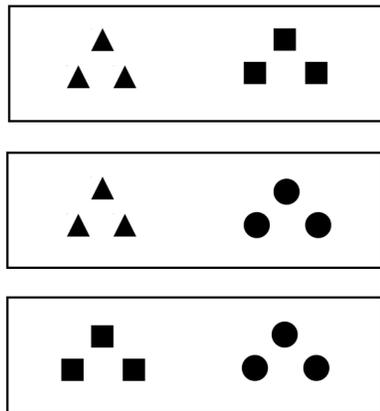
We installed stations on existing white-tailed deer snow trails. When deer did not visit the stations for 3–5 days, we moved stations to a newer trail. We changed the arrangements between the

Fig. 1. (a) Study areas (black dot: Outaouais; black star: Anticosti Island). White-tailed deer (*Odocoileus virginianus*) densities were estimated in 2006 in Outaouais (Ministère des Forêts, de la Faune et des Parcs, unpublished data) and on Anticosti Island (Rochette and Gingras 2007). Tree species in each bioclimatic domain are reported in Saucier et al. 2009. Species arrangements (view from above) used for (b) the preference experiment on white-tailed deer winter browsing and (c) associational effects and predation risk experiments. Black rectangles are stations, placed on existing deer snow trails. Plots inside the stations are separated by 2 m. Stations are independent and are located at least 200 m from another station. Branches are of similar height. The predation risk experiment has the same design as the associational effect experiment, but with half of the stations presenting a scent tag soaked in coyote (*Canis latrans*) urine for the Outaouais and one-third each with coyote and fisher (*Martes pennanti*) urine for Anticosti Island. The scent tag is placed in the middle of the station.

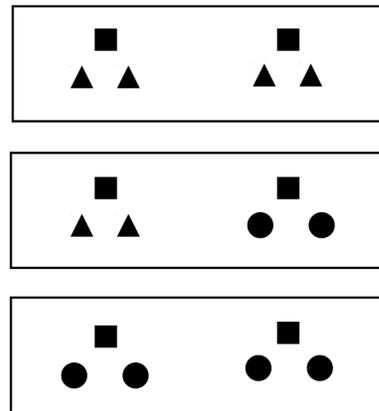


Predation	Yes (coyote, wolf)	No
Deer density	18 deer/km ²	>20 deer/km ²
Number of tree species in domain	49	8
■ Focal	White pine	Balsam fir
▲ Avoided	American beech	White spruce
● Preferred	Mountain maple	Paper birch

b) Preference experiment arrangements



c) Associational effects and predation risk experiment arrangements

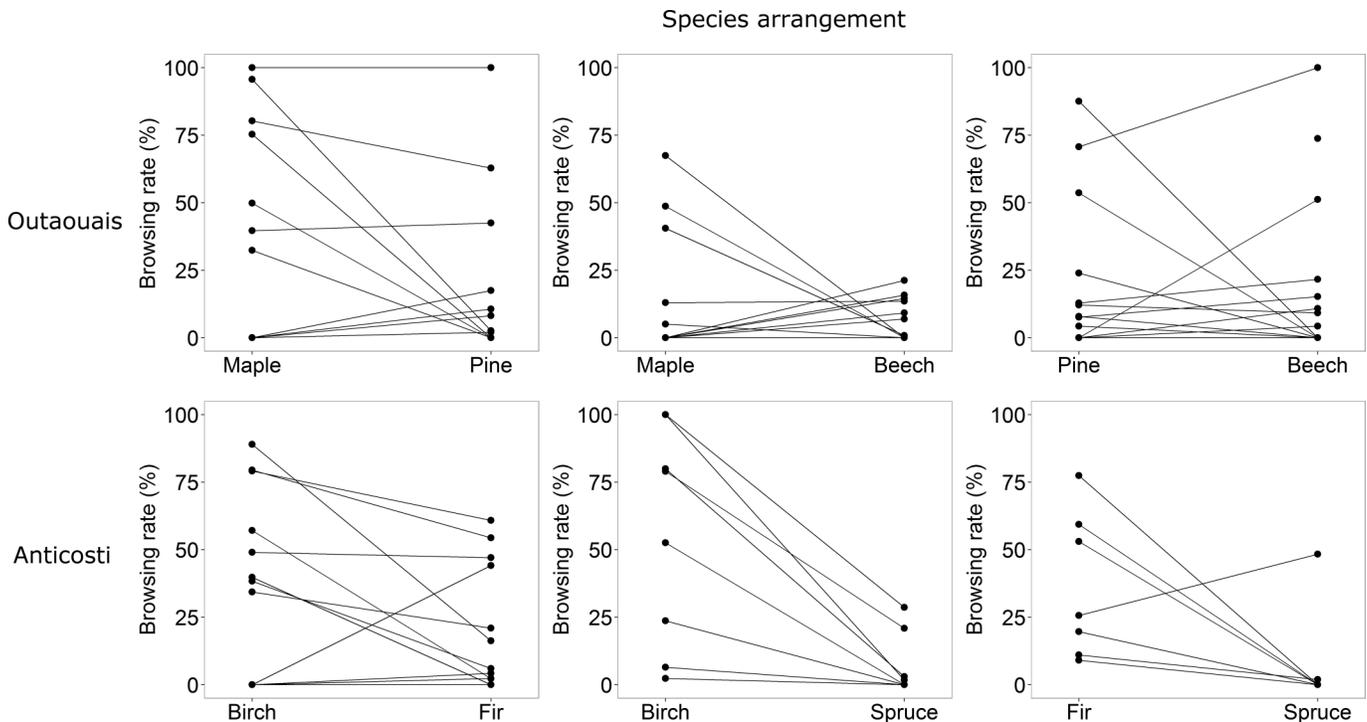


hours of 0900 and 1400, with each trial lasting approximately 24 h. We collected the branches used in the experiments in nearby areas, but not in the immediate vicinity of the stations. We picked branches randomly on different sections of trees, in the 0.25–2.25 m height interval considered to be available for deer in winter (Potvin 1995). We pooled branches from different trees and we distributed them randomly between trials. We reused unbrowsed

branches for a maximum of three trials. We reduced the potential confounding effect of human odour on the branches by limiting manipulations and keeping the branches outdoor while unused. Any effect of human odour would be equally present in all treatments.

During the predation risk experiment, we applied coyote urine to half of the stations in Outaouais to simulate increased risk of predation. Coyote urine can increase the predation risk perceived

Fig. 2. Winter browsing rates (estimated biomass browsed/available) per species in two-choice preference experiments in the Outaouais region (top panels) and on Anticosti Island (bottom panels). Each panel is one of the species arrangements, offering two plant species to white-tailed deer (*Odocoileus virginianus*) with each line corresponding to a trial (browsing in one station during 24 h). For Outaouais, we tested all combinations of white pine (*Pinus strobus*), mountain maple (*Acer spicatum*), and American beech (*Fagus grandifolia*). For Anticosti Island, we tested all combinations of balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*). Data presented are raw values of browsing.



and can elicit antipredator behaviour by white-tailed deer (Swihart et al. 1991). We placed scent tags soaked with urine (Maine Outdoor Solutions, LLC, Hermon, Maine, USA) on a stick between the two plots in randomly selected stations. We renewed the scent tags every day at the same time that we changed species arrangements. On Anticosti island, deer have not been in contact with coyotes and wolves since their introduction more than 120 years ago, and dogs (*Canis lupus familiaris* L., 1758) are prohibited. To distinguish between neophobia and antipredatory responses (Chamaillé-Jammes et al. 2014), we applied coyote urine to one-third of the stations, while another third was treated with fisher (*Martes pennanti* (Erxleben, 1777)) urine and the remaining third was untreated. Fishers are not predators of deer and are not present on the island.

Data collection

Before each trial, we counted the number of available shoots on each branch following Potvin (1995). After the trial, we counted the number of remaining shoots and the number of browsed shoots. For each browsed shoot, we measured the diameter at the point of browsing (DPB). Using a regression between shoot diameter and mass, we estimated the dry biomass browsed on each shoot from their DPB (Telfer 1969; Dumont et al. 2005). We sampled unbrowsed shoots ($n = 150\text{--}300$) on branches unused in feeding trials and measured the diameter at the growing node of each shoot. We cut the shoots at the node and weighed them after drying at $50\text{ }^{\circ}\text{C}$ for 48 h. For each species, we fitted a linear model with dry biomass of shoots as the response variable and diameter at the growth node as the explanatory variable with the gls function (Pinheiro et al. 2016) in R version 3.2.1 (R Core Team 2015). Model residuals were heteroscedastic; thus, we used the weight argument to adjust the within-group structure. When this adjustment was not sufficient to attain homoscedasticity, we used a square-root transformation of the response variable. To estimate

available biomass, we inferred a mean biomass per shoot using the mean diameter at the growing node of each species. When the browsed biomass exceeded the estimated available biomass ($n = 5$), we set the percentage of biomass browsed to 100%.

Video recording analysis

We used camera traps (Bushnell Trophy Cam, Bushnell Corporation, Overland Park, Missouri, USA) to record each trial, except when camera malfunction precluded it (20% of trials in Outaouais, 3% in Anticosti). Cameras were motion-triggered and filmed for 1 min at a time, with a 1 s interval between recordings.

We analyzed deer behaviour using JWATCHER version 1.0 (Blumstein et al. 2000). We combined consecutive recordings of the same individual during a trial into a single sequence. We excluded from the analysis videos with poor visibility or with more than one individual foraging at the same time (Kuijper et al. 2014). We kept videos with multiple deer when they were not foraging at the same time. We considered an absence longer than 5 min to be two separate visits and removed visits shorter than 10 s. We determined the total time spent by each individual at the station during a trial and we measured (i) time spent foraging on the focal species, (ii) time spent foraging on all species, and (iii) time spent vigilant. We considered a deer to be vigilant when it raised its head above its shoulders, without chewing (overt vigilance sensu Le Saout et al. 2015). A single observer (L.P.) analyzed all recordings.

Statistical analyses

We compared deer cumulative impact on plants (browsing rate = biomass browsed/biomass available) to percent time spent foraging by individual deer. For browsing rate analyses, we considered only the trials for which there was at least one shoot browsed; absence of browse can simply indicate that no deer visited the station during the trial. For foraging time analyses, we considered

Table 1. Results of the general linear models (GLM) and the general linear mixed models (GLMM) for the associational effects experiment and the predation risk experiment for white-tailed deer (*Odocoileus virginianus*) browsing in Outaouais (2014) on white pine (*Pinus strobus*) and on Anticosti Island (2015) on balsam fir (*Abies balsamea*).

Study area	Experiment	Response variables	Explanatory variables	df (numerator, denominator)	F	p		
Outaouais	Associational effect	Pine browsing rate	Overall model test	2, 46	0.6	0.58		
		All species browsing rate	Overall model test	2, 44	0.3	0.76		
		% Time spent foraging on pine	Species arrangement	2, 10	3.8	<i>0.06</i>		
		% Time spent foraging on all species	Species arrangement	2, 10	4.1	0.05		
	Predation risk	Pine browsing rate	Overall model test	5, 27	2.0	0.12		
		All species browsing rate	Overall model test	5, 27	5.4	0.001		
		% Time spent foraging on pine	Species arrangement	2, 11	0.6	0.55		
			Predation	1, 11	0.8	0.41		
		% Time spent foraging on all species	Species arrangement	2, 11	6.2	0.02		
			Predation	1, 11	0.0	0.92		
		% Time vigilant	Species arrangement	2, 11	2.0	0.18		
			Predation	1, 11	3.2	0.10		
		Anticosti	Associational effect	Fir browsing rate	Overall model test	2, 32	3.6	0.04
				All species browsing rate	Overall model test	2, 32	4.9	0.02
% Time spent foraging on fir	Species arrangement			2, 9	1.4	0.31		
% Time spent foraging on all species	Species arrangement			2, 9	2.4	0.14		
Predation risk	Fir browsing rate		Overall model test	8, 20	0.6	0.78		
	All species browsing rate		Overall model test	8, 20	8.5	<0.0001		
	% Time spent foraging on fir		Species arrangement	2, 9	0.8	0.48		
			Predation	2, 9	0.2	0.87		
			Species arrangement × Predation	4, 9	0.3	0.89		
	% Time spent foraging on all species		Species arrangement	2, 9	1.6	0.25		
			Predation	2, 9	0.3	0.74		
			Species arrangement × Predation	4, 9	0.1	0.98		
	% Time vigilant		Species arrangement	2, 9	0.4	0.67		
			Predation	2, 9	0.9	0.43		
	Species arrangement × Predation	4, 9	0.4	0.80				

Note: For the GLM, we report the F and p values of the overall model test. For the GLMM, we report F and p values for each independent variable. Significant p values are in boldface type ($\alpha = 0.05$) and statistical trends are in italic type ($\alpha = 0.10$).

the behaviour of the first group of deer that used the station, because previous deer browsing modified relative availability.

Preference experiment

We compared browsing rate on each species and percent time spent foraging on each species (time spent foraging/total time spent in the station) between the two species of interest in each independent arrangement using paired t tests.

Associational effects and predation risk experiment

We tested the effect of different neighbourhood composition on the browsing rate with a general linear model (GLM). We performed the analysis on the browsing rate of the focal species and of all species at the station. For data from video recordings, we tested the effect of the species arrangements on percent time spent foraging on the focal species and on all species with a general linear mixed model (GLMM). We included the trial as a random factor to take into account trials when more than one deer was recorded. We verified normality and heteroscedasticity and transformed response variables (square root or log transformation) when required. Analyses were performed using the GLM and the MIXED procedures of SAS version 9.4 (SAS Institute Inc. 2012). We set α at 0.05 and consider statistical trends at 0.10, as browsing rate is highly variable in natural environments. We repeated the same analyses for the predation risk experiment, adding the predation treatment and its interaction with the species arrangement as explanatory variables. We also tested the effect of the treatments on percent time spent vigilant in the station. We considered trials performed in the same station to be independent because video recording showed different individuals using the same station during different trials. We tested the impact of adding station as a random factor to analyses of browsing rates and of

time spent foraging. In half of the analyses, the effects of the station could not be estimated because of the low number of repetitions per station; 53% of the stations used in all analyses provided data three times or less. For all analyses, the effects of explanatory variables are identical to analyses without station as a random effect. We thus present results without station as a random effect. We present results as mean (95% confidence interval), unless specified otherwise.

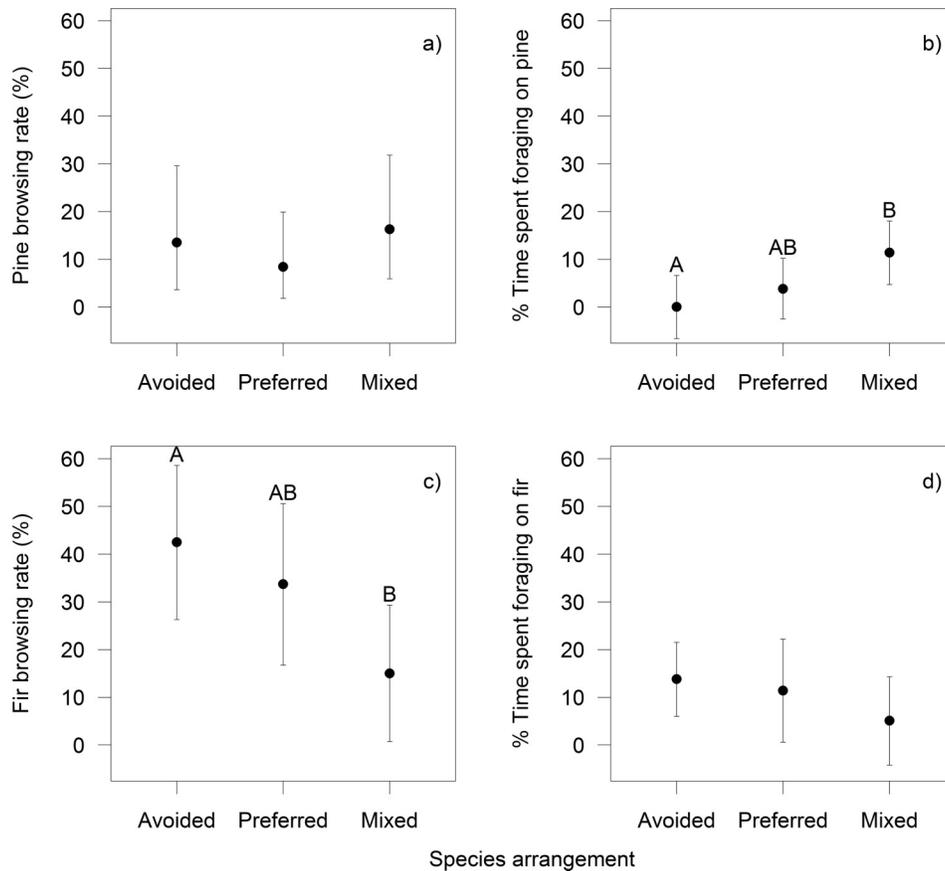
Results

Deer fed in the stations in 105 trials out of 262 in Outaouais (40%) and 79 out of 381 on Anticosti Island (21%). On average, 3 ± 3 (mean \pm SD) deer visited a station during a single trial in Outaouais ($n = 82$ trials with deer and available recordings) and 2 ± 1 deer on Anticosti Island ($n = 37$ trials with deer and available recordings).

Preference experiment

In Outaouais, browsing rate for the three species was variable among individuals (Fig. 2 top panels). Browsing rates did not follow our original prediction for this region. When offered in the same station, deer browsed similar proportions of maple and beech (mean difference between maple and beech in browsing rates: 8% (-12%, 28%), $t_{[11]} = 0.9$, $p = 0.37$) and pine and beech (5% (-16%, 26%), $t_{[12]} = 0.5$, $p = 0.60$). They tended to consume less pine than maple (-21% (-46%, 5%), $t_{[10]} = -1.8$, $p = 0.10$), but this result was variable between trials (Fig. 2). Analyses for the percent time spent foraging on each species confirmed this lack of preference; deer spent the same proportion of time foraging on maple and beech (mean difference between maple and beech foraging time: -6% (-20%, 9%), $t_{[3]} = -1.2$, $p = 0.30$), on pine and beech (7% (-42%, 55%),

Fig. 3. Winter browsing rates by white-tailed deer (*Odocoileus virginianus*) on focal species (estimated biomass browsed/available; *a, c*) and % time spent foraging on focal species (*b, d*) in the associational effects experiment in the Outaouais region (*a, b*) and on Anticosti Island (*c, d*). We tested significant differences with general linear models (*a, c*) and general linear mixed models (*b, d*) and performed a posteriori least square means differences when the treatment was significant (letters above the 95% confidence intervals (95% CI), $\alpha = 0.05$). Data are model estimates, back-transformed when required with 95% CI.



$t_{[4]} = -0.4, p = 0.73$), and on pine and maple (pine-maple: 7% (-38%, 52%), $t_{[6]} = -0.4, p = 0.72$).

On Anticosti Island, browsing rates fitted our predictions. Deer browsed more birch than spruce (Fig. 2, bottom panels; mean difference between birch and spruce browsing rates: 49% (18%, 78%), $t_{[7]} = 4.0, p = 0.005$) and tended to browse more fir than spruce (29% (-3%, 62%), $t_{[6]} = 2.2, p = 0.08$). Deer also tended to browse more birch than fir (17% (-2%, 37%), $t_{[11]} = -2.0, p = 0.08$). Analyses of foraging time revealed similar results: deer spent more time foraging on birch than spruce (mean difference between birch and spruce foraging time: 55% (30%, 80%), $t_{[5]} = 5.7, p = 0.002$) and on fir than spruce (40% (0%, 79%), $t_{[5]} = -2.6, p = 0.05$). They did not, however, spend more time foraging on birch compared with fir (2% (-68%, 73%), $t_{[5]} = 0.1, p = 0.94$).

Associational effects experiment

Species arrangement did not change the browsing rate on focal pine or on all species in Outaouais (Table 1, Fig. 3a). It modified, however, percent time spent foraging on pine and on all species (Table 1). Deer tended to spend less time foraging on pine when beech was in the neighbourhood than for mixed neighbourhoods (Fig. 3b). Time spent foraging on pine in stations with maple did not differ from beech or mixed neighbourhoods. Deer also spent less time foraging in stations with beech (0% (-16%, 16%) of their time) compared with stations with mountain maple or mixed neighbourhoods (23% (7%, 39%) and 25% (11%, 40%), respectively).

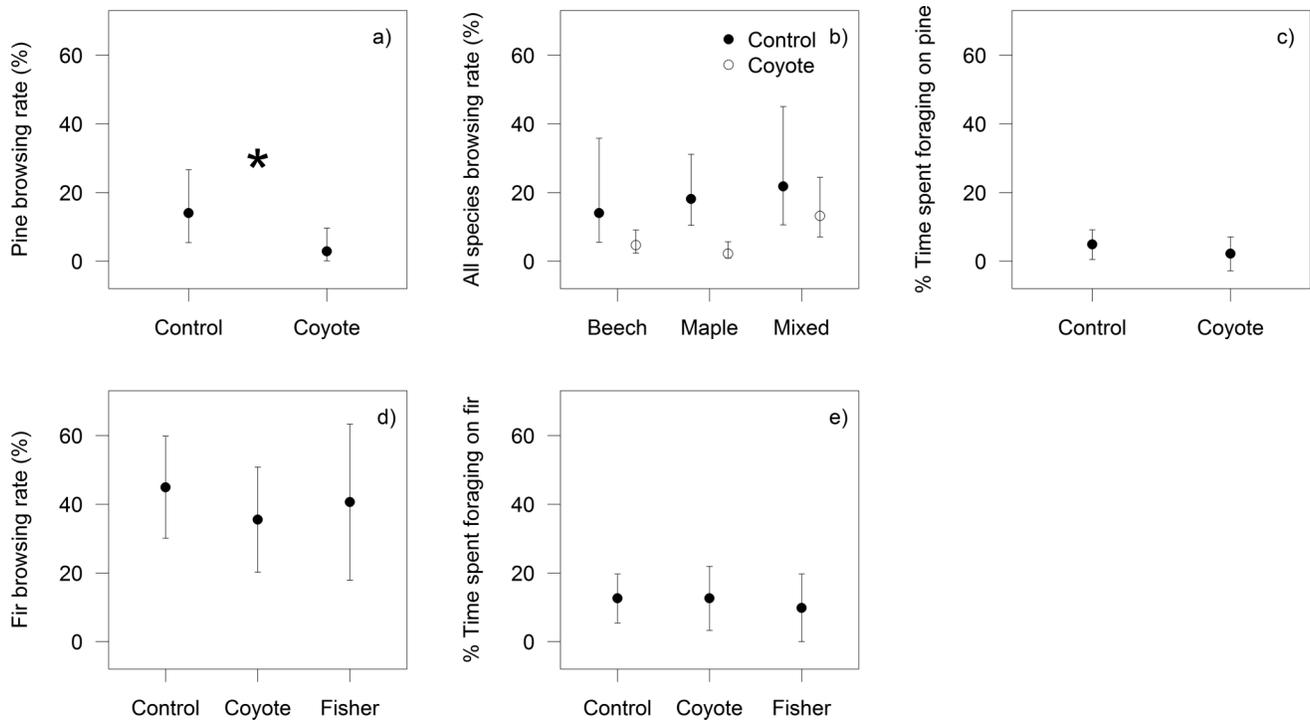
On Anticosti Island, species arrangement modified browsing rate on fir and overall browsing rate at the station, but not time

allocated to foraging (Table 1, Figs. 3c, 3d). Fir with avoided plants in the neighbourhood were more browsed than in mixed neighbourhoods (Fig. 3c). Browsing on fir in preferred neighbourhood did not differ from browsing in avoided and mixed neighbourhoods. Deer browsed more biomass in preferred neighbourhoods (30% (16%, 48%)) than in mixed and avoided neighbourhoods (7% (2%, 15%); 10% (3%, 21%), respectively).

Predation risk experiment

For Outaouais, the overall model test of the impact of treatments on pine browsing rate was not significant (Table 1). We observed, however, that the predation treatment decreased browsing rate on pine by 20% (0%, 41%) (predation $F_{[1,27]} = 4.4, p = 0.05$; Fig. 4a). In this model, the species arrangements and the interaction with perceived predation risk did not modify browsing rate on pine (species arrangement: $F_{[2,27]} = 2.1, p = 0.14$; interaction: $F_{[2,27]} = 0.9, p = 0.43$). Predation treatment reduced the overall browsing rate (Table 1; $F_{[1,27]} = 16.9, p = 0.0003$; with urine: 0% (0%, 0%); without urine: 2% (0%, 5%)) and deer browsed more biomass in mixed neighbourhoods (2% (0%, 5%)) than in single species neighbourhoods (with beech: 0% (0%, 1%); with maple: 0% (0%, 0%); $F_{[2,27]} = 4.4, p = 0.02$). There was a tendency for an interaction between species arrangement and predation treatment, but a graphical inspection revealed little biological relevance ($F_{[2,27]} = 2.6, p = 0.09$; Fig. 4b). The predation treatment had no effect on time allocation to foraging, although it tended to reduce time allocation to vigilance behaviour (Table 1); deer spent 18% (7%, 28%) of their time vigilant in stations without urine compared with 10% (4%, 16%) in stations

Fig. 4. Results of a predation risk experiment in the Outaouais region (a–c) and on Anticosti Island (d, e) on the focal species browsing rates (estimated biomass browsed/available) for white-tailed deer (*Odocoileus virginianus*) in winter (a, d), all species browsing rate (b), and % time spent foraging on focal species (c, e) in a predation risk experiment in the Outaouais region (a–c) and on Anticosti Island (d, e). We tested significant differences with general linear models (a, b, d) and general linear mixed models (c, e) and performed a posteriori least square means differences when the treatment was significant (* above 95% confidence interval (95% CI), $\alpha = 0.05$). Data are model estimates, back-transformed when required with 95% CI.



with urine. To understand this result, we calculated the total time spent in stations with and without urine: deer seemed to spend less time in stations with urine in Outaouais (0.22 min (0.08 min, 0.35 min)) compared with stations without urine (0.46 min (0.17 min, 0.76 min)). We could not test the interaction between species arrangements and the predation treatment with the video data of the Outaouais region because we had no video recording of trials for the combination “preferred” and “coyote urine”. Anticosti Island deer did not react to the predation risk treatment, whether they were in contact with coyote urine or fisher urine (Table 1, Fig. 4); the predation treatment for all species browsing rate was not significant (species arrangement: $F_{[2,28]} = 21.4$, $p < 0.0001$; predation: $F_{[2,28]} = 0.6$, $p = 0.56$; interaction: $F_{[4,28]} = 1.5$, $p = 0.25$).

Discussion

Using feeding trials with white-tailed deer in two contrasted regions, we found that differences in preference between neighbouring plants could generate associational effects. Perception of predation risk reduced the amount of biomass browsed by deer, but only in environments where deer co-occur with predators.

In Outaouais, deer spent more time foraging on pine in mixed neighbourhoods than in beech-only neighbourhoods, independently of predation risk. Because relative preferences for pine and beech were variable, this effect could be viewed both as a “classic” associational defence in presence of avoided neighbours (Atsatt and O’Dowd 1976; Champagne et al. 2016) or a neighbour contrast defence in presence of preferred neighbours (Bergvall et al. 2006). Time spent foraging in maple-only neighbourhood was intermediate between beech-only and mixed neighbourhood, potentially indicating a smaller, but similar, associational effect. On Anticosti Island, higher browsing on focal fir in avoided versus mixed neighbourhoods suggested a neighbour contrast susceptibility, i.e., an

increase in herbivory in the presence of a less palatable neighbour (Bergvall et al 2006). Again, the intermediate level of browsing in preferred neighbourhoods indicated a potential for associational effect and the slightly higher browsing on fir in preferred versus mixed neighbourhood suggested an associational susceptibility in the presence of preferred neighbours (Thomas 1986).

We suggest that variability in deer behaviour can explain the difference in associational effects between study areas. In the Outaouais region, preference for plant species varied among individuals (Fig. 2, top panels). Consequently, we observed associational effects only when looking at time allocation of individuals. On Anticosti Island, deer were more consistent in their preference for plant species (Fig. 2, bottom panels) and we observed associational effects in cumulative browse on plants. Selectivity for forage can differ among individual deer; Bergvall (2009) for instance demonstrated persistent individual variation in tannin intake in fallow deer (*Dama dama* (L., 1758)). Other differences, however, could explain the disparities in results between Outaouais and Anticosti Island. The two regions differed in bioclimatic domains and available plant species, with Outaouais being richer and more diverse in plant species than Anticosti. The relative abundance and densities of plant species can influence associational effects (Emerson et al. 2012; Hambäck et al. 2014; Underwood et al. 2014). Our stations provided a very small part of the deer’s daily diet, and other resources may have influenced deer selectivity. Moose (*Alces alces* (L., 1758)), for example, had decreased selectivity in diverse environments, leading to similar browsing among species in richer patches (Milligan and Koricheva 2013). Deer selectivity is variable and is known to decline during the winter, when resources become scarce (Dumont et al. 2005). Moreover, Outaouais deer aggregate during winter, whereas Anticosti Island deer do not and herbivore densities can influence associational effects. For example, domestic goats (*Capra hircus* L., 1758) at high densities grazed

almost all olive (*Olea europaea* L.) shoots regardless of their neighbouring plants, whereas associational defence occurred at lower goat densities (Aerts et al. 2007).

As expected in Outaouais, an increase in perceived predation risk reduced cumulative browse on plants (Swihart et al. 1991). It did not, however, modify time allocation to foraging and it reduced time allocation to vigilance. Vigilance can be combined to foraging activities such as chewing (Fortin et al. 2004), and thus, we could have missed increases in vigilance. Alternatively, herbivores can also reduce the overall time spent in a risky environment (Brown and Kotler 2004), which was the case in Outaouais. Black-tailed deer (*Odocoileus hemionus sitkensis* Merriam, 1898) also reduced the time that they spent in stations treated with wolf urine (Chamaillé-Jammes et al. 2014). The lack of interaction between associational effects and predation risk effects could be explained by their different impacts on the metrics measured: we report associational effects on foraging time and predation risk effects on cumulative browse. Although time spent foraging and biomass browsed are related, deer can modify the size and the rate at which they take bites, explaining the independence of these measures. It is also possible that we could not detect an interaction because of the avoidance of stations with urine by deer. Moreover, because deer preferences were variable, we could not determine how reduced foraging time influenced selectivity.

On Anticosti Island, deer did not adjust foraging behaviour in the presence of coyote urine. It is hypothesized that herbivores in predator-free areas can cease costly antipredator behaviours especially when resources are scarce (Lima and Dill 1990). Those results support the lack of antipredatory behaviour for deer on the island: deer ventured in large open areas (Casabon and Pothier 2007) and distance to forest edge was not a strong predictor of habitat selection (Massé and Côté 2009), a behaviour usually not seen in the presence of predators.

Our results help to identify factors influencing the individual fate of plants, a crucial issue in regions with high herbivore abundance. Associational effects are a widespread type of plant interactions mediated by large herbivores, but their effect size is highly variable (Champagne et al. 2016). Managers are exploring the application of associational effects as a management tool to reduce browsing rates on species of interest (e.g., Aerts et al. 2007; Perea and Gil 2014), but because of the variability in associational effects, managers need to perform site-specific studies. Exploring the impact of predation risk on forage selection and associational effects simultaneously may help, especially because these could interact to determine the impacts of herbivores on plants. Studies including both factors would represent more realistically trophic interactions in natural environments.

Acknowledgements

This project is part of the Natural Sciences and Engineering Research Council of Canada (NSERC) Chair in integrated resource management of Anticosti Island (<http://www.chaireanticosti.ulaval.ca/accueil/>). E.C. received scholarships from NSERC, EnviroNord, Bureau International de l'Université Laval and Centre d'Études Nordiques, and the Canadian Federation of University Women. We thank F. Parent-Paquet, A. Benoist-Chénier, B. Beaudoin, and M.A. Couillard for assistance with fieldwork; landowners of the Outaouais region for gracious use of their land; Anticosti Island inhabitants for valuable assistance; and M. Leblond, N. Underwood, M. Poulin, D. Fortin, and two anonymous reviewers for comments that improved the manuscript. We also thank H. Crépeau (Service de consultation statistique at Université Laval) who provided statistical guidance and J. Moreau (Université de Bourgogne) who provided assistance with JWwatcher analyses.

References

Aerts, R., Negussie, A., Maes, W.H., November, E., Hermy, M., and Muys, B. 2007. Restoration of dry afro-montane forest using pioneer shrubs as nurse-plants

for *Olea europaea* ssp. *cuspidata*. *Restor. Ecol.* **15**(1): 129–138. doi:10.1111/j.1526-100X.2006.00197.x.

Atsatt, P.R., and O'Dowd, D.J. 1976. Plant defense guilds. *Science*, **193**(4247): 24–29. doi:10.1126/science.193.4247.24. PMID:17793989.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., and Szendrei, Z. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annu. Rev. Ecol. Evol. Syst.* **40**: 1–20. doi:10.1146/annurev.ecolsys.110308.120242.

Beaupré, P., Bédard, C., Dufour, C., Gingras, A., Malenfant, C., and Potvin, F. 2004. Plan général d'aménagement intégré des ressources du milieu forestier de l'île d'Anticosti. Produits forestiers Anticosti Inc., Port-Menier, Que.

Bee, J.N., Tanentzap, A.J., Lee, W.G., Lavers, R.B., Mark, A.F., Mills, J.A., and Coomes, D.A. 2009. The benefits of being in a bad neighbourhood: plant community composition influences red deer foraging decisions. *Oikos*, **118**(1): 18–24. doi:10.1111/j.1600-0706.2008.16756.x.

Bergvall, U.A. 2009. Development of feeding selectivity and consistency in food choice over 5 years in fallow deer. *Behav. Processes*, **80**(2): 140–146. doi:10.1016/j.beproc.2008.11.004. PMID:19056473.

Bergvall, U.A., Rautio, P., Kesti, K., Tuomi, J., and Leimar, O. 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. *Oecologia*, **147**(2): 253–260. doi:10.1007/s00442-005-0260-8. PMID:16187104.

Blumstein, D.T., Evans, C., and Daniel, J.C. 2000. JWwatcher™ version 0.9. An introductory user's guide. Available from <http://www.jwatcher.ucla.edu> [accessed 1 May 2015].

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.*, **22**(1): 37–47. doi:10.1007/BF00395696.

Brown, J.S., and Kotler, B.P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* **7**(10): 999–1014. doi:10.1111/j.1461-0248.2004.00661.x.

Brown, J.S., Landré, J.W., and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80**(2): 385–399. doi:10.2307/1383287.

Casabon, C., and Pothier, D. 2007. Browsing of tree regeneration by white-tailed deer in large clearcuts on Anticosti Island, Quebec. *For. Ecol. Manage.* **253**(1–3): 112–119. doi:10.1016/j.foreco.2007.07.009.

Chamaillé-Jammes, S., Malcuit, H., Le Saout, S., and Martin, J.L. 2014. Innate threat-sensitive foraging: black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. *Oecologia*, **174**: 1151–1158. doi:10.1007/s00442-013-2843-0. PMID:24288079.

Champagne, E., Tremblay, J.-P., and Côté, S.D. 2016. Spatial extent of neighboring plants influences the strength of associational effects on mammal herbivory. *Ecosphere*, **7**: e01371. doi:10.1002/ecs2.1371.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* **35**: 113–147. doi:10.1146/annurev.ecolsys.35.021103.105725.

Doyon, F., and Bouillon, D. 2003. Stratégie d'aménagement, de restauration et de conservation du pin blanc et du pin rouge dans l'Outaouais. Institut Québécois d'Aménagement de la Forêt Feuillue, St-André-Avellin, Que.

Dumont, A., Ouellet, J.-P., Crête, M., and Huot, J. 2005. Winter foraging strategy of white-tailed deer at the northern limit of its range. *Ecoscience*, **12**(4): 476–484. doi:10.2980/i1195-6860-12-4-476.1.

Emerson, S.E., Brown, J.S., Whelan, C.J., and Schmidt, K.A. 2012. Scale-dependent neighborhood effects: shared doom and associational refuge. *Oecologia*, **168**(3): 659–670. doi:10.1007/s00442-011-2144-4. PMID:21987268.

Environment Canada. 1982. Canadian climate models, temperature and precipitation, 1951–1980. Québec. Atmospheric Environment Service, Ottawa, Ont.

Environment Canada. 2016a. Climate normals and averages, daily data report of Charteris' station for January 2014. Available from <http://www.climate.weatheroffice.ec.gc.ca> [accessed 17 February 2017].

Environment Canada. 2016b. Climate normals and averages, daily data report of Port-Menier's station for 1995–2015. Available from <http://www.climate.weatheroffice.ec.gc.ca> [accessed 10 June 2016].

Fortin, D., Boyce, M.S., and Merrill, E.H. 2004. Multi-tasking by mammalian herbivores: overlapping processes during foraging. *Ecology*, **85**(8): 2312–2322. doi:10.1890/03-0485.

Goudreault, F. 2007. Effet du broutement des cerfs sur la régénération d'espèces ligneuses de valeur commerciale. Ministère des Ressources Naturelles et de la Faune. Direction de l'aménagement de la faune de l'Outaouais, Gatineau, Que.

Hambäck, P.A., Inouye, B.D., Andersson, P., and Underwood, N. 2014. Effects of plant neighborhoods on plant–herbivore interactions: resource dilution and associational effects. *Ecology*, **95**(5): 1370–1383. doi:10.1890/13-0793.1. PMID:25000768.

Hébert, F., Hénault, M., Lamoureux, J., Bélanger, M., Vachon, M., and Dumont, A. 2013. Guide d'aménagement des ravages de cerfs de Virginie, 4e édition. Ministère des Ressources naturelles et Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, Québec, Que.

Hernández, L., and Landré, J.W. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildl. Biol.* **11**(3): 215–220. doi:10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2.

Kuijper, D.P., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jędrzejewska, B., and Dmit, C. 2014. What cues do ungulates use to assess predation risk in dense

- temperate forests? *PLoS ONE*, **9**(1): e84607. doi:10.1371/journal.pone.0084607. PMID:24404177.
- Le Saout, S., Martin, J.-L., Blanchard, P., Cebe, N., Hewison, A.J.M., Rames, J.-L., and Chamaillé-Jammes, S. 2015. Seeing a ghost? Vigilance and its drivers in a predator-free world. *Ethology*, **121**: 651–660. doi:10.1111/eth.12377.
- Lefort, S., Tremblay, J.-P., Fournier, F., Potvin, F., and Huot, J. 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of their distribution range. *Ecoscience*, **14**(1): 109–116. doi:10.2980/1195-6860(2007)14[109:IOBFAW]2.0.CO;2.
- Lima, S.L., and Bednekoff, P.A. 1999. Temporal variation in danger drives anti-predator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**(6): 649–659. doi:10.1086/303202.
- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**(4): 619–640. doi:10.1139/z90-092.
- Massé, A., and Côté, S.D. 2009. Habitat selection of a large herbivore at high density and without predation: trade-off between forage and cover? *J. Mammal.* **90**(4): 961–970. doi:10.1644/08-MAMM-A-148.1.
- Miller, A.M., McArthur, C., and Smethurst, P.J. 2007. Effects of within-patch characteristics on the vulnerability of a plant to herbivory. *Oikos*, **116**(1): 41–52. doi:10.1111/j.2006.0030-1299.15331.x.
- Milligan, H.T., and Koricheva, J. 2013. Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *J. Anim. Ecol.* **82**(4): 739–748. doi:10.1111/1365-2656.12049. PMID:23363076.
- Morrison, S., Barton, L., Caputa, P., and Hik, D.S. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. *Can. J. Zool.* **82**(4): 533–540. doi:10.1139/z04-024.
- Perea, R., and Gil, L. 2014. Tree regeneration under high levels of wild ungulates: the use of chemically vs. physically-defended shrubs. *For. Ecol. Manage.* **312**: 47–54. doi:10.1016/j.foreco.2013.10.022.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. 2016. nlme: linear and nonlinear mixed effects models. R package version 3.1-128 [computer program]. Available from <https://cran.r-project.org/web/packages/nlme/index.html>.
- Potvin, F. 1995. L'inventaire du brouet : revue des méthodes et description de deux techniques. Ministère de l'Environnement et de la Faune, Québec, Que.
- Potvin, F., Beaupré, P., and Laprise, G. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Québec: a 150-year process. *Ecoscience*, **10**(4): 487–495. doi:10.1080/11956860.2003.11682796.
- Pyke, G.H., Pulliam, H.R., and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**(2): 137–154. doi:10.1086/409852.
- R Core Team. 2015. R: a language and environment for statistical computing. Version 3.2.1 [computer program]. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>.
- Rautio, P., Kesti, K., Bergvall, U.A., Tuomi, J., and Leimar, O. 2008. Spatial scales of foraging in fallow deer: implications for associational effects in plant defences. *Acta Oecol.* **34**: 12–20. doi:10.1016/j.actao.2008.02.005.
- Rochette, B., and Gingras, A. 2007. Inventaire aérien du cerf de Virginie de l'île d'Anticosti – Été 2006. Ministère des Ressources Naturelles, Que.
- SAS Institute Inc. 2012. SAS for Windows. Version 9.4 [computer program]. SAS Institute Inc., Cary, N.C.
- Saucier, J.-P., Robitaille, A., and Grondin, P. 2009. Cadre bioclimatique du Québec. In Manuel de Foresterie, Deuxième édition. Edited by R. Doucet and M. Côté. Éditions Multimonde, Québec, Canada. pp. 186–205.
- Sauvé, D.G., and Côté, S.D. 2007. Winter forage selection in white-tailed deer at high density: balsam fir is the best of a bad choice. *J. Wildl. Manage.* **71**(3): 911–914. doi:10.2193/2006-056.
- Swihart, R.K., Pignatello, J.J., and Mattina, M.J.I. 1991. Aversive responses of white-tailed deer, *Odocoileus virginianus*, to predator urines. *J. Chem. Ecol.* **17**(4): 767–777. doi:10.1007/BF00994199. PMID:24258921.
- Telfer, E.S. 1969. Twig weight–diameter relationships for browse species. *J. Wildl. Manage.* **33**(4): 917–921. doi:10.2307/3799325.
- Thomas, C.D. 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia*, **70**(1): 113–117. doi:10.1007/BF00377118. PMID:28311294.
- Tremblay, J.-P., Huot, J., and Potvin, F. 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. *Oecologia*, **150**(1): 78–88. doi:10.1007/s00442-006-0504-2. PMID:16896768.
- Underwood, N., Inouye, B.D., and Hambäck, P.A. 2014. A conceptual framework for associational effects: when do neighbors matter and how would we know? *Q. Rev. Biol.* **89**(1): 1–19. doi:10.1086/674991. PMID:24672901.
- Vivås, H.J., Sæther, B.E., and Andersen, R. 1991. Optimal twig-size selection of a generalist herbivore, the moose *Alces alces*: implications for plant–herbivore interactions. *J. Anim. Ecol.* **60**(2): 395–408. doi:10.2307/5286.
- Wang, L., Wang, D., Bai, Y., Huang, Y., Fan, M., Liu, J., and Li, Y. 2010. Spatially complex neighboring relationships among grassland plant species as an effective mechanism of defense against herbivory. *Oecologia*, **164**(1): 193–200. doi:10.1007/s00442-010-1676-3. PMID:20552227.