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Manipulating forage and risk avoidance to increase white-tailed deer vulnerability to hunters

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A tradeoff between forage acquisition and predation avoidance contributes to shape space use by herbivores. The manipulation of structural components of the habitat, such as forage and forest cover may alter this tradeoff. The idea of influencing space use of herbivores is appealing for wildlife managers that aim to locally modify herbivore densities and increase their vulnerability to hunting. We attempted to manipulate the tradeoff between forage acquisition and risk avoidance of white-tailed deer *Odocoileus virginianus* on Anticosti Island (Québec, Canada) using experimental hunting fields varying in forage production (fertilized or unfertilized fields) and residual forest cover (30 or 60-m-wide forested strips between fields). In this system with high deer density, no natural predator and limited forage, fecal group surveys and camera traps demonstrated greater use of fertilized fields. Residual forest cover did not impact habitat use, suggesting that use of the experimental fields was mainly driven by the benefits of foraging compared to the costs of avoiding hunters. Deer vulnerability to hunting, however, differed with residual forest cover: hunters saw more deer per hour in fields separated by 30-m-wide forested strips compared to fields separated by 60-m-wide forested strips. That hunters did not detect the difference in deer use between fertilized and unfertilized fields suggests that deer vulnerability to hunting and deer use could be modified by different structural components of the habitat. Our results provide useful insights for wildlife managers that have to deal with conflicting goals such as maintaining hunter satisfaction with high observation rates of deer while reducing the negative impacts of high deer densities on their body condition and, on the composition and structure of forests.

Keywords: Anticosti, food plots, forage, habitat management, habitat use, hunting fields, *Odocoileus virginianus*, predation risk, tradeoff

For herbivores, space use is usually a tradeoff between forage acquisition and avoiding predation (Brown 1988, Verdolin 2006). Foraging may enhance prey vulnerability by reducing vigilance (Brown 1999). Prey can be forced to use suboptimal habitat types with decreased forage availability to avoid the use of risky ones (Kuijper et al. 2013). Several biotic and abiotic variables may modify the tradeoff over space and time, challenging ecologists in their understanding of space use by herbivores.

The structural components of habitat patches such as forest cover and soil properties modify forage acquisition and predation risk (Mysterud and Østbye 1999, Edwards et al. 2004). Forest cover conceals prey from predators, but cover

also hinders the growth of shade-intolerant plants and the lack of light can reduce forage quantity, quality and diversity (Tufto et al. 1996, Mysterud and Østbye 1999). On the other hand, open habitat patches generally produce a greater quantity of forage than dense forested patches (Massé and Côté 2009) but they also increase prey detectability (Johnson et al. 1995). In theory, herbivores should use habitats with structural components that allow them to make the most advantageous tradeoff between forage acquisition and risk avoidance (Lima and Dill 1990, Kauffman et al. 2007).

Sport hunting has been for many decades a socially acceptable, cost-efficient and common management tool to control cervid populations when natural predators are limited or absent (Brown et al. 2000). Now that broad regions experience high density of cervids (McCabe and McCabe 1997, Côté et al. 2004), the efficiency of hunting to control populations is questioned (Simard et al. 2013, Beguin et al. 2016). New habitat management practices are developed based on the observations that structural components of the

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habitat can mediate the tradeoff between forage acquisition and vulnerability to hunting (Miller and Marchinton 1995, Foster et al. 1997, Karns et al. 2016). For example, forage supplementation using food plots (Smith et al. 2007) and silvicultural practices such as prescribed fires (Edwards et al. 2004), clear-cutting (Lyon and Jensen 1980) and thinning (Heikkilä and Härkönen 2000) are aimed at increasing production and quality of forage and attracting herbivores to specific patches. Combining these practices with fertilization can further increase nutrient uptake by plants and the production of high-quality forage (Månsson et al. 2009). The fragmentation of continuous forest blocks into smaller forested patches with openings could create an advantageous tradeoff with increased forage access in open patches near protective forest cover (Lyon and Jensen 1980, Tufto et al. 1996). From the hunter's point of view, forage supplementation can also improve body condition and antler size (Putman and Staines 2004), while forest openings enhance visibility and accessibility to hunting grounds that can increase harvest probability (Lebel et al. 2012, Milner et al. 2014). Although manipulating the tradeoff for space use through habitat modifications is an attractive concept for hunters and wildlife managers, few empirical studies have tested it (but see Riginos 2015).

We established a network of experimental hunting fields within densely forested areas on Anticosti Island (Québec, Canada) to assess the effect of habitat modifications on white-tailed deer *Odocoileus virginianus* space use, vulnerability to hunting and body condition. Within the experimental hunting fields, we manipulated forage production and quality through fertilization of fields and perceived predation risk through two widths of forested patches between fields providing a variation of escape cover (Ball et al. 2000, Lebel et al. 2012). We hypothesized that deer space use is modified by the tradeoff between forage acquisition and risk avoidance. We predicted that high production and quality of forage would increase the use of riskier habitats represented by fields adjacent to narrow forest patches. We posited that deer use and vulnerability to hunting would be higher in experimental fields than in forested areas. We predicted that body condition and antler spread of harvested deer would be greater in the experimental fields than in the forested areas.

Material and methods

Study area

The experiment was conducted on public lands with exclusive rights over hunting and fishing delegated to Safari Anticosti Outfitter (49°17'N, 62°32'W) located in the eastern part of Anticosti Island, in the Gulf of St Lawrence, Québec, Canada. This 7943 km² island has a sub-boreal maritime climate characterized by cool summers and long mild winters with abundant snowfall (mean annual cumulative snowfall from winter 2006 to 2014 = 267 ± 57 cm [SD; Environment Canada 2016]). During our experiment (2013 and 2014), the average temperature near the study area varied between 17.7°C in July and -10.9°C in January (Société de protection des forêts contre le feu 2015). Harsh climatic conditions occurred during winter 2013–2014 in our study area (cumulative snowfall reached 372 cm versus 237 cm in 2012–2013

[Environment Canada 2016]); the deer population likely suffered heavier mortality in the second winter of our study. The topography of the island is a low plateau of calcareous rocks (average elevation = 126 m) intersected by several canyons (Copper and Long 1998).

The boreal forest on Anticosti Island belongs to the eastern part of the balsam fir *Abies balsamea* - white birch *Betula papyrifera* bioclimatic domain, characterized by a dominance of balsam fir, white spruce *Picea glauca* and black spruce *P. mariana* (Saucier et al. 2009). Selective deer browsing on balsam fir seedlings combined with natural disturbances has initiated a progressive conversion of balsam-fir-dominated stands into white-spruce-dominated stands (Barrette et al. 2014). The most palatable deciduous species of trees and shrubs normally found in this region, such as white birch, mountain maple *Acer spicatum*, and red-osier dogwood *Cornus stolonifera*, have also become scarce due to deer browsing (Potvin et al. 2003, Tremblay et al. 2005). In summer 1982, a forest fire burned 75 km² of the 2000 km² of lands under the exclusive rights of Safari Anticosti Outfitter. By 2012, thick white spruce-dominated stands with approximately 75% canopy cover density regenerated on this burned site to an average height of 2.5 m, greatly limiting access and reducing visibility for hunters. The soil at the study site has a thin layer of organic matter with low levels of nitrogen (N; 2 ± 1 g kg⁻¹ [95% CL]), phosphorus (P; 4 ± 1 mg kg⁻¹) and potassium (K; 104 ± 11 mg kg⁻¹) concentrations in the first 10 cm of the mineral horizon (see methods below), as often observed in coniferous forests (Jerabkova et al. 2006, Rosén et al. 2011).

Experimental design

In 2012, we created 38 km of trails and fields with a forestry mulching machine that shred aboveground vegetation. We established 16 experimental units within a completely randomized block design (four replicated blocks composed of four units each, uniform in percent cover of canopy trees [white spruce] and general topography; Fig. 1a). In each experimental unit, we created four parallel fields of 200 × 10 m with a residual forested strip between each field (Fig. 1b). We established experimental units >460 m apart, a distance greater than the mean radius of the summer home range of a female white-tailed deer on Anticosti Island (365 ± 27 m; Massé and Côté 2009). In each experimental unit, we tested a factorial combination of two treatments: 1) presence or absence of field fertilization, and 2) various widths of forest cover between fields (30 or 60-m-wide residual forested strips). We chose the width of the residual forest strip based on local ecological knowledge of professional hunting guides, in regards to average shot distance and desirable visibility. For each block, we randomly selected a paired control (2.6 or 4.4 ha) in the burned area with similar forest cover >800 m from the experimental units to avoid overlaps between control and experimental units within a deer home range (Massé and Côté 2009; Fig. 1a).

In fall 2012, we collected a composite sample of mineral soil in each experimental unit and analyzed total N through combustion at 1350°C (Carter 1993), and P and K concentrations with a Mehlich III extraction followed by spectrophotometry analyses (Mehlich 1984). We adjusted

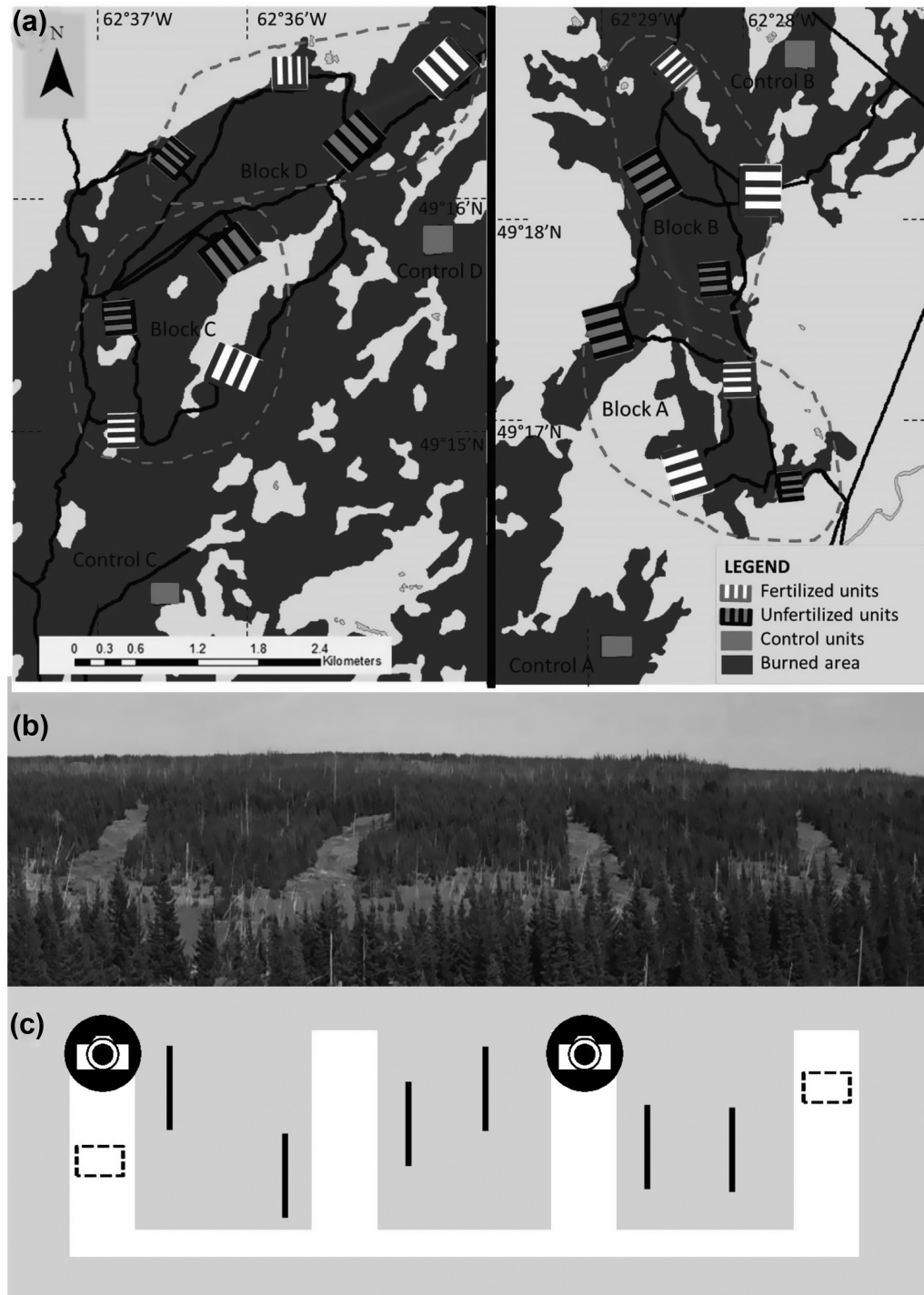


Figure 1. (a) Schematic representation of the experimental design illustrating the four replicated experimental blocks and their respective control. Dotted lines mark the block assignment of each fertilized and unfertilized units. Units with 60-m-wide forested strips have larger icons than units with 30-m-wide forested strips (not to scale). Black lines represent the network of trails between units. Light gray shading represents the matrix of unburned forests. (b) One experimental unit with the four 10×200 -m fields separated by three 30-m-wide forested strips. (c) Representation of measurement procedures established in an experimental unit (not to scale): two 2×2 -m deer exclosures within open fields (rectangles in white area) use to validate the effectiveness of the experimental manipulation (Supplementary material Appendix 1), six 4×80 -m fecal pellet group transects in forested strips (lines in grey area), and one or two camera traps within fields.

the quantity of fertilizer based on the nutrient requirements of legumes (Association des fabricants d'engrais du Québec 1999). In spring 2013, we applied a pelleted mixture of N, P and K at a rate of 450 kg ha^{-1} with a 8%:22%:25% ratio. We performed fertilization with a spreader mounted on an all-

terrain vehicle. No seeds were sown; herbaceous pioneer species such as Canadian bunchberry *Cornus canadensis*, dwarf raspberry *Rubus pubescens*, and many other native forbs recolonized the fields (Supplementary material Appendix 1 for all the information regarding vegetation analyses).

Deer use of the experimental units and controls

During 2013 and 2014, we estimated deer use of the experimental and control units with fecal pellet group surveys. We randomly positioned six 4×80-m strip transects per unit among the three forested strips of each experimental unit and in controls ($n_{\text{total}} = 120$ transects, Fig. 1c). We cleared transects of all fecal pellet groups in June. In October, we counted the fecal pellet groups defined as a dung or an accumulation of more than 15 pellets within a 10 cm radius (Marques et al. 2001). We maintained the same transect locations in 2013 and 2014. In addition to pellet group surveys, we used camera traps to evaluate use of hunting fields by deer according to the fertilization and forest cover treatments. We did not use cameras to measure deer use of forested control units because dense vegetation would have prevented us from seeing deer. In June 2013 and 2014, we randomly dispatched one or two cameras (Trophy Cam, Bushnell) per experimental unit for a total of 24 camera traps (Fig. 1c). We placed cameras 1.1 m above ground at the end of one or two of the four fields composing an experimental unit with no more than one camera per field. We adjusted the cameras to systematically trigger every 30 min during daylight from June to November (Hamel et al. 2013). We assured the same sampling effort for each treatment combination by selecting periods for which all cameras within a block worked without technical problems (from 42 to 168 days, depending on the block; Supplementary material Appendix 2). We used the number of deer seen per camera within these periods as estimates of deer use.

Deer vulnerability to hunters

From September to November 2013 and 2014 respectively, we monitored the observations of deer by 82 volunteer hunters inside the experimental design and 83 hunters in unmanaged areas (but not specifically in paired controls) to estimate deer vulnerability to hunting. We tracked the movements of hunters using GPS devices. Movements of hunters in a vehicle were not included in the study. After each hunting period, we interviewed hunters to validate their itinerary and record the number, sex and approximate location of observed deer with a possibility of shooting. We used the number of harvestable deer seen per hour as a measure of deer vulnerability to hunting (Lebel et al. 2012). We assigned observations of deer seen >460 m and >1 km from an experimental field for females and males, respectively, as animals with no access to the experimental units. Although we have no data on the movements of males, we assumed they were larger than those of females (Whitman et al 2018). We recorded the date, hunter age and years of experience as a deer hunter on Anticosti Island and elsewhere. We detailed weather conditions prevailing during the hunt, using data provided by a weather station located ca 12 km from the study area (Société de protection des forêts contre le feu 2015). We noted air temperature, peak wind speed and presence/absence of rain, ground frost and snow on the ground.

Body condition of harvested deer

To assess the effect of the experimental fields on the body condition of deer, we performed body measurements on mature

deer (≥ 2.5 -years-old) harvested by the monitored hunters in 2013 (26 males, 8 females) and 2014 (17 males, 7 females) within four days of the kill. We assigned each deer to a harvest zone considering that individuals harvested at <460 m from an experimental unit were using the experimental design ($n = 29$) and females harvested elsewhere in the burned area were controls ($n = 6$); we considered males harvested at ≥ 1 km from an experimental unit ($n = 23$) as controls to reduce the chance that they used these treated areas. We registered the date of the kill to use this information as a covariate. We weighed dressed body mass (without viscera) with a spring scale (± 0.25 kg) and measured the length of deer from the tip of the snout to the tip of the tail. We measured the thickness of the rump fat at 5 and 10 cm from the base of the tail (Simard et al. 2014). We weighed the peroneus muscle with a Pesola scale (± 0.5 g) as an index of muscle mass (Crête et al. 1993). We measured the exterior width of the antlers at the widest point and tallied the number of points exceeding 2.5 cm. We assessed deer age using counts of cementum layers in incisor teeth (Hamlin et al. 2000).

Data analyses

Effects of treatments

We used GLMM to analyze the effects of fertilization, residual forest cover, year and their interactions on deer use of experimental fields, that is 1) the number of fecal pellet groups, and 2) the number of deer observed on cameras. We used 1) blocks and transects, and 2) blocks and cameras, respectively, as random factors. We used year as a repeated measure for both models. We performed a posteriori mean comparisons using least square mean differences (LSMEANS statement). We compared the number of harvestable deer seen per hunter-day between year and treatment combinations using generalized estimating equations (GEE; PROC GENMOD) taking into account the repeated measures by a same hunter. We modeled the repeated effect with the independent type of correlation matrix considering that all measures from the same hunter were independent. We used a negative binomial distribution, the logarithm of hours spent hunting in a day as an offset variable (Agresti 1996) and the hunter information (age and hunting experience on Anticosti island and elsewhere), weather conditions, and date as covariates. To reduce redundancy between covariates, we performed two principal component analyses (PCA). First, the three hunter characteristics were substituted by a single component explaining 66% of the variance between these covariates. Second, the five weather conditions were replaced by two components explaining 73% of their variance: the first component represented temperature and presence/absence of snow and ground frost, the second discriminated between rainy and windy days.

Experimental areas versus controls

We compared the abundance of fecal pellet groups between experimental units and controls, combining the variables fertilization and residual forest cover into one explanatory variable with 5 levels (4 treatment combinations + control). Year and its interaction with this 5-level variable were also explanatory variables. We used blocks and transects as random factors and year as a repeated measure. We analyzed the effects

of the experimental design on deer vulnerability using the number of deer with possibility of shooting seen per hunter-day in the experimental design and in the control zones with GEE. We used observation zone (experimental design versus control), year and their interaction as explanatory variables. Again, we used a negative binomial distribution, the independent matrix for repeated measures, the logarithm of hours spent hunting in a day as offset variables and date, hunter information and weather conditions as covariates. The covariate date did not respect the homogeneity of slopes, thus the interaction $\text{date} \times \text{year} \times \text{observation zone}$ was kept in the model and used as a covariate (Quinn and Keough 2002). Finally, we assessed the effects of harvest zone (experimental design versus control), year, sex and their interactions on the six indices of body condition using a GLMM with harvest date and deer age as covariates (PROC MIXED). All data were checked for normality of errors and homoscedasticity and data transformations were used when required. Degrees of freedom were calculated with the Kenward–Roger approximation for GLMM. We performed all analyses with SAS 9.4 (SAS Inst.) and we used 0.05 as alpha value.

Results

Deer use of the experimental fields

Fertilization had no effect on the number of fecal pellet groups deposited in year 1 ($F_{1,23.4}=0.00$, $p=0.97$), but in year 2 fertilized units (379 ± 65 groups ha^{-1}) tended to have more fecal pellet groups than unfertilized units (263 ± 49 groups ha^{-1} ; $F_{1,9.51}=3.79$, $p=0.08$; Fig. 2, Table 1). There was no significant difference in the number of fecal pellet groups between controls (416 ± 80 groups ha^{-1}) and experimental units (544 ± 60 groups ha^{-1} ; $F_{4,13.1}=1.77$, $p=0.20$) in both years. A significant reduction in fecal pellet groups occurred in the experimental units and in the controls from year 1 (719 ± 76 groups ha^{-1}) to year 2 (283 ± 33 groups ha^{-1} ; $F_{1,139}=206.02$, $p \leq 0.001$).

In both years, there were more deer observed per camera in fertilized units (185 ± 109 deer) compared to unfertilized units (68 ± 31 deer; Fig. 3, Table 1). The number of deer seen per camera significantly declined from 216 ± 99 deer in 2013 to 37 ± 15 deer in 2014 (Fig. 3, Table 1). Both indices of deer use showed no effect of residual forest cover with 122 ± 101 deer seen per camera and 572 ± 90 fecal pellet groups ha^{-1} in units with 30-m-wide strips and 132 ± 71 deer seen per camera and 515 ± 80 fecal pellet groups ha^{-1} in units with 60-m-wide strips (Table 1).

Deer vulnerability to hunters

Hunters observed more harvestable deer h^{-1} in fields separated by 30-m-wide forested strips (1.47 ± 0.05 deer h^{-1}) than in the fields with 60-m-wide forested strips (0.96 ± 0.03 deer h^{-1} ; Table 1). Fertilization had no effect on the number of harvestable deer h^{-1} seen per hunter ($\chi^2=0.38$, $p=0.54$). There was no significant difference in the number of deer h^{-1} observed by hunters between controls and the experimental design ($\chi^2=0.02$, $p=0.88$). The number of deer h^{-1} observed in the controls and in the experimental design significantly

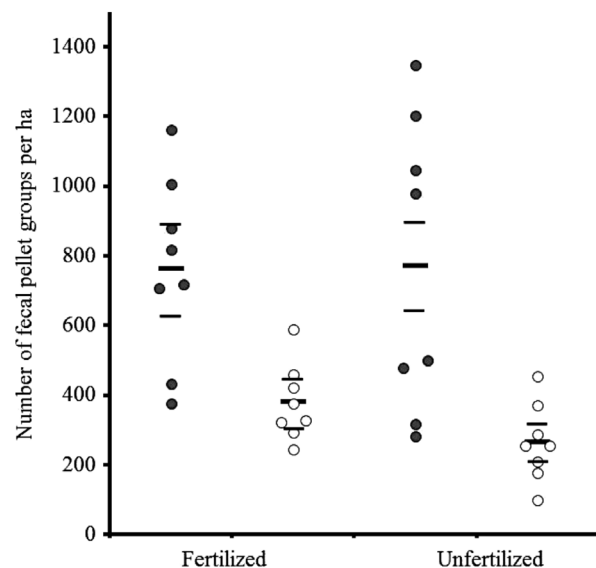


Figure 2. Effect of fertilization on deer space use estimated from feces count in fertilized units or unfertilized units over two years (year 1 grey dots, year 2 white dots) on Anticosti Island, Québec, Canada. Each dot represents the annual mean of the six transects per experimental unit and the black bars represent the overall mean of every combination of fertilization and year with the 95% CI (thinner bars).

decreased from 1.17 ± 0.01 deer h^{-1} in year 1 to 0.50 ± 0.01 deer h^{-1} in year 2 ($\chi^2=4.99$, $p=0.03$).

Body condition of harvested deer

Harvest zone (experimental design versus controls) or the interactions between harvest zone and the other explanatory variables had no effect on eviscerated body mass (51 ± 4 kg versus 47 ± 3 kg in the experimental design and controls, respectively), body length (184 ± 5 cm versus 181 ± 4 cm), peroneus muscle mass (109 ± 9 g versus 107 ± 7 g), mean thickness of rump fat (1.7 ± 0.3 cm versus 1.6 ± 0.2 cm) and the number of points (6.4 ± 0.8 versus 5.9 ± 1.0 ; Table 2; $n=65$ and $p \geq 0.16$ in all cases). Antler spread was similar between harvest zones in year 1 (39 ± 5 cm versus 35 ± 4 cm; $F_{1,36}=0.36$, $p=0.55$), but larger in the experimental design (37 ± 5 cm) than in controls in year 2 (29 ± 7 cm; $F_{1,36}=4.39$, $p=0.04$).

Discussion

Based on a large scale experimental manipulation of forage production and forest cover, our results show that creation of hunting fields in dense regenerating forests and fertilization can increase the use of these habitat patches. However, we could not detect a clear tradeoff between forage acquisition and avoidance of hunters in deer use of the experimental fields under the relatively light hunting pressure applied in our study area. Deer did not increase the use of fertilized fields adjacent to narrow forest patches. Vulnerability to hunting was rather a simple response to the width of residual forest cover between fields. Our results suggest that deer use and vulnerability to hunting are driven by different struc-

Table 1. Effects of fertilization, residual forest cover, year and their interactions on white-tailed deer use of the experimental design and on deer vulnerability to hunters in experimental fields on Anticosti Island, Québec, Canada.

Source	Fecal pellet groups			Deer seen on cameras			Deer observed by hunters	
	df _{num,den}	F	p	df _{num,den}	F	p	χ^2	p
Fertilization (F)	1,11	0.83	0.38	1,9.79	8.79	0.01*	0.38	0.54
Residual forest cover (RFC)	1,11	0.72	0.42	1,9.85	0.14	0.71	3.73	0.05*
RFC×F	1,11	1.13	0.31	1,9.81	1.72	0.22	1.43	0.23
Year (Y)	1,92	118.94	≤0.001*	1,15.1	161.20	≤0.001*	6.84	0.01*
F×Y	1,92	3.86	0.05*	1,15.1	1.08	0.32	0.05	0.82
RFC×Y	1,92	0.02	0.89	1,15.1	3.24	0.09	0.00	0.96
RFC×F×Y	1,92	0.01	0.92	1,15.1	0.00	0.95	0.83	0.36

tural components of a habitat, respectively forage production and forest cover.

We observed a large inter-annual variability in forage production, deer use and vulnerability to hunters. Within a given year, habitat use by deer in the boreal forest of Anticosti Island is mainly determined by forage abundance and not expected to vary seasonally during the snow-free period, at least in females (Massé and Côté 2009). Males could change their habitat use during the rut, but this period is short and later on Anticosti Island than elsewhere on the distribution range of white-tailed deer in North America (Goudreau 1980). The harsh climatic conditions prevailing during the winter between year 1 and year 2 of our experiment led to high winter mortality and a major decline in the deer population of the island, as demonstrated by the yearly average of deer seen with possibility of shooting per hunter-day on Anticosti Island (6.5 deer/hunter-day in year 2 compared to 11.3 ± 1.2 deer/hunter-day in the 5 preceding years; Ministère des Forêts, de la Faune et des Parcs du Québec, unpublished report). Similar high winter mortality also occurred on the island in 2003 (Simard et al. 2010). From year 1 to year 2 of our experiment, the number of fecal pellet groups deposited and the number of deer seen with possibility of shooting per hunter decreased by more than

50% in the experimental units and the controls. This decline in deer population relaxed browsing pressure on forage and contributed to increase the production of forage. Also, forage production likely increased with time due to the natural revegetation of the fields.

Forage availability

The combination of fecal pellet group surveys and camera traps demonstrated that the manipulation of forage availability with fertilization can lead to higher deer use of hunting fields. Other studies have demonstrated that an increase in forage availability after fertilization can enhance the production of biomass in an habitat patch and allow a greater use of this patch by herbivores (Miller and Marchinton 1995, Ball et al. 2000, Månsson et al. 2009). Furthermore, in a system like Anticosti Island with strong competition for food, forage availability is likely to be a strong determinant of habitat use (Massé and Côté 2009).

With regards to the fertilization postulate, our experiment showed that N, P and K amendments to the soil tended to increase forage production, while maintaining forage quality as evaluated by foliar N and NDF concentrations (Supplementary material Appendix 1). Other studies using factorial experiments reported positive, negative or no effect of fertilization on N and NDF concentrations depending on forage composition (Schellberg et al. 1999), soil characteristics (Assefa and Ledin 2001), nutrient ratio and application rate of fertilizers (Carpici and Tunali 2014). Similarly, it is likely that other fertilizer ratios and application rates could have changed forage composition and increased forage quality in our experimental fields. Forage quality also change over time with natural revegetation, as demonstrated by the increase in NDF concentration in unfertilized fields in year 2 in phase with the increase in grasses production (Supplementary material Appendix 1).

The number of harvestable deer h^{-1} seen by hunters did not increase with fertilization suggesting that hunters could not detect small differences in deer use within the experimental design. The number of deer seen by hunters is widely used to monitor fluctuations in cervid density at the regional scale (Sage et al. 1983, Mysterud et al. 2007). Similarly, in our study, this index detected the decline in deer population of the island after year 1, although it failed to detect the smaller differences in deer use at a finer scale between fertilized and unfertilized fields revealed by feces surveys and camera traps. Several factors such as habitat visibility, hunting methods, prey behavior, or, as in our study, residual

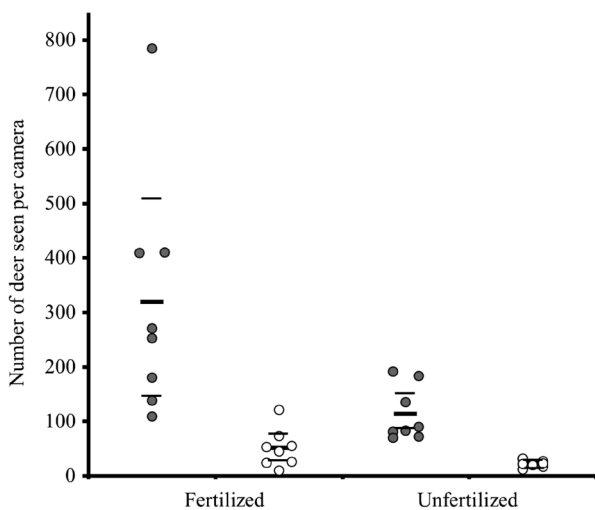


Figure 3. Number of white-tailed deer seen per camera traps in fertilized and unfertilized fields over two years (year 1 grey dots, year 2 white dots) on Anticosti Island, Québec, Canada. Each dot represents the annual mean of one or two cameras per unit and the black bars represent the mean of every combination of year and fertilization with the 95% CI (thinner bars).

Table 2. Effects of harvest zone, year, sex and their interactions on six indices of body condition of deer harvested (n=65) through recreational hunting on Anticosti Island, Québec, Canada.

Source	Eviscerated body mass			Length of deer			Peroneus muscle mass		
	df _{num,den}	F	p	df _{num,den}	F	p	df _{num,den}	F	p
Zone (Z)	1,48	1.85	0.18	1,47	0.00	0.95	1,48	0.00	0.98
Year (Y)	1,48	1.99	0.16	1,47	0.00	0.99	1,48	0.36	0.55
Sex (S)	1,48	49.00	≤0.001*	1,47	28.69	≤0.001*	1,48	27.89	≤0.001*
Z×Y	1,48	0.02	0.88	1,47	0.43	0.52	1,48	0.32	0.57
Z×S	1,48	1.48	0.23	1,47	0.07	0.79	1,48	1.02	0.32
Y×S	1,48	0.58	0.45	1,47	0.65	0.43	1,48	0.10	0.76
Z×Y×S	1,48	1.12	0.30	1,47	0.84	0.36	1,48	0.92	0.35
Source	Mean thickness of rump fat			Antler spread			Number of points		
	df _{num,den}	F	p	df _{num,den}	F	p	df _{num,den}	F	p
Z	1,48	1.53	0.22	1,36	1.23	0.28	1,37	0.64	0.43
Y	1,48	1.05	0.31	1,36	2.12	0.15	1,37	5.27	0.03*
S	1,48	1.08	0.30						
Z×Y	1,48	0.90	0.35	1,36	4.04	0.05*	1,37	0.99	0.33
Z×S	1,48	1.56	0.22						
Y×S	1,48	0.00	0.99						
Z×Y×S	1,48	0.44	0.51						

forest cover can affect the number of harvestable deer h^{-1} seen by hunters and modify the correlation of this index with local deer abundance (Hansen et al. 1986, Myrsetrud et al. 2007, Simard et al. 2012).

Residual forest cover

The manipulation of residual forest cover with various widths of forested strips increased the number of harvestable deer h^{-1} seen by hunters in the fields with narrower forested strips, but had no effect on sight distance or deer use. Other studies have shown that a reduction in forest cover increases prey detectability (Hansen et al. 1986, Brinkman et al. 2009). Visibility is inversely correlated with forest cover and it is a common factor known to increase prey harvest opportunities (Lebel et al. 2012). The mean sight distance was not significantly reduced in the 30-m-wide forested strips (36 ± 5 m) compared to the 60-m-wide forested strips (31 ± 5 m). However, the mean sight distance was long enough in most 30-m-wide forested strips to see through one strip from one field to the adjacent one, which was not possible in the 60-m-wide forested strips. It may explain why observations of deer decreased with the width of forested strips. The use of forest thinning that reduces stand density could potentially be another technique to decrease forest cover and increase deer observations (Miller and Marchinton 1995).

Residual forest cover had no detectable effect on deer use of the experimental fields. Anticosti is a predator-free island where sport hunters harvest about 5% of the deer population annually (Simard et al. 2008). Previous studies performed on Anticosti Island demonstrated no effect of cover on deer habitat selection (Massé and Côté 2009) and foraging (Potvin et al. 2003) during the snow free period. Similarly, our study suggests that without natural predators the costs of risk avoidance are outweighed by the benefits of forage acquisition in the tradeoff for space use. A lower ratio of forest cover/openings or a more intensive hunting pressure could have demonstrated an effect of risk avoidance on deer use of the experimental fields.

Managed versus natural landscapes

The experimental design had a positive but non-significant effect on deer use and vulnerability to hunting based on the mean number of fecal pellet groups and deer with possibility of shooting per hour seen by hunters in the experimental fields and in the controls. Natural revegetation of the fields is a slow process and forage production may not have increased enough yet to enhance deer use, thus explaining the lack of a significant effect on this variable. To better understand the effects of experimental fields on deer use and vulnerability to hunting, other spatial organisations and shapes of fields, and smaller proportions of forest cover/openings should be tested. Longer experimental periods should also be considered to measure the long-term effects of increased deer vulnerability on deer use and of higher deer use on forage production.

On the other hand the overall presence of experimental fields had a positive effect on antler spread of deer shot in this landscape in year 2 compared to unmanaged control areas. Other studies revealed positive effects of food supplementation on antler size, depending on the quality and quantity of the forage provided and on the degree of initial mineral and nutrient limitations (Putman and Staines 2004). Thus, natural revegetation of the fields combined with the fertilization of the mineral-poor soils of the experimental fields with phosphorus, a high component of antlers, may have contributed to increase antler spread in year 2 (Miller and Marchinton 1995) during their growth in spring and summer months. Also, the availability of forage in the experimental fields could have attracted males with larger antlers that defend their food resources and chase away males with smaller antlers (Donohue et al. 2013).

Management implications

Our study suggests that a reduction in residual forest cover increases deer vulnerability to hunting without modifying deer use of the habitat. These results can be used by wildlife

managers dealing with conflicting goals such as maintaining hunter satisfaction with high observation rates of deer while reducing the negative impacts of high deer densities on their body condition and, on the composition and structure of forests. To increase deer vulnerability to hunting, forested strips that are narrow or thinned enough to see through them, from one field to another should be considered. However, reducing forest cover should be performed as long as it does not cause avoidance of the habitat, which could decrease deer observations.

Natural revegetation of experimental fields should be considered as an alternative to cultivating crops in food plots to attract deer because it is a low-cost approach with low maintenance and reduced risk of introducing exotic species. Finally, fertilization of fields provides deer with abundant forage and could favor the local deer population if performed over large areas and over a long period of time (Mathisen et al. 2014).

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References

- Agresti, A. 1996. An introduction to categorical data analysis. – Wiley.
- Assefa, G. and Ledin, I. 2001. Effect of variety, soil type and fertiliser on the establishment, growth, forage yield, quality and voluntary intake by cattle of oats and vetches cultivated in pure stands and mixtures. – *Anim. Feed. Sci. Technol.* 92: 95–111.
- Association des fabricants d'engrais du Québec. 1999. Guide de fertilisation, 5th edn. – CRAAQ.
- Ball, J. P. et al. 2000. Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. – *J. Appl. Ecol.* 37: 247–255.
- Barrette, M. et al. 2014. Cumulative effects of chronic deer browsing and clear-cutting on regeneration processes in second-growth white spruce stands. – *For. Ecol. Manage.* 329: 69–78.
- Beguín, J. et al. 2016. Management of forest regeneration in boreal and temperate deer-forest systems: challenges, guidelines and research gaps. – *Ecosphere* 7: e01488.
- Brinkman, T. J. et al. 2009. Linking hunter knowledge with forest change to understand changing deer harvest opportunities in intensively logged landscapes. – *Ecol. Soc.* 14: 36.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk and competition. – *Behav. Ecol. Sociobiol.* 22: 37–47.
- Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. – *Evol. Ecol. Res.* 1: 49–71.
- Brown, T. L. et al. 2000. The future of hunting as a mechanism to control white-tailed deer populations. – *Wildl. Soc. Bull.* 28: 797–807.
- Carpici, E. B. and Tunali, M. M. 2014. Effects of the nitrogen and phosphorus fertilization on the yield and quality of the hairy vetch (*Vicia villosa* Roth.) and barley (*Hordeum vulgare* L.) mixture. – *Afr. J. Biotechnol.* 11: 7208–7211.
- Carter, M. R. 1993. Soil sampling and methods of analysis. – Lewis and CRC.
- Copper, P. and Long, D. G. F. 1998. Sedimentology and paleontology of the Late Ordovician through Early Silurian shallow water carbonates and reefs of the Anticosti Island, Québec. – In: Desrochers, A. et al. (eds), *Sedimentology and paleontology of the Late Ordovician through Early Silurian shallow water carbonates of the Mingan Islands National Park and Anticosti Island, Québec. Field Trip B8 Guidebook*. Geological Association of Canada-Mineralogical Association of Canada, Québec, Québec, Canada, pp. 55–97.
- Côté, S. D. et al. 2004. Ecological impacts of deer overabundance. – *Annu. Rev. Ecol. Evol. Syst.* 35: 113–147.
- Crête, M. et al. 1993. Reproduction, growth and body composition of Rivière George caribou in captivity. – *Arctic* 46: 189–196.
- Donohue, R. N. et al. 2013. Aggressive behavior of white-tailed deer at concentrated food sites as affected by population density. – *J. Wildl. Manage.* 77: 1401–1408.
- Edwards, S. L. et al. 2004. White-tailed deer forage production in managed and unmanaged pine stands and summer food plots in Mississippi. – *Wildl. Soc. Bull.* 32: 739–745.
- Environment Canada. 2016. Climate normals and averages, daily data reports of Port-Menier's station from 2013 to 2014. – Canada's Climate Archives. <<http://climate.weather.gc.ca>>, accessed 12 Jan 2016.
- Foster, J. R. et al. 1997. Factors influencing efficiency of white-tailed deer harvest in Illinois. – *J. Wildl. Manage.* 61: 1091–1097.
- Goudreau, F. 1980. Reproduction and dynamic of deer population on Anticosti Island. – MSc thesis, Dept of biology, Univ. Laval, Québec, CA, in French.
- Hamel, S. et al. 2013. Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. – *Methods Ecol. Evol.* 4: 105–113.
- Hamlin, K. L. et al. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. – *J. Wildl. Manage.* 64: 441–449.
- Hansen, L. P. et al. 1986. Factors affecting daily and annual harvest of white-tailed deer in Illinois. – *Wildl. Soc. Bull.* 14: 368–376.
- Heikkilä, R. and Härkönen, S. 2000. Thinning residues as a source of browse for moose in managed forests in Finland. – *Alces* 36: 85–92.
- Jerabkova, L. et al. 2006. Nitrogen availability in soil and forest floor of contrasting types of boreal mixedwood forests. – *Can. J. For. Res.* 36: 112–122.
- Johnson, A. S. et al. 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. – *Am. Midl. Nat.* 133: 18–35.
- Karns, G. R. et al. 2016. Factors influencing spatial heterogeneity of female white-tailed deer harvest dynamics. – *Wildl. Soc. Bull.* 40: 758–763.
- Kauffman, M. J. et al. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. – *Ecol. Lett.* 10: 690–700.
- Kuijper, D. P. J. et al. 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. – *Ecography* 36: 1–13.
- Lebel, F. et al. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. – *J. Wildl. Manage.* 76: 1431–1440.

- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Lyon, L. J. and Jensen, C. E. 1980. Management implications of elk and deer use of clear-cuts in Montana. – *J. Wildl. Manage.* 44: 352–362.
- Månsson, J. et al. 2009. Fertilization – effects on deciduous tree growth and browsing by moose. – *For. Ecol. Manage.* 258: 2450–2455.
- Marques, F. F. et al. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. – *J. Appl. Ecol.* 38: 349–363.
- Massé, A. and Côté, S. D. 2009. Habitat selection of a large herbivore at high density and without predation: tradeoff between forage and cover? – *J. Mamm.* 90: 961–970.
- Mathisen, K. et al. 2014. Long-term effects of supplementary feeding of moose on browsing impact at a landscape scale. – *For. Ecol. Manage.* 314: 104–111.
- McCabe, T. R. and McCabe, R. E. 1997. Recounting whitetails past. – In: Meehan, W. J. et al. (eds), *The science of overabundance: deer ecology and population management*. Smithsonian Inst. Press, pp. 11–26.
- Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. – *Commun. Soil Sci. Plant Anal.* 15: 1409–1416.
- Miller, K. V. and Marchinton, R. L. 1995. Quality whitetails: the why and how of quality deer management. – *Stackpole*.
- Milner, J. M. et al. 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. – *J. Wildl. Manage.* 78: 1322–1334.
- Mysterud, A. and Østbye, E. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. – *Wildl. Soc. Bull.* 27: 385–394.
- Mysterud, A. et al. 2007. Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. – *Wildl. Biol.* 13: 285–298.
- Potvin, F. et al. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Québec: a 150-year process. – *Ecoscience* 10: 487–495.
- Putman, R. J. and Staines, B. W. 2004. Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. – *Mamm. Rev.* 34: 285–306.
- Quinn, G. P. and Keough, M. J. 2002. *Experimental design and data analysis for biologists*. – Cambridge Univ. Press.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. – *J. Anim. Ecol.* 84: 124–133.
- Rosén, K. et al. 2011. Long-term effects of single potassium fertilization on ¹³⁷Cs levels in plants and fungi in a boreal forest ecosystem. – *J. Environ. Radioact.* 102: 178–184.
- Sage Jr., R. W. et al. 1983. White-tailed deer visibility and behavior along forest roads. – *J. Wildl. Manage.* 47: 940–953.
- Saucier, J.-P. et al. 2009. Cadre bioclimatique du Québec. – In: Doucet, R. and Côté, M. (eds), *Manuel de foresterie*, 2nd edn. Ordre des ingénieurs forestiers du Québec. Multimondes, pp. 186–205, in French.
- Schellberg, J. et al. 1999. Long-term effects of fertilizer on soil nutrient concentration, yield, forage quality and floristic composition of a hay meadow in the Eifel mountains, Germany. – *Grass Forage Sci.* 54: 195–207.
- Simard, A. et al. 2014. Influences of habitat composition, plant phenology and population density on autumn indices of body condition in a northern white-tailed deer population. – *Wildl. Monogr.* 187: 1–28.
- Simard, M. A. et al. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. – *J. Anim. Ecol.* 77: 678–686.
- Simard, M. A. et al. 2010. Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. – *J. Wildl. Manage.* 74: 1671–1685.
- Simard, M. A. et al. 2012. Tests of density dependence using indices of relative abundance in a deer population. – *Oikos* 121: 1351–1363.
- Simard, M. A. et al. 2013. Is hunting an effective tool to control overabundant deer? A test using an experimental approach. – *J. Wildl. Manage.* 77: 254–269.
- Smith, J. R. et al. 2007. Diets, movements and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. – *J. Wildl. Manage.* 71: 2719–2726.
- Société de protection des forêts contre le feu. 2015. Climate normals and averages, hourly data reports of a weather station located at 49°21'N and –62°26'W. – Québec's Forest Protection Service.
- Tremblay, J.-P. et al. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternate food sources that preclude density-dependent feedbacks? – *Can. J. Zool.* 83: 1087–1096.
- Tufto, J. et al. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. – *J. Anim. Ecol.* 65: 715–724.
- Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. – *Behav. Ecol. Sociobiol.* 60: 457–464.
- Whitman, B. J. et al. 2018. Movement behavior preceding autumn mortality for white-tailed deer in central New York. – *J. Mamm.* 99: 675–683.

Supplementary material (available online as Appendix wlb-00554 at <www.wildlifebiology.org/appendix/wlb-00554>). Appendix 1–2.