



Is Hunting an Effective Tool to Control Overabundant Deer? A Test Using an Experimental Approach

M. ANOUK SIMARD,¹ NSERC-Produits Forestiers Anticosti Industrial Research Chair, Département de biologie, Centre d'études nordiques, Université Laval, Québec, QC G1V 0A6, Canada

CHRISTIAN DUSSAULT, Direction générale de l'expertise sur la faune et ses habitats, Ministère des Ressources naturelles et de la Faune, Québec, QC G1S 4X4, Canada

JEAN HUOT, NSERC-Produits Forestiers Anticosti Industrial Research Chair, Département de biologie, Centre d'études nordiques, Université Laval, Québec, QC G1V 0A6, Canada

STEEVE D. CÔTÉ, NSERC-Produits Forestiers Anticosti Industrial Research Chair, Département de biologie, Centre d'études nordiques, Université Laval, Québec, QC G1V 0A6, Canada

ABSTRACT Overabundant populations of cervids have induced drastic negative effects on plant communities in several regions worldwide. Antlerless deer harvest by sport hunters has been proposed as a potential solution to overabundance because the philopatric behavior of female deer is expected to limit recolonization of hunted zones. The efficiency of this method, however, has rarely been tested in the wild. Using a large-scale experimental design, we reduced white-tailed deer (*Odocoileus virginianus*) density within 5 20-km² areas on Anticosti Island (Québec, Canada). Our objective was to harvest 50% of antlerless deer in each site during the first year of the study in 2002, and 30% from 2003 to 2006. We monitored deer density, vegetation abundance and growth as well as deer life-history traits during 6 years in these experimental sites and in 5 control sites where harvest rate was 5–7%. Overall, we achieved 93% of harvest objectives. Contrary to our expectations, however, deer density, vegetation abundance and growth, and deer life-history traits did not vary differently in experimental and control sites during the study period. They rather varied stochastically but synchronously. We discuss several alternative hypotheses that may explain these results, including 1) compensatory mechanisms, 2) biases in density estimates, 3) limited access to territory for hunters, 4) large target areas for localized management, 5) low hunter density, 6) recolonization by surrounding deer, 7) slow plant response under canopy cover, and 8) bottom-up mechanisms. Given the large efforts invested in this study, we conclude that the local control of abundant cervid populations through sport hunting may be difficult to achieve in many natural environments. © 2012 The Wildlife Society.

KEY WORDS Anticosti Island, body condition, density, forest regeneration, hunting, localized management, *Odocoileus virginianus*, overabundance, population control, white-tailed deer.

Anthropogenic activities have modified ecosystems and trophic relationships worldwide. Although such disruptions have resulted in population declines of many plant and animal species, they also benefited other populations that increased in abundance or expanded their distribution (Garrott et al. 1993, Nugent et al. 2011). In North America and Europe, the intensification of agriculture and the near extirpation of large predators have favored the increase of vertebrate herbivore populations, thereby increasing their negative impacts on vegetation communities (Jefferies 1999, Côté et al. 2004). For example, grubbing by increasing geese populations (e.g., lesser snow geese [*Chen caerulescens caerulescens*]) has resulted in soil degradation and

erosion (Kerbes et al. 1990, Fox et al. 2005). Selective browsing by large ungulates has not only affected the diversity and abundance of herbaceous plants, but also induced compositional shifts of dominant tree species in boreal and temperate forests (e.g., moose [*Alces alces*], Brandner et al. 1990; sika deer [*Cervus nippon*], Takatsuki and Gorai 1994; white-tailed deer [*Odocoileus virginianus*], Alverson and Waller 1997; reindeer [*Rangifer tarandus*], Engelmark et al. 1998). Abundant populations of large herbivores can also affect human health and economy through car accidents, disease transmission, crop damages, and inhibition of timber regeneration (Ankney 1996, Côté et al. 2004, Nugent et al. 2011).

Issues involving overabundant wildlife populations are often socially complex since they are embedded within human perception or judgment regarding both diagnosis and solutions (McShea et al. 1997). Solutions may involve the killing of animals, which is often not well perceived by the public (Garrott et al. 1993, Rutberg 1997b). Current

Received: 3 January 2012; Accepted: 2 August 2012
Published: 6 December 2012

Additional supporting information may be found in the online version of this article.

¹E-mail: marie-anouk.simard.1@ulaval.ca

management tools to reduce deer density include culling (Kilpatrick et al. 1997, Nugent et al. 2011), contraception (Merrill et al. 2006, Nugent et al. 2011), and predator reintroductions (Bangs and Fritts 1996, Ripple and Beschta 2003), but the most popular and common method remains sport hunting (Woolf and Roseberry 1998, Heusmann 1999). Sport hunting is primarily recognized as a leisure activity, in association to an industry that confers economic benefits, but it has also been used by wildlife managers as a population management tool (Rutberg 1997b).

In North America, hunting has been employed for decades as a tool to reduce white-tailed deer populations and their impacts on vegetation (Woolf and Roseberry 1998, Côté et al. 2004, Warren 2011). Management hunts have traditionally focused on females or antlerless deer to reduce the reproductive potential of populations (Brown et al. 2000). A study conducted in the Adirondacks (New York, USA) has also suggested that localized antlerless deer harvest should limit the recolonization of hunted areas because of the philopatric behavior of females (Porter et al. 1991, McNulty et al. 1997). Young females are known to establish their home range adjacent to that of their mother (Tierson et al. 1985, Mathews and Porter 1993), such that colonization of new areas should occur through the gradual expansion of home ranges of daughters surrounding a matriarch (Porter et al. 1991). The Adirondack study, where initial hunting pressure was low, suggested that harvesting a whole matriline should maintain low density for 2–10 years (Porter et al. 1991, McNulty et al. 1997). Isolated experiments successfully maintained low deer density for at least 2 years by removing about 80% of females in 1–3-km² areas (McNulty et al. 1997, Kilpatrick et al. 2001). Others have been less successful as deer recolonized the hunted zone (Miller et al. 2010) or increased reproductive rate (Killmaster et al. 2007). Although regional control of deer browsing is needed, and not only for protecting small pristine sites (Côté et al. 2004), few studies have assessed whether localized management through hunting could work in areas as large as 20 km², as suggested by Porter et al. (1991).

Despite the potential of localized sport hunting to reduce deer density, this method has received little scientific evaluation (Campbell et al. 2004, Miller et al. 2010). The assessment of population control often lacks crucial elements of scientific methodology such as replicates, control sites, or baseline data, against which to evaluate treatment effects (Rutberg 1997b, Côté et al. 2004). Because several decades of deer hunting did not succeed in controlling deer density throughout most of their range (Woolf and Roseberry 1998, Nugent et al. 2011, Warren 2011), some authors have challenged the role and efficiency of hunting to control deer populations, and proposed to rigorously test hunting management through scientific studies (Rutberg 1997b, Brown et al. 2000).

Here, we report the results of an experiment aimed at locally reducing white-tailed deer densities through sport hunting on a large predator-free island. Following their introduction on Anticosti Island (Québec, Canada; 7,943 km²) at the end of the 19th century, the deer popula-

tion grew very rapidly and today reaches very high densities despite low habitat productivity and harsh winter conditions (Simard et al. 2008). Deer have greatly modified vegetation communities; most palatable species have disappeared, especially in the shrub layer (Tremblay et al. 2005). Balsam fir (*Abies balsamea*), the main component of deer's winter diet (Lefort et al. 2007), is being gradually replaced by the less palatable white spruce (*Picea glauca*; Potvin et al. 2003).

Our objective was to assess the feasibility and efficiency of decreasing the local deer population through targeted sport hunting and to assess potential vegetation recovery and improved deer condition following density reduction. We increased antlerless deer harvest during 5 years in 5 experimental sites (20 km² each), expecting that low density would persist because of the philopatric behavior of females (Porter et al. 1991). We also established 5 control sites receiving the regular hunting pressure to compare density variations with that of experimental sites, predicting that deer density would decrease and remain low in experimental but not in treatment sites. Following a reduction in deer density in the experimental sites, we predicted an increase in the abundance of preferred herbaceous plants and balsam fir seedlings, as well as in plant size and reproductive performance (Augustine and Frelich 1998, Augustine and McNaughton 1998). Such plant response would be expected to reduce intraspecific competition, and therefore increase deer body condition and fecundity (Ashley et al. 1998, Swihart et al. 1998). Our experiment used a complex study design involving replicates, controls, and permanent plots, to measure the cascading effects of localized management on deer density, vegetation, and deer life-history traits.

STUDY AREA

Anticosti Island, Québec, Canada (49°N, 62°W; 7,943 km²), is located in the eastern balsam fir-white birch (*Betula papyrifera*) bioclimatic region where the dominant trees are balsam fir, white spruce, and black spruce (*Picea mariana*). The climate is maritime sub-boreal with cool rainy summers (630 mm/yr) and long snowy winters (406 cm/yr; Environment Canada 2006). Although the island is at the northern limit of the species' range, deer introduction has been highly successful and mean population density was estimated at >20 deer/km² locally in the last aerial surveys (Rochette and Gingras 2007). Annual population growth rate (λ) varies between years, but has remained slightly above 1 in the last 2 decades (Simard et al. 2010).

Because of chronic browsing, deer body size and fecundity rate are lower on Anticosti Island than in mainland populations and they respond rapidly to annual changes in deer density (Simard et al. 2010). Annual survival rate of adult female deer on Anticosti Island is 77% (Simard et al. 2010). Sport hunters only harvest about 5% of the population annually (approx. 8,000 deer), 65% being males (Simard et al. 2008).

METHODS

Experimental Design

Five hunting zones occur on the island, each managed by a different outfitter under the supervision of the Québec Government. We replicated our experiment 5 times, with 1 experimental block in each of the 5 hunting zones. Each zone included an experimental site (E), where hunting effort was increased, and we used the rest of the hunting zone as a large control site (C) where hunting pressure remained similar for the entire period. The hunting zones were: Western end (WW; $C = 452 \text{ km}^2$ and $E = 24 \text{ km}^2$), West (W; $C = 564 \text{ km}^2$ and $E = 21 \text{ km}^2$), Central-South (CS; $C = 557 \text{ km}^2$ and $E = 23 \text{ km}^2$), Northeast (NE; $C = 709 \text{ km}^2$ and $E = 26 \text{ km}^2$), and Southeast (SE; $C = 466 \text{ km}^2$ and $E = 25 \text{ km}^2$; Fig. 1). Harvest intensity in the controls averaged 1.3 deer/km², which was about 5–7% of the population (i.e., WW = 1.2, W = 1.3, CS = 1.6, NE = 1.1, SE = 1.1 deer/km²; Simard 2010). We randomly selected experimental and control sites that were easily accessible and had at least 50% forest cover, including a minimum of 40% stands dominated by balsam fir, to make sure we could assess the response in forest regeneration. We avoided recent forest openings (i.e., clearcut or burned areas) as they may attract deer (Lyon and Jensen 1980). We

first selected sites using 1:20,000 forest maps and later validated their characteristics through field visits.

Initial Densities and Harvest Objectives

Our objective was to harvest 50% of antlerless deer in experimental sites in the first treatment year (i.e., autumn 2002), and 30% in the subsequent years (i.e., 2003–2006) to maintain low density (Brown et al. 2000). We determined harvest quotas based on density estimates obtained through aerial surveys conducted in 2002, 2003, and 2005, assuming that antlerless deer comprised 70% of the population (Potvin 2001; Table 1). We used the upper limit of the 95% confidence interval of density estimates to fix quota objectives, but we did not set any upper limit to the number of harvested deer. We conducted aerial surveys by helicopter in mid-August using the double count technique (Potvin and Breton 2005), along 3.5-km long by 60-m wide transects, equally spaced every 250 m. We surveyed 24–30 transects in each experimental site and 18–23 transects in each control site. Average detection rate for aerial surveys on Anticosti are, respectively, $52 \pm 3\%$ and $61 \pm 4\%$ for the front and the rear observers.

Outfitters used various strategies to harvest the appropriate quotas in the different experimental sites. Some used a bonus license allowing hunters to harvest an antlerless deer in

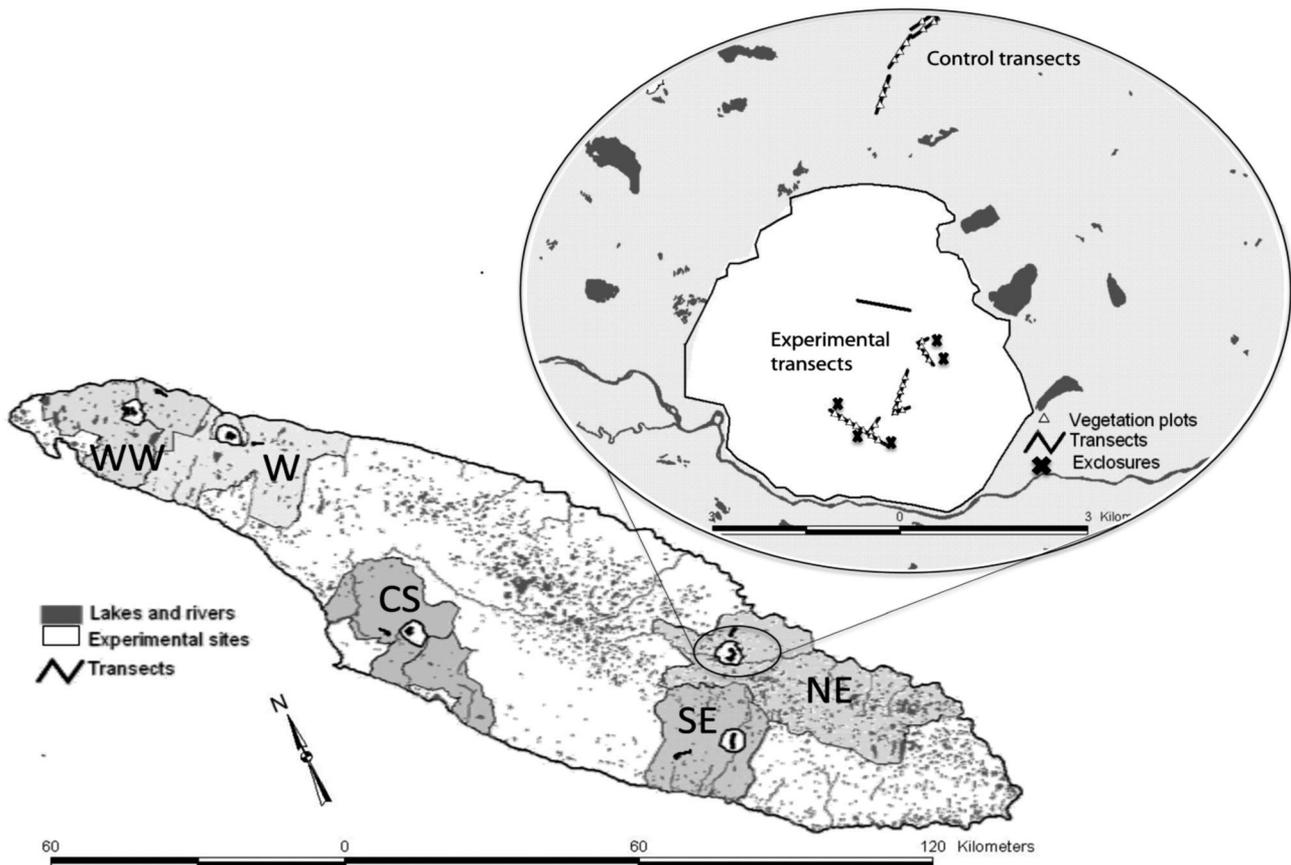


Figure 1. Anticosti Island (Québec, Canada) with the 5 hunting zones: West end (WW), West (W), Central-South (CS), Northeast (NE), and Southeast (SE) that corresponded to control sites with regular hunting pressure. We established a 20-km² experimental site where antlerless white-tailed deer harvest was locally increased within each zone. To assess variation in deer density and vegetation response to deer browsing, we established fecal transects, vegetation plots, and exclosures, 2002–2007.

Table 1. White-tailed deer density (deer/km²) and coefficient of variation (CV) obtained by aerial surveys in control and experimental hunting sites on Anticosti Island (Québec, Canada). Density estimates were used to set objectives for antlerless (females and fawns) white-tailed deer harvest. Success (%) in the application of the treatment within experimental sites was calculated by dividing the number of harvested antlerless deer by the harvest objective in each zone (WW = West end, W = West, CS = Central-South, NE = Northeast and SE = Southeast). We also present the total number of deer harvested (i.e., males included).

Year	Zone	Density from surveys				Density used to set harvest quotas (deer/km ²)	Harvest objective in experimental sites (<i>n</i>)	No. of deer harvested in experimental sites and % of success			
		Control		Experimental				Antlerless deer		All deer	
		Deer/km ²	CV (%)	Deer/km ²	CV (%)			<i>n</i>	%	<i>n</i>	%
2002	WW	15 ^a	33	10	31	13	100	107	107	113	113
	W			5	111	10	70	62	89	69	99
	CS	8	44	4	70	10	70	71	101	73	104
	NE	23 ^a	38	8	33	11	80	150	188	160	200
	SE			21	26	21	150	143	95	150	100
2003	WW	6 ^a	40	5	35	6	45	50	111	61	136
	W			4	50	6	45	48	107	68	151
	CS	3	50	4	39	6	45	29	64	50	111
	NE	6 ^a	41	4	47	6	45	4	9	16	36
	SE			6	31	8	60	19	32	55	92
2004	WW	NA ^b		NA		NA	45	59	131	65	144
	W	NA		NA		NA	45	43	96	74	164
	CS	NA		NA		NA	45	41	91	63	140
	NE	NA		NA		NA	45	17	38	25	56
	SE	NA		NA		NA	60	59	98	77	128
2005	WW	9 ^a	42	12	27	15	45	49	109	67	149
	W			14	25	17	45	37	82	69	153
	CS	11	42	11	25	14	45	22	49	29	64
	NE	18 ^a	24	11	19	13	45	15	33	36	80
	SE			28	18	28	60	39	65	56	93
2006	WW	27 ^a	34	NA ^b		NA ^b	45	113	251	132	293
	W			NA		NA	45	46	102	88	196
	CS	21	37	NA		NA	45	37	82	61	136
	NE	21 ^a	34	NA		NA	45	39	87	48	107
	SE			NA		NA	60	69	115	91	152

^a Values represent both WW and W or both NE and SE.

^b Aerial surveys were not conducted in 2004 and in experimental sites in 2006.

addition to the 2 deer allowed by their regular license (sites WW, CS, NE, and SE), whereas others used a specific license allowing a hunter to shoot antlerless deer only (sites W, WW, and CS). Residents from Anticosti achieved harvest at site WW, whereas hunters visiting the island for a 3–5-day period achieved harvest in all other sites (see Fig. 2 for an example of hunting pressure in the experimental sites).

Changes in Deer Relative Density

Because aerial surveys could not be performed each year, we used 2 other indices to monitor variations in deer density in control and experimental sites. We used the yearly average number of deer seen per hunter per day, which was correlated with density estimates from aerial surveys, both spatially (Pettorelli et al. 2007) and temporally (Simard et al. 2012). This index also correlated with population estimates in other ungulate populations (Solberg et al. 1999, Myrsetrud et al. 2007). A larger number of observers collected the data in control sites (300 hunters × 4 days annually) than in experimental sites (20–50 hunters × 3 days annually). We had no estimate of the number of deer seen per day

in 2 experimental sites in 2003 and in all the experimental sites in 2007, so we excluded that last year from the analysis.

We also estimated deer density by measuring the density of summer feces along line transects of 3.5–4 km in the central part of experimental sites to limit edge effect, and along 1–2-km transects in controls (Fig. 1). We established transects in June 2002, and revisited them in August each year up to 2007. In both control and experimental sites, we ensured that transects ran through mature balsam fir stands and circumvented areas of reduced visibility on the ground (adjusted angle zigzag design; Plumptre 2000). We subdivided each transect into a series of successive 200-m sample plots. We measured the perpendicular distance between each summer pellet group and the middle of the transect (distance = 0 m), up to a maximum of 2 m. We cleared transects from feces of previous years each June to prevent overestimating deer density (Acevedo et al. 2008), except in 2002, so we discarded data collected in that year. We estimated summer feces density in each site using Distance 5.0 (Buckland et al. 2001), which models a detection function taking into account a decrease in detection rate with increasing distance from the transect line (Bailey and Putman 1981, Buckland et al. 2001). Detection functions varied

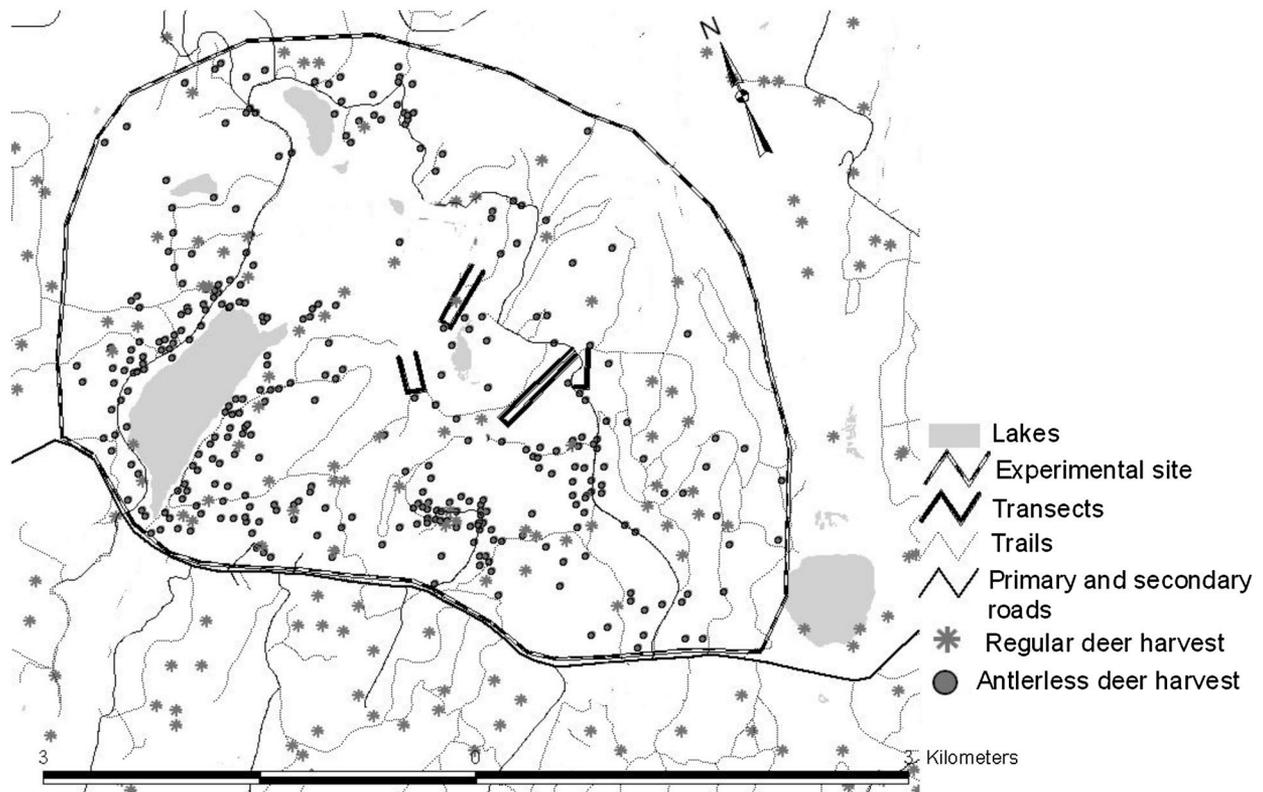


Figure 2. Locations of harvest sites for white-tailed deer taken from regular (females and males) or antlerless (females and fawns) deer licenses in autumns 2002–2005 in experimental and control sites of the West zone on Anticosti Island.

between habitats and observers. The program determined the statistical distribution that best fitted the distribution of perpendicular distances, specific to each site and year, based on Akaike's Information Criterion (AIC; Buckland et al. 2001). It then estimated the average feces density for each site and year by bootstrapping (500 repetitions). We did not transpose feces density into deer density because our goal was to assess changes in relative abundance.

Changes in Vegetation at Ground Level

We assessed the effect of antlerless deer hunting on ground vegetation by establishing a network of 4-m² permanent plots spaced 120 m–150 m apart along fecal transects, in which we measured vegetation every August from 2002 to 2007. We established plots for vegetation measurements in balsam fir stands both in experimental and control sites. We used 20 sample plots per experimental site ($n = 100$) and 7–10 plots per control site ($n = 41$; Fig. 1). We added 5 4-m² exclosures in each experimental site ($n = 24$, 1 exclosure was removed the first year) to determine the response of vegetation in the absence of deer. We characterized the tree layer by estimating the basal area of tree species with a prism (Grosenbaugh 1952) and by measuring the height (m; using a clinometer), age (with a Pressler borer), and diameter at breast height (cm) of a representative tree. We estimated percent canopy closure by counting the number of times that tree canopy cover exceeded 50% at every meter along a 20-m north-south transect (Vales and Bunnell 1988). We mea-

sured percentage of horizontal cover towards the north and south with a profile board (2.5 m × 0.3 m with sections of 0.5 m) positioned at 15 m from the plot center (Nudds 1977).

We estimated percent ground cover ($\pm 5\%$) and average height (± 5 cm) of browse-sensitive broadleaf plants and low shrubs (Viera 2003, Tremblay et al. 2006). We built an index of forbs abundance by summing the ground cover of most forbs and low shrubs present in deer diet (i.e., *Cornus canadensis*, *Coptis groenlandica*, *Rubus pubescens*, *Trientalis borealis*, *Maianthemum canadense*, *Clintonia borealis*, *Aralia nudicaulis*, *Fragaria* spp., *Gallium* spp., *Viola* spp., *Vaccinium* spp., and *Ribes* spp.; Huot 1982). We also analyzed bunchberry (*C. canadensis*) ground cover separately because this species alone comprised 25–40% of deer diet between May and November (Huot 1982) and it was the most common plant in vegetation plots.

Because changes in deer density might affect plant physiology and morphology more rapidly than plant abundance in forest stands (Kraft et al. 2004), we collected data on plant growth from 2004 to 2007, including reproductive performance and leaf area. We assessed the reproductive performance of browse-sensitive broadleaf herbs and shrubs by counting reproductive structures (i.e., flower shoots or fruits) in each plot. We estimated leaf area of Canadian bunchberry (Cc) and wild lily-of-the-valley (*M. canadense*; Mc). We measured leaf maximal width (W_l) and length (L_l) of 10–30 individuals in each plot. For bunchberry, we counted the

number of leaves per whorl (N_l) and measured 1 leaf for every whorl (n of whorl = k). We used the following equations to estimate leaf area:

$$\sqrt{\text{leaf area}_{Cc}} = \sum_k^1 -1.36 \pm 0.09 + 0.43 \pm 0.2 \times N_l + 0.64 \pm 0.06 \times L_l + 0.62 \pm 0.09 \times W_l$$

$$\sqrt{\text{leaf area}_{Mc}} = -4.5 \pm 0.4 + 2.2 \pm 0.1 \times L_l + 1.4 \pm 0.2 \times W_l + 0.8 \pm 0.1 \times [(L_l - 2.5) \times (W_l - 2.2)]$$

We developed these regressions by scanning 211 leaves of bunchberry ($R^2 = 0.93$) and 129 leaves of lily-of-the valley ($R^2 = 0.92$) and measuring their area. We averaged the leaf area of each species in each plot.

We assessed forest regeneration from 2002 to 2007 by counting the number of balsam fir seedlings in plots and exclosures using the following height classes, I: <10 cm, II: 10–30 cm, III: 30–60 cm, and IV: 60–100 cm. We only used the total number of seedlings in classes I and II, because very few seedlings were taller than 10 cm. Balsam fir is a good indicator of deer browsing pressure on Anticosti Island (Tremblay et al. 2005). Because of severe windthrow in autumn 2005, especially in the WW experimental and W control sites, we could not monitor several fecal transects and/or vegetation plots after 2006, resulting in an unbalanced design.

Changes in Deer Life-History Traits

To assess the effect of experimental hunting treatment on deer body condition, we measured different indices of body condition on deer harvested in control and experimental sites during autumns 2002–2006 (i.e., years 1–5; Simard 2010). We measured dressed body mass of fawns and rump fat thickness of adult (i.e., ≥ 1.5 -yr-old) females because they were the most likely to respond to changes in forage abundance (Therrien et al. 2007, Simard 2010). Dressed body mass (i.e., body mass minus viscera and bleedable blood; spring scale ± 0.25 kg) is a common index of body condition integrating variation in fat content, muscular mass, and skeletal growth (Chan-McLeod et al. 1995, Simard 2010). Rump fat thickness is a good index of fat reserves (Cook et al. 2001) and was measured by inserting a ruler (± 0.25 cm) in subcutaneous fat at 5 and 10 cm from the base of the tail, at a 45° angle with the backbone. We aged fawns and yearlings based on tooth replacement and used cementum layers in incisor teeth to age adults (Hamlin et al. 2000).

For most females harvested during autumns 2002–2006, hunters noted the presence of milk during evisceration, which could indicate whether females successfully raised their fawns throughout the summer, a proxy of weaning success involving a prolonged reproductive investment (Simard 2010, Simard et al. 2010). We assumed no difference in the probability of milk detection throughout autumn,

considering that the percentage of lactating females did not differ between early ($65 \pm 6\% < 15$ Oct) and late autumn ($69 \pm 7\% > 15$ Oct, $F_{1,4} = -1.55$, $P = 0.2$). Simard et al. (2010) demonstrated that lactation rate is negatively influenced by local deer density of the previous year; an increase in lactation rate could therefore be a good indicator of density changes in experimental sites. We also collected ovaries from 2002 to 2005 to obtain fecundity rate of reproductive females (1 or 2 ovulations) the preceding autumn by counting the number of *Corpus rubrum* (Langvatn et al. 1994, Simard et al. 2008).

Statistical Analyses

We assessed the effects of hunting treatment using mixed effect models (lme in package nlme R version 2.10.1; R Development Core Team 2009). We included the 5 hunting zones as a random effect. In vegetation models, which involved replicated plots, we used the treatment nested within the hunting zone as a random term because we were interested in assessing variations at the plot level (Pinheiro and Bates 2000, Quinn and Keough 2002). The random term indicates what is the smallest unit on which to measure the treatment and consider autocorrelation. For plant reproductive structures, we averaged the number of flowers or fruits among plots for each treatment, zone, and year because they were too rare. Because we applied the hunting treatment from year 1 to 5 (i.e., 2002–2006) and monitored it from year 1 to 6 (i.e., 2002–2007, with a few exceptions), we used a repeated measures design to control for the effect of confounding factors, such as site characteristics (Pinheiro and Bates 2000). We accounted for temporal correlation within sites using a correlation matrix with a first-order autoregressive structure because sites at year t of the treatment were more likely to be correlated to themselves at years $t - 1$ or $t + 1$ than at years $t - i$ or $t + i$ (where $i > 1$; Pinheiro and Bates 2000). To assess changes in body condition and reproductive status, we used different individuals each year, and therefore year was not considered a repeated measure. We used a general linear mixed model (i.e., glmer) in lme4 package of R version 2.10.1 (Pinheiro and Bates 2000) for the analysis of lactation status, which was a binary variable, and we tested the significance of fixed effects with Chi-squared (χ^2) deletion tests.

In each analysis, we tested the following fixed effects: the treatment (experimental, control, and exclosure for vegetation), the year of treatment (between 4 and 6 levels), and the year by treatment interaction, to test for the effect of treatment while considering year and site effects. We were specifically interested in year \times treatment interactions to test the effect of hunting management on response variables. For the models on body condition and lactation status, we also included sex, date, age, and lactation status (for body condition only) as covariables (including non-linear effects) based on Simard (2010). We investigated the structure of the relation between response variables and time by testing, using AIC (Burnham and Anderson 2002), whether year best fitted response variables as a factor, suggesting stochastic temporal variation (null model), as opposed to a linear,

exponential, or logarithmic increase involving a directional response in time (Tremblay et al. 2006).

For each response variable, we selected the transformation that best improved the distribution of residuals, based on Sokal and Rohlf (1995) or a boxcox procedure (generally log or arcsin [square-root]; Crawley 2007). In the few cases where we could not improve the distribution of residuals with a transformation, we confirmed the results by conducting a similar analysis using ranks, but for brevity, we only present results from parametric models (Sokal and Rohlf 1995). In the results section, we present *F*-statistics from analysis of variance (ANOVA) tables and, in some occasions, *t*-statistics from the table of estimates associated with each treatment level (respectively, χ^2 and *Z* for lactation; Tables 2–4).

This research project complies with all legal requirements and was approved by the Canadian Council for Animal Care committee of Université Laval (Protocol No. 2005-024).

RESULTS

Experimental Hunting Treatment

Before the experiment (Aug 2002), deer density within experimental sites varied between 13 deer/km² and 21 deer/km² (Table 1). Overall, the harvest objective for antlerless deer was reached in 93% of the cases over the 5 years of the experiment with variations among sectors (mean proportional harvest relative to objective, WW = 142%, W = 95%, CS = 78%, NE = 71%, SE = 81%) and years (1 = 116%, 2 = 65%, 3 = 91%, 4 = 68%, 5 = 127%; Table 1). In most experimental sites, hunters also harvested adult males in addition to antlerless deer (Table 1).

Changes in Relative Deer Density

The number of deer seen per hunter per day (log-transformed) was greater in control (10 ± 2) than in experimental sites (6 ± 1; $F_{1,34} = 4.5$, $P = 0.04$), but showed stochastic vari-

ation through years ($F_{4,34} = 12.6$, $P < 0.001$; AIC values in Appendix 1 available online at www.onlinelibrary.wiley.com), which were similar in both control and experimental sites (year × treatment interaction not significant, $F_{4,34} = 0.9$, $P = 0.5$; Table 2, Fig. 3A). In both sites, the number of deer seen per day was on average greater during years 1 and 5 (control = 15 ± 3, experimental = 9 ± 2) than in years 2, 3, and 4 (control = 8 ± 2, experimental = 5 ± 1; Table 2, Fig. 3A).

Feces density (log-transformed) did not differ between control and experimental sites ($F_{1,32} = 0.2$, $P = 0.6$) and showed stochastic variation through years ($F_{4,32} = 5.0$, $P = 0.003$; Appendix 1 available online at www.onlinelibrary.wiley.com), which were similar in control and experimental sites ($F_{4,32} = 0.2$, $P = 0.9$; Fig. 3B, Table 2). Feces density suggested the greatest deer density at year 3 (control = 228 ± 53, experimental = 167 ± 38) and the lowest densities during years 4 and 6 (control = 81 ± 20, experimental = 62 ± 15; Fig. 3B, Table 2). The correlation between our 2 density indices was low ($r = 0.12$, $P = 0.4$). Feces density did not correlate with aerial surveys ($r = -0.10$, $P = 0.4$), whereas the number of deer seen per hunter per day did ($r = 0.57$, $P < 0.001$).

Changes in Vegetation at Ground Level

Most vegetation plots were located in forest stands of similar characteristics: mature balsam fir forest with a relatively high canopy closure, low lateral cover, predominance of moss germination beds, and a high tree basal area composed predominantly of balsam fir of similar age and diameter at breast height (Appendix 2 available online at www.onlinelibrary.wiley.com).

The percentage ground cover of palatable forbs (log-transformed) was lesser in control (8 ± 2%) than in experimental sites (29 ± 7%, $t = 6.2$, $P < 0.001$) or exclosures (27 ± 7%, $t = 5.0$, $P < 0.001$), the latter 2 being similar

Table 2. Coefficients ($\beta \pm SE$), *t*-statistic, and associated degree of significance of the variables used to explain variations in white-tailed deer density on Anticosti Island (Québec, Canada). Models compared control (*C*) with experimental sites (*E*) in which we increased antlerless deer harvest. We tested for changes in response variables among years 1–6 of treatment (2002–2007) and verified if treatment affected temporal changes. We log-transformed variables to normalize residuals.

	Deer seen per day			Feces density		
	β	SE	<i>t</i>	β	SE	<i>t</i>
Intercept	2.8	0.2	15.4***	4.8	0.2	20.7***
<i>E</i>	-0.5	0.2	-2.1*	-0.2	0.3	-0.5
Year ^a						
2	-1.0	0.2	-5.9***			
3	-0.5	0.2	-2.2*	0.7	0.3	2.5
4	-0.7	0.2	-3.2**	-0.4	0.3	-1.4
5	-0.1	0.2	-0.3	<0.1	0.3	0.1
6				-0.4	0.3	-1.1
<i>E</i> × year						
2	0.4	0.3	1.3			
3	-0.1	0.3	-0.2	-0.2	0.4	-0.4
4	<-0.1	0.3	-0.1	-0.3	0.4	-0.6
5	-0.2	0.3	-0.5	-0.3	0.5	-0.7
6				<0.1	0.5	<0.1

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

^a Year 1 was the reference except for feces density where reference was year 2.

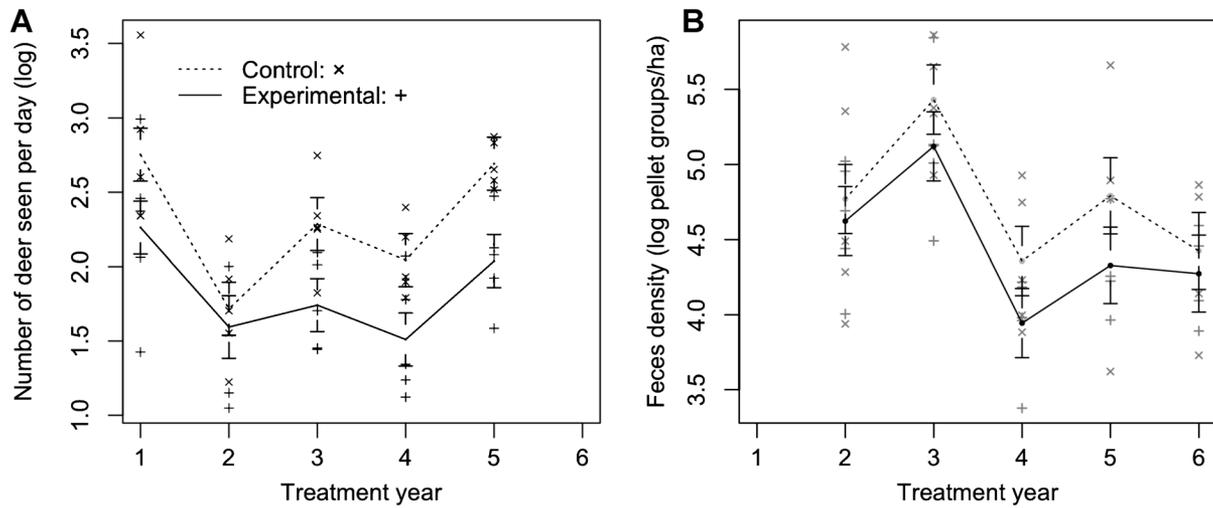


Figure 3. Temporal variations in white-tailed deer density (estimates and SE) predicted from models using relative indices of deer density: (A) number of deer seen per hunter per day and (B) density of fecal pellet groups. Models compared density between control (i.e., natural deer density) and experimental sites (i.e., intensified antlerless deer harvest) on Anticosti Island (Québec, Canada) over 6 years (2002–2007). Symbols in gray represent the average density for the different zones.

($t < 0.1$, $P = 1.0$ [t -test between each level]; $F_{2,8} = 21.5$, $P < 0.001$ [main effects ANOVA]; Fig. 4A and Table 3). Forbs ground cover changed stochastically through years ($F_{5,903} = 19.6$, $P < 0.001$; Appendix 1 available online at www.onlinelibrary.wiley.com) and variations were not significantly related to treatment ($F_{10,903} = 1.6$, $P = 0.1$;

Fig. 4A, Table 3). Experimental plots differed from control plots at the beginning of the project, but the lack of difference in temporal trends between treatment and control plots indicate that vegetation did not respond to reduced browsing pressure. We also observed similar results for most vegetation measurements. Notably, the percentage cover of bunchberry

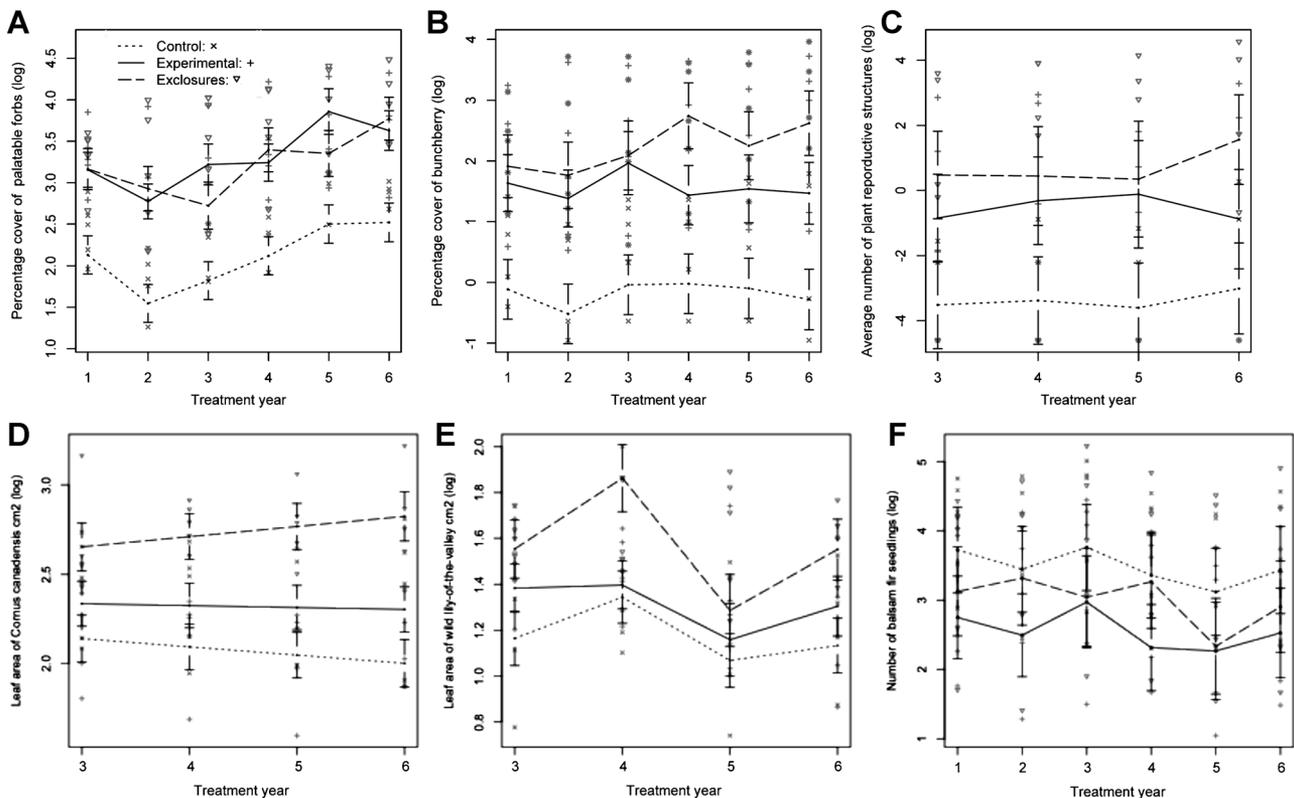


Figure 4. Temporal variations in vegetation growth and abundance (estimates and SE) predicted by models for (A) percent ground cover in palatable forbs and low shrubs and (B) in bunchberry, (C) number of reproductive structures in forbs and low shrubs, (D) leaf area of bunchberry and (E) wild lily-of-the-valley, and (F) abundance of balsam fir seedlings. Models compared vegetation characteristics between control sites (i.e., natural deer density), experimental sites (i.e., increased antlerless white-tailed deer harvest), and exclosures (i.e., deer exclusion) on Anticosti Island (Québec, Canada) during 6 years (2002–2007). Symbols in gray represent the average vegetation growth and abundance for the different zones.

Table 3. Coefficients ($\beta \pm SE$), t -statistic, and associated degree of significance of the variables used to explain variations in vegetation abundance, vegetation growth, and balsam fir regeneration on Anticosti Island (Québec, Canada). Models compared control (C) with experimental sites (E) in which we increased antlerless white-tailed deer harvest. We also established exclosures (EX; vegetation plots free of deer browsing) within experimental sites. We tested for changes in response variables among years 1–6 of treatment (2002–2007; year was factorial or continuous) and verified if treatment affected temporal changes. We log-transformed variables to normalize residuals.

	Vegetation abundance (% ground cover)									Vegetation growth						Regeneration		
	Forbs (log)			Bunchberry (log)			No. of reproductive structures (log)			Leaf area (log)						No. of fir seedlings (log)		
	β	SE	t	β	SE	t	β	SE	t	β	SE	t	β	SE	t	β	SE	t
Intercept	2.1	0.2	9.3***	-0.1	0.5	-0.2	-4	1	-2.6*	2.3	0.2	13.8***	1.3	0.1	12.9***	3.7	0.6	6***
E	1.0	0.2	6.2***	1.8	0.3	5.5***	3	1	2.5*	0.1	0.2	0.6	0.2	0.1	1.7	-1.0	0.5	-1.8
EX	1.0	0.2	4.9***	2.0	0.4	5.3***	4	1	3.7***	0.2	0.2	1.2	0.3	0.1	2.7*	-0.6	0.6	-1
Year ^a										Linear								
2	-0.6	0.1	-7.5***	-0.4	0.1	-3.0**				-0.05	0.02	-1.9****				-0.3	0.2	-1.6
3	-0.3	0.1	-3.0**	0.1	0.2	0.4										<0.1	0.2	0.2
4	-0.1	0.1	-0.1	0.1	0.2	0.4	0.1	0.6	0.2				0.15	0.07	2.2*	-0.4	0.3	-1.5
5	0.4	0.1	2.7**	<0.1	0.2	0.1	-0.1	0.9	-0.1				-0.09	0.08	-1.1	-0.6	0.3	-2.2*
6	0.4	0.2	2.7**	-0.2	0.3	-0.7	1.5	1.0	0.5				-0.03	0.09	-0.4	-0.3	0.3	-1.0
$E \times \text{year}^a$										Linear								
2	0.2	0.1	2.2*	0.2	0.2	0.9				0.04	0.03	1.3				<0.1	0.2	0.1
3	0.1	0.1	0.8	-0.3	0.2	-1.4										-0.1	0.3	-0.3
4	0.1	0.1	0.6	<0.1	0.3	0	0.4	0.9	0.4				-0.14	0.08	-1.8****	0.1	0.3	0.2
5	-0.1	0.2	-0.8	0.1	0.3	0.4	-0.5	1.0	-0.4				-0.03	0.09	-0.4	-0.1	0.3	-0.4
6	-0.2	0.2	-1.0	0.3	0.3	1.1	<0.1	1.4	0				-0.1	0.1	-1.4	-0.2	0.3	-0.6
EX \times year ^a										Linear								
2	0.4	0.1	2.9**	0.3	0.2	1.1				0.10	0.04	2.7**				0.2	0.3	0.7
3	0.3	0.2	1.9*	-0.1	0.3	-0.4										0.1	0.4	0.3
4	0.4	0.2	1.8****	0.3	0.3	0.8	0.8	0.9	0.9				-0.1	0.1	-1.0	0.5	0.4	1.2
5	0.2	0.2	1.1	0.7	0.4	1.9*	-0.2	1.2	-0.1				0.1	0.1	1.0	0.5	0.4	1.1
6	0.2	0.2	0.9	0.9	0.4	2.1*	0.6	1.4	0.4				<0.1	0.1	0.2	0.1	0.5	0.1

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

**** $P < 0.1$.

^a Year 1 was the reference except for vegetation growth where reference was year 3.

(log-transformed) was lesser in control ($1 \pm 0\%$, $t = 5.5$, $P < 0.001$) than in experimental sites ($5 \pm 2\%$, $t = 5.5$, $P < 0.001$) or exclosures ($10 \pm 5\%$, $t = 5.0$, $P < 0.001$), the latter 2 being similar ($t = 0.7$, $P = 0.5$; $F_{2,8} = 19.3$, $P < 0.001$; Fig. 4B, Table 3). Bunchberry cover showed stochastic variations over time ($F_{5,903} = 4.0$, $P = 0.001$; Appendix 1 available online at www.onlinelibrary.wiley.com), and significant interactions suggested that inter-annual variations differed among treatments ($F_{10,903} = 1.9$, $P = 0.05$). Bunchberry cover increased more rapidly in exclosures than in control or experimental sites (Fig. 4B, Table 3).

The number of plant reproductive structures in forbs or low shrubs (log-transformed) was fewer in control (0.03 ± 0.05) than in experimental sites (0.6 ± 0.9 , $t = 2.4$, $P = 0.02$) or exclosures (2.3 ± 3.4 , $t = 3.7$, $P < 0.001$), the latter 2 being not statistically different ($t = 1.2$, $P = 0.2$; $F_{2,41} = 12.4$, $P < 0.001$). The abundance of plant reproductive structures did not vary over time ($F_{3,41} = 0.2$, $P = 0.9$; factorial and exponential relationships had equivalent AIC values, Appendix 1 available online at www.onlinelibrary.wiley.com) in any treatment ($F_{6,41} = 0.4$, $P = 0.9$; Fig. 4C, Table 3).

The leaf area of bunchberry changed linearly from 2004 to 2007 (year as a linear effect: $F_{1,388} = 3.7$, $P = 0.06$;

Appendix 1 available online at www.onlinelibrary.wiley.com), with slopes varying in relation to treatment (interaction: $F_{2,388} = 3.6$, $P = 0.02$, treatment: $F_{2,8} = 0.7$, $P = 0.5$; Fig. 4D, Table 3). Over the 6-year study, leaf area of bunchberry increased by $19 \pm 22\%$ in exclosures, whereas it decreased by $5 \pm 20\%$ in experimental sites ($t = -2.0$, $P = 0.04$) and by $15 \pm 20\%$ in control sites ($t = -2.7$, $P < 0.001$), the last 2 decreasing similarly ($t = 1.3$, $P = 0.2$; Fig. 4D, Table 3). The leaf area of wild lily-of-the-valley showed stochastic annual variation ($F_{3,547} = 8.9$, $P < 0.001$; Appendix 1 available online at www.onlinelibrary.wiley.com), unrelated to treatment ($F_{6,547} = 1.5$, $P = 0.2$; Table 3). Leaf area of lily-of-the-valley was similar in control ($3.3 \pm 0.4 \text{ cm}^2$) and experimental sites ($3.7 \pm 0.5 \text{ cm}^2$, $t = -1.7$, $P = 0.1$), and greater in exclosures ($4.9 \pm 0.7 \text{ cm}^2$, $t = 2.7$, $P = 0.03$), although the difference between experimental sites and exclosures was not significant ($t = 1.3$, $P = 0.2$; $F_{2,8} = 6.0$, $P = 0.03$; Fig. 4E, Table 3).

The number of balsam fir seedlings did not differ among control sites (32 ± 20), experimental sites (13 ± 8 , $t = -1.8$, $P = 0.1$), and exclosures (21 ± 14 , $t = -1.0$, $P = 0.3$; $F_{2,8} = 2.7$, $P = 0.2$), and varied stochastically over time ($F_{5,901} = 2.7$, $P = 0.02$; Appendix 1 available

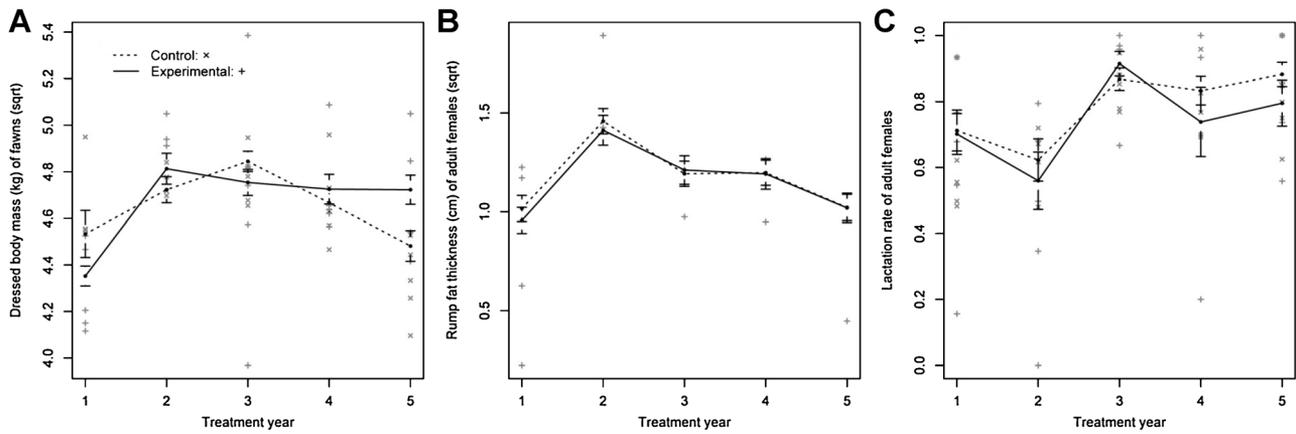


Figure 5. Temporal variations in white-tailed deer life-history traits predicted from models of (A) fawn dressed body mass, (B) female rump fat thickness, and (C) female lactation rate. Models compared life-history traits between control (i.e., natural deer density) and experimental sites (i.e., increased antlerless deer harvest) on Anticosti Island (Québec, Canada) over 5 years (2002–2006). Symbols in gray represent the average deer life-history traits for the different zones.

online at www.onlinelibrary.wiley.com) in control and experimental sites ($F_{10,901} = 0.5$, $P = 0.9$; Fig. 4F, Table 3).

Changes in Deer Life-History Traits

Dressed body mass of white-tailed deer fawns varied stochastically through time ($F_{4,588} = 7.6$, $P < 0.001$; Appendix 1 available online at www.onlinelibrary.wiley.com). After controlling for date and sex, inter-annual variation in mass differed according to treatment ($F_{4,588} = 3.7$, $P = 0.006$), but the average mass was similar in control (21.5 ± 2.5 kg) and experimental sites (21.7 ± 2.6 kg;

$F_{1,588} = 2.9$, $P = 0.09$; Fig. 5A, Table 4). In experimental sites, fawn body mass increased from year 1 to 2, and remained high and constant in consecutive years, whereas in control sites it increased up to year 3 and decreased thereafter (Fig. 5A). After controlling for date, age, and lactation status, rump fat thickness of adult females was 1.4 ± 0.2 cm in both control and experimental sites ($F_{1,1953} = 2.5$, $P = 0.1$), and varied stochastically through years ($F_{4,1953} = 60.8$, $P < 0.001$) in a similar manner in experimental and control sites ($F_{4,1953} = 0.6$, $P = 0.7$; Fig. 5B, Table 4).

Table 4. Coefficients ($\beta \pm$ SE), t - or Z -statistic and associated degree of significance of the variables used to explain variation in white-tailed deer life-history traits on Anticosti Island (Québec, Canada). Models compared control (C) with experimental sites (E) in which we increased antlerless deer harvest. We tested for changes in response variables among years 1–5 of treatment (2002–2006; year was factorial or continuous) and verified if treatment affected temporal changes. Models were corrected for the effect of age, date in autumn (number of days since 1 Sep), sex (fawn model), and lactation status. We square root-transformed variables to normalize residuals, except for lactation, which was binomial.

	Fawn body mass (sqrt)			Female rump fat (sqrt)			Lactation rate		
	β	SE	t	β	SE	t	β	SE	Z
Intercept	4.0	0.1	31.3***	0.45	0.08	5.6***	-1.3	0.5	-2.4*
E	-0.2	0.1	-1.7***	-0.06	0.04	-1.6	-0.1	0.3	-0.2
Year ^a									
2	0.2	0.1	1.7****	0.44	0.03	12.9***	-0.4	0.4	-1.0
3	0.3	0.1	2.9**	0.18	0.03	5.4***	1.0	0.4	2.4*
4	0.1	0.1	1.3	0.18	0.03	5.6***	0.7	0.4	1.7
5	-0.1	0.1	-0.4	0.02	0.04	0.1	1.1	0.5	2.5**
E × year ^a									
2	0.3	0.1	2.0*	0.01	0.06	0.2	-0.2	0.4	-0.6
3	0.1	0.1	0.7	0.08	0.06	1.3	0.5	0.5	1.1
4	0.2	0.1	1.9****	0.05	0.06	0.8	-0.5	0.6	-0.9
5	0.4	0.1	3.1**	0.06	0.06	0.9	-0.6	0.5	-1.3
Day ^a	0.01	0.03	4.1***	0.013	0.002	8.4***			
Day ²	9×10^{-5}	3×10^{-5}	2.7**	-7×10^{-5}	2×10^{-5}	-3.6***			
Age				0.14	0.02	7.7***	0.6	0.2	3.4***
Age ²				-0.011	0.002	-7***	-0.04	0.02	-2.5**
Sex (male)	0.16	0.03	4.8***						
Lactation				-25×10^{-4}	8×10^{-4}	3.1**			

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

**** $P < 0.1$.

^a Year 1 was the reference.

Female lactation rate was similar in control ($78 \pm 5\%$) and experimental sites ($74 \pm 7\%$; $\chi^2 = 6.0$, $P = 0.3$) when controlling for age. Lactation rate varied over time ($\chi^2 = 20.3$, $P < 0.01$), but similarly in experimental and control sites ($\chi^2 = 4.9$, $P = 0.3$; Fig. 5C, Table 4). Lactation rate was the lowest in 2003 and the highest in 2004, showing a 1-year lag relative to changes in density and female rump fat. Fecundity of reproductive females (litter size at ovulation from ovaries collected from 2002 to 2005) was similar in control (1.22 ± 0.04) and experimental sites (1.27 ± 0.06 ; $\chi^2 = 1.2$, $P = 0.5$), and it increased linearly from 2001 (1.16 ± 0.04) to 2004 (1.34 ± 0.07 ; $\chi^2 = 6.8$, $P = 0.03$), and similarly in treatment and control sites ($\chi^2 = 0.08$, $P = 0.8$; estimates and graph not shown).

DISCUSSION

Because of the philopatric behavior of white-tailed deer females (Porter et al. 1991), we expected that increasing antlerless deer harvest during 5 years would generate low-density areas where understory forb abundance, forest regeneration, and deer body condition would increase compared with control sites with a regular hunting pressure. Based on aerial survey estimates, hunters successfully harvested about 50% of antlerless deer in experimental sites in year 1 and 25% thereafter (years 2–5), which was close to our original objective of 50% and 30%, respectively. Despite this harvest effort, our results showed no evidence that we reduced deer densities enough to favor habitat regeneration. Relative deer density varied stochastically among years and synchronously in experimental and control sites. Vegetation abundance and growth, as well as forest regeneration, also varied stochastically over time at all sites, even in exclosures. Only ground cover and leaf area of bunchberry increased through years in exclosures, but not in experimental sites. Deer life-history traits did not improve in experimental sites. Our study was one of the most complete to date testing for the efficiency of localized management, addressing topics from hunting harvest to local density estimates, and assessment of vegetation, body condition, and reproductive responses.

Wildlife managers usually consider that appropriate hunting regulations can be used to control deer populations (Witmer and deCalesta 1992). Our results showed that reducing and controlling overabundant white-tailed deer density within medium-sized areas (i.e., 20 km²) could be very difficult, at least using localized antlerless deer hunting. Our experiment covered large spatial and temporal extents, with 5 well-dispersed replicates distributed in varied environments and 5 years of treatment that should have been appropriate to detect, at least, a preliminary response. We propose several alternative non-exclusive hypotheses to explain the low efficiency of antlerless deer hunting, underlying either technical or ecological issues: 1) compensatory mechanisms, 2) biases in density estimates, 3) limited access to territory for hunters, 4) large target areas for localized management, 5) low hunter density, 6) recolonization by surrounding deer, 7) slow plant response under canopy cover, and 8) bottom-up mechanisms.

A prerequisite for the regulation of a population through harvest is that harvest should be high enough to be an additive source of mortality rather than mostly a compensatory one (Bartmann et al. 1992). Compensation occurs when density-dependent factors maintain similar population growth as before harvest, by increasing survival or reproduction (Bartmann et al. 1992). We are unsure whether harvest mortality in our study was sufficient to induce additive mortality; however, we observed strong density-dependent mortality in control sites in winter 2002–2003 when natural mortality of adult females was 10% greater than the normal average of 23% (Simard et al. 2010). Relative density indices also suggested that the population decline observed in 2003 was similar in control and experimental sites, indicating that the experimental harvest was likely compensatory, removing a surplus of individuals that would likely have died anyway during winter. Another antlerless deer harvest program conducted over 4 years in Colorado (USA) suggested compensatory mortality; 2 years after reducing deer density by 75% in a 21.4-km² treatment area, the population in the control area also started to decline as fawn mortality was greater than in the treatment (White and Bartmann 1998). Other studies have also attributed failure to control deer populations to density-dependent mechanisms in survival or reproductive rates (Giles and Findlay 2004, Killmaster et al. 2007). In the present study, however, we did not detect signs of compensation in lactation rate or litter size.

Another possibility is that we underestimated initial deer densities, which we used to determine harvest targets. Aerial survey data from populations of known size have shown that few density estimates are unbiased and precise (Hone 2008). Summer aerial surveys on Anticosti Island had, accordingly, a large coefficient of variation and have been demonstrated to generally underestimate densities by about 30% (Potvin and Breton 2005). This would mean that 38% of antlerless deer were harvested in the first year and 23% afterwards, as opposed to our original objectives of, respectively, 50% and 30%. Underestimation of deer density was also a management issue in the study by Kaji et al. (2010).

Although we possibly underestimated initial densities, and therefore harvest targets, it should not have been a major issue, especially as Ueno et al. (2010) suggested that 30% hunting mortality could be sufficient at least for some populations to reduce total population size. Moreover, antlerless deer licenses were unlimited, such that if densities were greater than first assumed, hunters should have been able to harvest more deer than the original target, which rarely happened. Harvest success in some experimental sites was sometimes low. Harvest might have been low because hunters did not spend enough time hunting (generally 4 days) considering the low hunter efficiency at relatively low deer density. Contiguous forested sectors, such as those found on Anticosti Island, are expected to reduce deer vulnerability to harvest compared with heavily fragmented forested areas (Foster et al. 1997). Moreover, deer harvested in experimental sites were not distributed randomly but clustered along trails and roads (Fig. 2; see also Lebel et al. 2012). Hunters, therefore, probably failed to harvest deer that had their home

range in dense forest patches far from a road or trail, thereby allowing recolonization from these inaccessible areas.

Because chances of removing whole matriline by hunting are greater in small areas (i.e., 1–2 km²), hunting is perhaps more likely to reduce deer density in small areas (Kilpatrick et al. 1997, McNulty et al. 1997) than in large areas (approx. 20 km²; this study, White and Bartmann 1998). Porter et al. (1991) nevertheless suggested that localized hunting should allow the control of deer density in areas of 4–20 km². Although large areas may reduce hunter efficiency, size may not be the only reason explaining difficulties in controlling deer density through hunting, as localized management has failed in study sites of 6 km² (Killmaster et al. 2007) and 1 km² (Miller et al. 2010), but apparently succeeded in a large area of 160 km² (McDonald 2007). A study on sika deer suggested that a minimal hunting effort is necessary to decrease deer density (i.e., 3,500 hunter days for that particular study), but that it could vary for different populations and habitat types (Ueno et al. 2010).

The limitations of hunting as a management method to reduce browsing damage locally may be explained by the observation that, unlike predators, hunters are active during a limited time period (daily and seasonally), which limits their capacity to generate a fear factor strong enough to modify space-use patterns of animals all year long, day and night (Ripple and Larsen 2000). In Yellowstone National Park, the intensification of elk (*Cervus canadensis*) harvest between 1923 and 1968 failed to reduce browsing pressure, but wolf (*Canis lupus*) reintroduction allowed aspen (*Populus tremuloides*) regeneration to reestablish in areas avoided by elk but where density was previously high (Ripple and Larsen 2000). These results suggest that wolf predation, but not hunters, modified space-use patterns of elk, confining them to lower quality habitats (Ripple et al. 2001, Hernandez and Laundre 2005). In another study, hunting seemed to have allowed red cedar (*Thuja plicata*) regeneration to escape black-tailed deer (*Odocoileus hemionus sitchensis*) browsing, but only in areas where deer were more exposed to hunters (Martin and Baltzinger 2002). According to these authors, the positive impact of hunting on tree regeneration was attributable to changes in deer behavior rather than a reduction in density because only 10% of animals were harvested each year. The relatively low hunter density encountered in our experimental sites on Anticosti Island (i.e., approx. 0.2 hunter/km²) may not have been high enough to modify deer habitat use, limiting the effect of hunting on vegetation growth (Hansen et al. 1986).

The success of the experiment was largely dependent on the assumption that the philopatric behavior of white-tailed deer females would limit the recolonization of harvested zones, as observed in the Adirondacks (McNulty et al. 1997). We could not verify this assumption on Anticosti Island since we did not install radio-collars on deer near experimental sites. Miller et al. (2010), however, showed that after localized management hunting, deer outside the treated area moved their home range closer to the treated area, resulting in a gradual recolonization of hunted zones. Other authors have shown that deer may increase home-range size in the

absence of intact matriline (Williams et al. 2008). Intraspecific competition in overabundant populations like on Anticosti Island could result in a greater frequency of dispersers (Lesage et al. 2001). Many studies, however, found no relationship between density and dispersal (Hawkins and Klimstra 1970, Clutton-Brock et al. 1982, Nixon et al. 1991), whereas others suggested decreased dispersal at high density (Wahlström and Liberg 1995). Dispersal patterns and seasonal movements of radio-collared females at the periphery of harvested sites should be further investigated, similarly to Miller et al. (2010).

Hunting possibly created low-density areas that we could not detect using vegetation indices. A browsing-controlled experiment on Anticosti Island measured plant responses to deer browsing pressure in reduced known-density enclosures. After 3 years, few signs of vegetation response were found under forest cover, whereas plant reproductive structures, bunchberry, and balsam fir biomass increased exponentially in cutovers (Tremblay et al. 2006). Studies in hardwood forests of Pennsylvania (Tilghman 1989, Horsley et al. 2003) and southern Québec (Collard et al. 2010) obtained similar results for understory vegetation. Likewise, species richness and understory plant abundance were reported to respond rapidly to canopy openings, but not to deer browsing, and only plant size and reproductive structures were sensitive to deer density (Rooney 1997, Kraft et al. 2004, Koh et al. 2010). Accordingly, after 6 years of monitoring vegetation growth and abundance under forest cover, the only parameter that changed was leaf area of bunchberry that increased in enclosures. Other factors besides deer density may have delayed the recovery of seedlings and forbs in our sites such as initial vegetation density (Augustine et al. 1998, Martin and Baltzinger 2002), light regime (Tremblay et al. 2006, 2007), or other site characteristics (Vellend 2005). Nevertheless, although monitoring vegetation in open habitats may have provided a better response than under cover (Horsley et al. 2003), we are confident that vegetation did not change greatly in experimental sites because fat reserves in female deer remained similar to control sites. Indeed, deer should have been much better than we were at sampling vegetation, both under cover and in open areas, such that actual changes in deer density or in vegetation abundance should have rapid consequences on deer body condition or productivity, which was not the case (Albon et al. 1983, Swihart et al. 1998).

We based our experiment on the top-down principle, which implies that modifying predation or harvest on herbivores should modify vegetation abundance (reviewed in Underwood 2000). More specifically, several authors suggested that high predation pressure should reduce ungulate density resulting in lower density-dependent fluctuations, particularly at northern latitudes with low primary productivity (Crête 1999, Melis et al. 2009, Wang et al. 2009). Nevertheless, the weak effect of increased hunting pressure on vegetation characteristics could suggest that we overestimated the importance of top-down compared with bottom-up processes. Herbivores could be primarily regulated through plant productivity and nutrient availability, whereas

predation would rather act as a secondary mechanism (Sinclair and Krebs 2002). On Isle Royale (Michigan, USA), for example, wolf predation surprisingly had a weaker influence on moose population growth rate than spring forage quality in relation to climatic conditions (Vucetich and Peterson 2004). In Europe, roe deer (*Capreolus capreolus*) are influenced both by food supply and predation, but bottom-up processes appear stronger in productive environments and during mild winters (Melis et al. 2009). On Anticosti Island, despite the harsh northern climate at the limit of deer range, spring vegetation and habitat characteristics strongly influenced deer reproduction and body condition (Simard 2010, Simard et al. 2010). As both top-down and bottom-up processes operate simultaneously in natural systems (Tveraa et al. 2003, Wang et al. 2009), the development of management approaches acting on both processes could improve population control methods (Hobbs 1996, Augustine and McNaughton 1998, Nugent et al. 2001). One factor among the several we discussed was unlikely solely responsible for the low impact of localized antlerless deer harvest. We rather suspect multiple causes. Yet, factors acting during the first phase of the experiment, when we established harvest objectives, were likely determinant.

MANAGEMENT IMPLICATIONS

Our experiment clearly demonstrated the complexity of using localized management to control deer density. Based on our results, we propose several guidelines to increase the success of deer control through localized management and other hunting-based methods. We suggest, along with other authors, that 1) harvest mortality should be large enough to be additive (i.e., at least 50% [White and Bartmann 1998], although 30% seems sufficient in some populations [Ueno et al. 2010]), 2) control programs should be conducted during more than 1 year and be adaptive (McDonald 2007, Kaji et al. 2010), 3) estimations of herbivore density should be validated or assessed with more than 1 index and followed during several years after treatment (Cederlund et al. 1998, Hone 2008), 4) programs should involve a high density of hunters, instructed to harvest antlerless deer (Brown et al. 2000, Ueno et al. 2010), 5) hunted areas should be small, accessible, and with good visibility (Martin and Baltzinger 2002, Lebel et al. 2012), 6) deer movements should be monitored to assess recolonization from surrounding areas and seasonal movements (Miller et al. 2010), 7) vegetation responses should be measured both in open and forested areas, and on plant parameters sensitive to browsing such as leaf area (Tremblay et al. 2006), and 8) environmental factors limiting the herbivore population should be well understood (Vucetich et al. 2005, Wang et al. 2009). Research should be directed to enhance our understanding of how management tools induce changes in overabundant populations, and to improve their efficiency (Rutberg 1997b, Giles and Findlay 2004).

Considering the apparent difficulties of using localized management to reduce deer density in overabundant populations (this study, Killmaster et al. 2007, Miller et al. 2010), other management methods should be evaluated.

An approach involving culling or commercial hunting at different periods of the year might be a more viable option to effectively reduce deer density (Nugent and Choquenot 2004, Killmaster et al. 2007, Williams et al. 2008, Miller et al. 2010), although it may face public opposition (Rutberg 1997b). Kaji et al. (2010) suggested a combination of hunting and culling under adaptive management. The reintroduction of predators could also be an efficient option (White and Garrott 2005, Nilsen et al. 2007), but again is subject to negative public opinion and it would not apply to insular systems where predators have never been present (Lohr et al. 1996, Nilsen et al. 2007). Researchers have suggested that tolerance towards overabundant populations could sometimes be the only possible option (Rutberg 1997a, Killmaster et al. 2007). Nevertheless, with increasing issues with native and exotic overabundant populations of different species, and their numerous impacts on communities and ecosystems (Garrott et al. 1993, Côté et al. 2004, Valéry et al. 2009), developing and testing management solutions that are efficient and economically viable is urgently needed (Mack et al. 2000, Forsyth 2006).

ACKNOWLEDGMENTS

This study was funded by the NSERC-Produits forestiers Anticosti Industrial Research Chair and the Ministère des Ressources naturelles et de la Faune du Québec. A.S. received scholarships from: Fonds québécois de recherche sur la nature et les technologies, Fondation de l'Université Laval, Association des biologistes du Québec, Fondation de la faune du Québec, Fédération de la faune du Québec, Centre d'études nordiques, Fonds Richard-Bernard, Société Provancher, and Université Laval. We thank A. Gingras, C. Raymond, B. Rochette, F. Potvin, G. Laprise, and Y. Birkly for their collaboration, G. Daigle for statistical advice, A. Lussier for estimation of deer age, and F. Potvin, J.-P. Tremblay, and A. Massé for advice and discussion. We are grateful to J. Taillon, A. Hidding, M. Festa-Bianchet, G. Beuplet, and K. Parker for comments on earlier versions of the manuscript. We are thankful for the precious help of S. de Bellefeuille throughout the redaction and publication process. Data collection was possible with the help of M.-E. Paquet, R. Pouliot, D. Morin, M. Huot, C. Pinnel, M.-A. Giroux, V. Viera, M. Renière, G. Gagnon, D. Chambers, A. Goupil, C. Bajzak, J. Lavergne, N. Marois, R. Lesmerises, L. Plourde, J. Motard-Côté, B. Savary, C. Caux, G. Chrétien, F. Lebel, S. de Bellefeuille, V. St-Pierre, J.-F. Therrien, J. Taillon, V. Laroche, M. Nolin-Veilleux, and D. Duteau. Special thanks to hunting guides, local residents, hunters and outfitters of Anticosti Island: Pourvoirie du Lac Geneviève, Sépaq Anticosti, Safari Anticosti and Cerf-Sau.

LITERATURE CITED

Acevedo, P., F. Ruiz-Fons, J. Vicente, A. R. Reyes-Garcia, V. Alzaga, and C. Gortázar. 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *Journal of Zoology* 276:37–47.

- Albon, S. D., B. Mitchell, and B. W. Staines. 1983. Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology* 52:969–980.
- Alverson, W. S., and D. M. Waller. 1997. Deer population and the widespread failure of hemlock regeneration in northern forests. Pages 280–297 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- Ankney, C. D. 1996. An embarrassment of riches: too many geese. *Journal of Wildlife Management* 60:217–223.
- Ashley, E. P., G. B. McCullough, and J. T. Robinson. 1998. Morphological responses of white-tailed deer to a severe population reduction. *Canadian Journal of Zoology* 76:1–5.
- Augustine, D. J., and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conservation Biology* 12:995–1004.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165–1183.
- Augustine, D. J., L. E. Frelich, and P. A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. *Ecological Applications* 8:1260–1269.
- Bailey, R. E., and R. J. Putman. 1981. Estimation of fallow deer populations from faecal accumulation. *Journal of Applied Ecology* 18:697–702.
- Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* 24:402–413.
- Bartmann, R. M., C. W. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs* 121:1–39.
- Brandner, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. *Ecology* 71:155–164.
- Brown, T. L., D. J. Decker, S. J. Ripley, J. W. Enck, T. B. Lauber, P. D. Curtis, and G. F. Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. *Wildlife Society Bulletin* 28:797–807.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and D. C. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford, UK.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2004. Movements of female white-tailed deer (*Odocoileus virginianus*) in relation to timber harvests in the central Appalachians. *Forest Ecology and Management* 199:371–378.
- Cederlund, G., J. Bergqvist, P. Kjellander, R. Gill, J. M. Gaillard, B. Boisaubert, P. Ballon, and P. Duncan. 1998. Managing roe deer and their impact on the environment: maximising the net benefits to society. Pages 337–367 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, Norway.
- Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1995. Body mass and composition indices for female barren-ground caribou. *Journal of Wildlife Management* 59:278–291.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1982. Competition between female relatives in a matrilineal mammal. *Nature* 300:178–180.
- Collard, A., L. Lapointe, J.-P. Ouellet, M. Crête, A. Lussier, C. Daigle, and S. D. Côté. 2010. Slow responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. *Forest Ecology and Management* 260:649–662.
- Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Nutritional condition models for elk: which are the most sensitive, accurate, and precise? *Journal of Wildlife Management* 65: 988–997.
- Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review in Ecology, Evolution, and Systematics* 35:113–147.
- Crawley, M. J. 2007. *The R book*. John Wiley and Sons Ltd, Chichester, UK.
- Crête, M. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. *Ecology Letter* 2:223–227.
- Engelmark, O., A. Hofgaard, and A. Tore. 1998. Successional trends 219 years after fire in an old *Pinus sylvestris* stand in northern Sweden. *Journal of Vegetation Science* 9:583–592.
- Environment Canada. 2006. Climate normals and averages, daily data reports of Port-Menier's station from 1995 to 2005. Canada's National Climate Archive. <<http://climate.weatheroffice.gc.ca>>. Accessed 5 Dec 2006.
- Forsyth, D. M. 2006. Controls on the population dynamics of invading mammals. Pages 179–193 in R. Allen, and W. Lee, editors. *Biological invasions in New Zealand*. Springer-Verlag, Heidelberg, Germany.
- Foster, J. R., J. L. Roseberry, and A. Woolf. 1997. Factors influencing efficiency of white-tailed deer harvest in Illinois. *Journal of Wildlife Management* 61:1091–1097.
- Fox, A. D., J. Madsen, H. Boyd, E. Kuikens, D. W. Norriss, and I. M. Tombre. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology* 11:881–893.
- Garrott, R. A., P. J. White, and C. A. Vanderbilt White. 1993. Overabundance: an issue for conservation biologists? *Conservation Biology* 7:946–949.
- Giles, B., and C. Findlay. 2004. Effectiveness of a selective harvest system in regulating deer populations in Ontario. *Journal of Wildlife Management* 68:266–277.
- Grosenbaugh, L. R. 1952. Plotless timber estimates—new, fast, easy. *Journal of Forestry* 50:32–37.
- Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *Journal of Wildlife Management* 64:441–449.
- Hansen, L. P., C. M. Nixon, and F. Loomis. 1986. Factors affecting daily and annual harvest of white-tailed deer in Illinois. *Wildlife Society Bulletin* 14:368–376.
- Hawkins, R. E., and W. D. Klimstra. 1970. A preliminary study of the social organization of white-tailed deer. *Journal of Wildlife Management* 34:407–419.
- Hernandez, L., and J. Laundre. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* 11:215–220.
- Heusmann, H. W. 1999. Special hunting seasons and resident Canada goose populations. *Wildlife Society Bulletin* 27:456–464.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- Hone, J. 2008. On bias, precision and accuracy in wildlife aerial surveys. *Wildlife Research* 35:253–257.
- Horsley, S. B., S. L. Stout, and D. S. deCalesta. 2003. White-tailed deer impact on vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13:98–118.
- Huot, J. 1982. Body condition and food resources of white-tailed deer on Anticosti Island, Québec. Dissertation, University of Alaska, Fairbanks, USA.
- Jefferies, R. L. 1999. Herbivores, nutrients and tropic cascades in terrestrial environments. Pages 301–330 in H. Olff, V. K. Brown, and R. H. Drent, editors. *Herbivores: between plants and predators*. Thirty-Eighth Symposium of the British Ecological Society in cooperation with the Netherlands Ecological Society, Wageningen 1997. Blackwell Science Ltd, Oxford, UK.
- Kaji, K., T. Saitoh, H. Ueno, H. Matsuda, and K. Yamamura. 2010. Adaptive management of sika deer populations in Hokkaido, Japan: theory and practice. *Population Ecology* 52:373–387.
- Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* 27:242–258.
- Killmaster, C. H., D. A. Osborn, R. J. Warren, and K. V. Miller. 2007. Deer and understory plant responses to a large-scale herd reduction on Georgia State Park. *Nature Areas Journal* 27:161–168.
- Kilpatrick, H. J., M. S. Shelley, and G. G. Chasko. 1997. A controlled deer hunt on a state-owned coastal reserve in Connecticut: controversies, strategies, and results. *Wildlife Society Bulletin* 25:451–456.
- Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effect of population reduction on home ranges of female white-tailed deer at high densities. *Canadian Journal of Zoology* 79:949–954.

- Koh, S., D. R. Bazely, A. J. Tanentzap, D. R. Voigt, and E. Da Silva. 2010. *Trillium grandiflorum* height is an indicator of white-tailed deer density at local and regional scales. *Forest Ecology and Management* 259:1472–1479.
- Kraft, L. S., T. R. Crow, D. S. Buckley, E. A. Nauertz, and J. C. Zasada. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. *Forest Ecology and Management* 199:219–230.
- Langvatn, R., Å. Bakke, and S. Engen. 1994. Retrospective studies of red deer reproduction using regressing luteal structures. *Journal of Wildlife Management* 58:654–663.
- Lebel, F., C. Dussault, A. Massé, and S. D. Côté. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. *Journal of Wildlife Management* 76:1431–1440.
- Lefort, S., J.-P. Tremblay, F. Fournier, F. Potvin, and J. Huot. 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of its distribution range. *Écoscience* 14:109–116.
- Lesage, L., M. Crête, J. Huot, and J.-P. Ouellet. 2001. Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia* 126:30–41.
- Lohr, C., W. B. Ballard, and A. Bath. 1996. Attitudes toward gray wolf reintroduction to New Brunswick. *Wildlife Society Bulletin* 24: 414–420.
- Lyon, J., and C. E. Jensen. 1980. Management implications of elk and deer use of clear-cuts in Montana. *Journal of Wildlife Management* 44: 352–362.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- Martin, J. L., and C. Baltzinger. 2002. Interaction among deer browse, hunting, and tree regeneration. *Canadian Journal of Forest Research* 32:1254–1264.
- Mathews, N. E., and W. F. Porter. 1993. Effect of social structure on genetic structure of free-ranging white-tailed deer in the Adirondack Mountains. *Journal of Mammalogy* 74:33–43.
- McDonald, J. E. J. 2007. Reduction and maintenance of a white-tailed deer herd in central Massachusetts. *Journal of Wildlife Management* 71:1585–1593.
- McNulty, S. A., W. F. Porter, N. E. Mathews, and J. A. Hill. 1997. Localized management for reducing white-tailed deer populations. *Wildlife Society Bulletin* 25:265–271.
- McShea, W. J., H. B. Underwood, and J. H. Rappole. 1997. Deer management and the concept of overabundance. Pages 1–7 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- Melis, C., B. Jedrzejewska, M. Apollonio, K. A. Barton, W. Jedrzejewski, J. D. C. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykky, K. Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvrya, V. E. Sidorovich, B. Zawadzka, and S. Zhylya. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global Ecology and Biogeography* 18:724–734.
- Merrill, J., E. Cooch, and P. Curtis. 2006. Managing an overabundant deer population by sterilization: effects of immigration, stochasticity and the capture process. *Journal of Wildlife Management* 70:268–277.
- Miller, B. F., T. A. Campbell, B. R. Laseter, W. M. Ford, and K. V. Miller. 2010. Test of localized management for reducing deer browsing in forest regeneration areas. *Journal of Wildlife Management* 74:370–378.
- Mysterud, A., E. L. Meisingset, V. Veiberg, R. Langvatn, E. J. Solberg, L. E. Loe, and N. C. Stenseth. 2007. Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. *Wildlife Biology* 13:285–298.
- Nilsen, E. B., E. J. Milner-Gulland, L. Schofield, A. Mysterud, N. C. Stenseth, and T. Coulson. 2007. Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. *Proceedings of the Royal Society B* 274:995–1002.
- Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelvig. 1991. Ecology of white-tailed deer in a intensively farmed region of Illinois. *Wildlife Monographs* 118:30–77.
- Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* 5:113–117.
- Nugent, G., and D. Choquenot. 2004. Comparing cost-effectiveness of commercial harvesting, state-funded culling, and recreational deer hunting in New Zealand. *Wildlife Biology Bulletin* 32:481–492.
- Nugent, G., W. Fraser, and P. Sweetapple. 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and terrestrial ruminants on native forests in New Zealand. *Biological Conservation* 99:65–79.
- Nugent, G., W. J. McShea, J. Parkes, S. Woodley, J. Waithaka, J. Moro, R. Gutierrez, C. Azorit, F. Mendez Guerrero, W. T. Flueck, and J. M. Smith-Flueck. 2011. Policies and management of overabundant deer, (native or exotic) in protected areas. *Animal Production Science* 51:384–389.
- Petorelli, N., S. D. Côté, A. Gringras, F. Potvin, and J. Huot. 2007. Aerial surveys vs hunting statistics to monitor deer density: the example of Anticosti Island (Québec, Canada). *Wildlife Biology* 13:321–327.
- Pinheiro, J. C., and D. Bates. 2000. *Mixed-effects models in S and S-plus*. Springer, New York, New York, USA.
- Plumptre, A. J. 2000. Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology* 37:356–368.
- Porter, W. F., N. E. Mathews, H. B. Underwood, R. W. Sage, and D. F. Beherd. 1991. Social organization in deer: implications for localized management. *Environmental Management* 15:809–814.
- Potvin, F. 2001. Inventaire aérien à Anticosti. Direction générale de la ressource faunique. Ministère du Loisir, de la Chasse et de la Pêche, Québec, Québec, Canada. [In French.]
- Potvin, F., and L. Breton. 2005. Testing two aerial survey techniques on deer in fenced enclosures—visual double-counts and thermal infrared sensing. *Wildlife Society Bulletin* 33:317–325.
- Potvin, F., P. Beaupré, and G. Laprise. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island Québec: a 150-year process. *Écoscience* 10:487–495.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184:299–313.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95:361–370.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227–234.
- Rochette, B., and A. Gringras. 2007. Inventaire aérien du cerf de Virginie de l'île d'Anticosti- été 2006. Direction de l'aménagement de la faune de la Côte-Nord, Ministère des Ressources naturelles et de la Faune, Québec, Québec, Canada. [In French.]
- Rooney, T. P. 1997. Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. *Journal of Torrey Botanical Society* 124:280–285.
- Rutberg, A. T. 1997a. Lessons from the urban deer battlefield: a plea for tolerance. *Wildlife Society Bulletin* 25:520–523.
- Rutberg, A. T. 1997b. The science of deer management: an animal welfare perspective. Pages 37–54 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- Simard, M. A. 2010. Dynamique de population d'un ongulé nordique à haute densité : les déterminants environnementaux de la démographie et des composantes biodynamiques. Dissertation, Université Laval, Québec, Canada.
- Simard, M. A., S. D. Côté, R. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on the life history traits of a large herbivore. *Journal of Animal Ecology* 77:678–686.
- Simard, M. A., S. D. Côté, A. Gringras, and T. Coulson. 2012. Tests of density dependence using indices of relative abundance in a deer population. *Oikos* 121:1351–1363.
- Simard, M. A., T. Coulson, A. Gringras, and S. D. Côté. 2010. Influence of density and climate on the population dynamics of a large herbivore under harsh environmental conditions. *Journal of Wildlife Management* 74: 1671–1685.

- Sinclair, A. R. E., and C. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society Biological Sciences* 357:1221–1231.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Third edition. Freeman, New York, New York, USA.
- Solberg, E. J., B.-E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* 68:186–204.
- Swihart, R. K., H. P. J. Weeks, A. L. Easter-Pilcher, and A. J. DeNicola. 1998. Nutritional condition and fertility of white-tailed deer (*Odocoileus virginianus*) from areas with contrasting histories of hunting. *Canadian Journal of Zoology* 76:1932–1941.
- Takatsuki, S., and T. Gorai. 1994. Effects of sika deer on the regeneration of a *Fagus crenata* on forest on Kinkazann Island, northern Japan. *Ecology Research* 9:115–120.
- Therrien, J.-F., S. D. Côté, and M. Festa-Bianchet. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. *Behavioural Ecology and Sociobiology* 62:193–199.
- Tierson, W. C., G. F. Mattfeld, R. W. J. Sage, and D. F. Behrend. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. *Journal of Wildlife Management* 49:760–769.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53:524–532.
- Tremblay, J.-P., I. Thibeault, C. Dussault, J. Huot, and S. D. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks? *Canadian Journal of Zoology* 83:1087–1096.
- Tremblay, J.-P., J. Huot, and F. Potvin. 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. *Oecologia* 150:78–88.
- Tremblay, J.-P., J. Huot, and F. Potvin. 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. *Journal of Applied Ecology* 44:552–562.
- Tveraa, T., P. Fauchald, C. Henaug, and N. Yoccoz. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. *Oecologia* 137:370–376.
- Ueno, M., K. Kaji, and T. Saitoh. 2010. Culling versus density effects in management of a deer population. *Journal of Wildlife Management* 74:1472–1483.
- Underwood, A. J. 2000. Experimental ecology of rocky intertidal habitats: what are we learning? *Journal of Experimental Marine Biology and Ecology* 25:51–76.
- Valéry, L., H. Fritz, J. C. Lefeuvre, and D. Simberloff. 2009. Invasive species can also be native. *Trends in Ecology and Evolution* 24:585.
- Vales, D. J., and F. L. Bunnell. 1988. Comparison of methods for estimating forest overstory cover. 1. Observer effects. *Canadian Journal of Forest Research* 18:606–609.
- Vellend, M. 2005. Land-use history and plant performance in populations of *Trillium grandiflorum*. *Biological Conservation* 124:217–224.
- Viera, V. 2003. Effets à long terme du cerf de Virginie (*Odocoileus virginianus*) sur les communautés végétales de l'île d'Anticosti. Thesis, Université Laval, Québec, Canada.
- Vucetich, J., and R. Peterson. 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of Royal Society B* 271:183–189.
- Vucetich, J., D. Smith, and D. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* 111:259–270.
- Wahlström, L. K., and O. Liberg. 1995. Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). *Journal of Zoology* 235:455–467.
- Wang, G., N. Hobbs, S. Twombly, R. Boone, A. Illius, I. Gordon, and J. Gross. 2009. Density dependence in northern ungulates: interactions with predation and resources. *Population Ecology* 51:123–132.
- Warren, R. J. 2011. Deer overabundance in the USA: recent advances in population control. *Animal Production Science* 51:259–266.
- White, G. C., and R. M. Bartmann. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *Journal of Wildlife Management* 62:214–225.
- White, P. J., and R. Garrott. 2005. Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biological Conservation* 125:141–152.
- Williams, S., A. DeNicola, and I. M. Ortega. 2008. Behavioral responses of white-tailed deer subjected to lethal management. *Canadian Journal of Zoology* 86:1358–1366.
- Witmer, G. W., and D. S. deCalesta. 1992. The need and difficulty of bringing the Pennsylvania deer herd under control. Pages 130–137 in *Proceedings of the Eastern Wildlife Damage Control Conference, Fifth Eastern Wildlife Damage Control Conference*. University of Nebraska, Lincoln, USA.
- Wolf, A., and J. L. Roseberry. 1998. Deer management: our profession's symbol of success or failure? *Wildlife Society Bulletin* 26:515–521.

Associate Editor: Gary White.