

Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks

Jean-Pierre Tremblay, Isabel Thibault, Christian Dussault, Jean Huot, and Steve D. Côté

Abstract: Selective browsing by cervids has persistent impacts on forest ecosystems. On Anticosti Island, Quebec, Canada, introduced white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) have caused massive changes to the native boreal forest. Despite the apparent stability of the deer population over recent decades, we suspected that they were not at equilibrium with their browse supply and that further degradation of the habitat had occurred. A comparison of two browse surveys conducted 25 years apart showed a strong decline in browse availability. Although balsam fir (*Abies balsamea* (L.) P. Mill.) remained the most available browse species, it declined or disappeared from most stands ($n = 13$). Preferred deciduous species that were still available 25 years ago have almost disappeared. The continuous decline of the browse supply confirmed our hypothesis. This situation may be exacerbated by a subsidy from the winter litterfall, a significant and stable alternative food source. The abundance of litterfall from mature trees is independent of browsing over a long time period, which introduces a temporal uncoupling between the impact of deer browsing on balsam fir seedlings and the negative feedback from recruitment failure of mature balsam fir on the deer population. This means that the system is susceptible to being forced into an alternative regime.

Résumé : Le broutement sélectif des cervidés produit des impacts persistants sur les écosystèmes forestiers. À l'île d'Anticosti, Québec, Canada, une population introduite de cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) a modifié considérablement la communauté végétale de la forêt boréale indigène. Malgré la stabilité apparente de la population de cerfs au cours des dernières décennies, nous soupçonnons l'existence d'un déséquilibre entre le cerf et le brout disponible, ainsi qu'une détérioration persistante de l'habitat. La comparaison de deux inventaires réalisés à 25 ans d'intervalle montre un fort déclin de la disponibilité du brout. Le sapin baumier (*Abies balsamea* (L.) P. Mill.) demeure la source de nourriture dominante, bien qu'il soit en déclin ou ait disparu de la plupart des peuplements ($n = 13$). Les espèces décidues préférées du cerf et encore disponibles il y a 25 ans sont pratiquement disparues. La réduction continue du brout confirme notre hypothèse. En contrepartie, les lichens et ramilles qui tombent des sapins matures en hiver constituent une source de nourriture de rechange dont l'apport est indépendant de la pression de broutement sur une période prolongée. Cela introduit un découplage temporel entre les impacts du cerf sur les jeunes pousses de sapins et la rétroaction négative associée à l'absence de recrutement des sapinières sur les populations de cerf. Cette situation est susceptible d'entraîner le système vers un régime d'équilibre différent.

Introduction

In plant–herbivore systems, interactive relationships between animals and their food resources usually generate dynamic changes in population growth at both trophic levels (Caughley and Sinclair 1994). Woody browse is the basic food source in winter for most free-ranging vertebrate herbivores of northern forests, especially cervids, and is usually

considered a limiting resource (Huot 1974, 1982; Renecker and Schwartz 1997). Equilibrium theory predicts that browsing will reduce the resources available down to a critical threshold where the rate of increase of woody browse and herbivore populations reaches zero (carrying capacity sensu Macnab 1985). In spite of these dynamic changes, high fecundity, time lags in the rate of increase of ungulate populations relative to the decline in resources, and a high neonatal

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J.-P. Tremblay,¹ I. Thibault, C. Dussault,² J. Huot, and S.D. Côté. Chaire de recherche industrielle CRSNG – Produits forestiers Anticosti, Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC G1K 7P4, Canada.

¹Corresponding author (e-mail: jean-pierre.tremblay@bio.ulaval.ca).

²Present address: Ministère des ressources naturelles, de la faune et des parcs, 675 boulevard René-Lévesque est (11^e), Québec, QC G1R 5V7, Canada.

survival rate are likely to cause populations to exceed the carrying capacity of their habitat (Caughley 1970; McCullough 1979; Clutton-Brock et al. 1997). Clutton-Brock et al. (1997) predicted that oscillations around carrying capacity will occur in systems with a high ungulate recruitment rate and a lack of early density-dependent constraint on fecundity, while relative population stability is expected when fecundity is more closely linked to herbivore population density. However, environmental stochasticity in weather severity or the timing of spring green-up can influence the dynamics of forest–deer systems by changing the rate of increase of deer and plant populations independently of population density (Macnab 1985; Sæther 1997). Sæther (1997) suggested that equilibrium between ungulates and their resources is unlikely in a predator-free environment because of the strong influence of environmental stochasticity. In any case, systems in which plant and herbivore populations are far from equilibrium (Caughley 1981) and where chronic heavy browsing has led to strong and persistent impacts on forest vegetation have been widely reported worldwide (reviewed in Côté et al. 2004).

Anticosti Island is an extreme example of how an overabundant cervid population, and its associated heavy browsing pressure, can have long-lasting impacts on a forest ecosystem. In the absence of predators, the introduced population of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) irrupted and reached a peak ca. 30 years following its introduction in 1896–1897. The deer remained abundant thereafter (~20/km²) in spite of annual fluctuations related to winter severity (Potvin and Breton 2005). In the long term, selective browsing has induced dramatic changes in the native plant community. Some preferred or less-tolerant deciduous shrubs and herbaceous plant species that were abundant prior to the introduction of the deer had been either extirpated or greatly reduced in abundance by the mid-1950s (Pimlott 1963; Marie-Victorin and Rolland-Germain 1969). Deer browsing on balsam fir (*Abies balsamea* (L.) P. Mill.) seedlings during the snow-free period (26%–48% of seedlings/year) also generated recruitment failure and a progressive conversion of balsam fir stands into white spruce (*Picea glauca* (Moench) Voss) stands (Potvin et al. 2003). In the mid-1970s, balsam fir was the most abundant and used browse species (Huot 1982). Balsam fir, which is usually considered a starvation forage (Ullrey et al. 1968), has accounted for at least 70% of deer winter diet on the island during the last 25 years (Huot 1982; Lefort 2002). Other coniferous species are either completely avoided (e.g., black spruce, *Picea mariana* (P. Mill.) B.S.P.) or rarely browsed (white spruce). The apparent stability of the deer population during the past 25 years (Potvin et al. 2003) suggests that the system is now close to carrying capacity. Under these conditions, Lesage et al. (2001) predicted that browse availability will be stable. We suspected, however, that further degradation of the habitat had occurred over the last 25 years, leading to a paradox: how can deer maintain a relatively stable population while the availability of their main food sources appears to be seriously declining?

This paradox required an explanation; could there be alternative food sources that could explain the absence of density-dependent feedback between the white-tailed deer population and the integrity of its habitat? Although body re-

serves are critical for over-winter survival (Huot 1982), it was suggested that arboreal lichens are decisive for the winter survival of many cervids, especially caribou (*Rangifer tarandus* (L., 1758)), in northern areas (Van Daele and Johnson 1983; Hodgman and Bowyer 1985; Ouellet et al. 1996; Rominger et al. 1996). Arboreal lichens contain more digestible energy than woody browse (Hodgman and Bowyer 1985; Robbins 1987; Ditchkoff and Servello 1998; Kumpala 2001). According to Ditchkoff and Servello (1998), lichens and litterfall deposited during winter may account for more than 85% of the forage available to deer in unharvested forest stands in Maine. There, arboreal lichens accounted for 6% of the total litterfall biomass but contributed 31% of the available energy for overwintering white-tailed deer. Jenks and Leslie (1989) reported a decrease in digesta-retention time for white-tailed deer fawns fed with lichens, although they could not find any lichen-induced synergisms using in-vitro digestion. For white-tailed deer, litterfall is usually not included in the assessment of carrying capacity. However, the standing biomass of arboreal lichens and twigs in the litterfall is usually high in old-growth conifer stands and could therefore constitute an important energy supply in boreal forests (Lang et al. 1980; Ouellet et al. 1996). Miyaki and Kaji (2004) concluded that large populations of sika deer (*Cervus nippon* Temminck, 1838) are maintained by litterfall in deciduous forests.

The objectives of this study were (i) to quantify the changes in availability and use of white-tailed deer forage over a 25-year period to evaluate the extent of habitat modifications still occurring on Anticosti Island almost a century after deer introduction and (ii) to estimate the potential of winter litterfall in mature forest stands as an alternative food source that could contribute to sustaining a high deer density.

Material and methods

Study area

Anticosti Island (7943 km²) is located in the Gulf of St. Lawrence, Quebec, 70 km northeast of the northeastern limit of the white-tailed deer distribution range on the mainland. About 220 deer were introduced on the predator-free island in 1896–1897. In 2001, the population was estimated at 125 000 deer (coefficient of variation 90% = 7%), which represents an average density of ~20 deer/km² (Potvin and Breton 2005).

The climate on Anticosti Island is maritime and characterized by cool summers and long but relatively mild winters. Mean annual snowfall is 406 cm, while rainfall averages 63 cm. Mean air temperature is –13.6 °C in January and 14.8 °C in July (Environment Canada 1993).

Anticosti Island forests belong to the boreal zone and are part of the eastern balsam fir – paper birch (*Betula papyrifera* Marsh.) bioclimatic region (Grondin et al. 1996). On mesic and xeric sites, the forests are dominated by balsam fir, white spruce, black spruce, and paper birch (Huot 1982). The shrub layer is almost entirely absent and the most palatable woody-plant species normally found in that region, such as mountain maple (*Acer spicatum* Lam.), redosier dogwood (*Cornus sericea* L.), beaked hazel (*Corylus cornuta* Marsh.), and Canada yew (*Taxus canadensis* Marsh.), have

been almost extirpated by deer (Pimlott 1963; Potvin et al. 2003).

Browse surveys

Annual browse surveys were conducted by Huot (1982) between 1975 and 1978 (hereinafter 1975) in forest stands representative of key deer habitat types (Table 1). We repeated the surveys in 2001–2002 (hereinafter 2001) in the same stands ($n = 13$). The position of sample plots (29–32) within stands was randomly determined in both periods. In 2001, tree basal area and density were estimated according to Bitterlich's method (Grosenbaugh 1952). The tree and shrub overstory cover were estimated from the vertical projection of 20 points spaced 3 m apart along a 15 m long calibrated rope originating from the center of the plot and directed in the four main cardinal headings (Vales and Bunnell 1988). We estimated the relative age and height of one codominant tree per plot using an increment borer and clinometer.

We counted all stems (individual saplings or trees) with at least one twig between 25 and 225 cm from the ground, and all twigs >5 cm from those stems, for balsam fir, paper birch, and other deciduous species, including American mountain ash (*Sorbus americana* Marsh.), balsam poplar (*Populus balsamifera* L.), quaking aspen (*Populus tremuloides* Michx.), northern bush honeysuckle (*Diervilla lonicera* P. Mill.), chokecherry (*Prunus virginiana* L.), pin cherry (*Prunus pensylvanica* L. f.), squashberry (*Viburnum edule* (Michx.) Raf.), serviceberry (*Amelanchier* spp.), and willows (*Salix* spp.). Browse below 25 cm was regarded as unavailable in winter because of snow cover, while twigs at a height of over 225 cm were considered to be out of deer reach (Huot 1982). In 1975, stems and twigs on stems originating within a 1.5 m × 1.5 m plot were tallied. In 2001, we used a 1 m × 10 m plot because of the low number of observations expected. To take into account the change in food accessibility as snow depth increases, we further divided the winter feeding stratum into three substrata: 25–75, 76–125, and 126–225 cm. We counted the deer-browsed and unbrowsed twigs per feeding substratum.

Litterfall

We estimated the abundance of arboreal lichens and balsam fir twigs in the winter litterfall. Sampling was conducted during the winters of 2001–2002, 2002–2003, and 2003–2004 in four balsam fir stands aged 90–120 years. Stands were selected based on their description on forest-cover maps and their accessibility.

We collected litterfall in 1-m² litter traps (15 traps per stand per year), which consisted of fine-mesh textile netting mounted on a wooden frame. Traps were set up each fall at 40-m intervals along two parallel transects separated by 40 m, offset by 20 m, and starting at least 20 m from stand edges. Lefort (2002) used similar traps set inside deer enclosures and showed that the potential consumption of lichens and browse in the traps did not bias biomass estimates (2.8 ± 3.0 g/m² out vs. 3.5 ± 7.3 g/m² in; $t_{[0.05,14]} > 0.3$, $P > 0.1$). We harvested trap contents in late May after snowmelt was complete. Trap contents were air-dried and sorted according to lichen genus (*Alectoria* Ach. + *Bryoria* Brodo and D.D. Hawksw., *Ramalina* Ach., and *Lobaria* (Schreb.)

Hoffm.). We cut balsam fir twigs at a diameter of 5 mm (Dumont 2004) and rejected those exceeding that diameter, as well as dead parts. We air-dried samples for 24 h at 55 °C before weighing them (± 0.0001 g).

Statistical analyses

We used the Kruskal–Wallis test to compare the availability of balsam fir, paper birch, and other deciduous browse between periods for each stand (stems only) and feeding substratum within stands (twigs only). We regarded sampling plots as true replicates within a stand. We compared the balsam fir browsing rate between 1975 and 2001 with a Kruskal–Wallis test.

We compared the relative proportions of fruticose arboreal lichens (genera *Alectoria* + *Bryoria* and *Ramalina*) and balsam fir twigs in the winter litterfall using repeated-measures ANOVAs. We verified the normality and homogeneity of variance assumptions of parametric statistics and log-transformed data ($\ln + 0.1$) when needed. We verified the sphericity of the variance–covariance matrix using Mauchly's test and performed both univariate F tests adjusted with the Greenhouse–Geisser epsilon and multivariate analyses as suggested by Quinn and Keough (2002). All results are presented as the mean \pm SE, unless otherwise stated. Statistical analyses were performed using SAS[®] system release 8.02 (SAS Institute Inc. 1999–2001).

Results

Browse availability

The density of stems with available twigs declined for all tree and shrub species between the two sampling periods (Table 2). Many species that were present in the 1975 survey were absent in 2001.

Balsam fir was the most abundant browse in both periods (Tables 2, 3). However, stem density decreased significantly in 6 out of 13 forest stands (Table 2). In the remaining 7 stands, balsam fir was already scarce or absent in 1975, and remained so thereafter. Similarly, twig density strongly decreased between the two surveys (Table 3). The apparent increase in twig density in the 25- to 75-cm substratum of stand 20 was not significant ($F_{[1,49]} = 0.83$, $P = 0.37$).

Paper birch was the most abundant deciduous species in both sampling periods (Table 2). In 1975, paper birch stems with available browse were observed in 4 stands, but this species was either absent (stand 12: $F_{[1,59]} = 5.38$, $P = 0.02$; stand 14: $F_{[1,59]} = 14.7$, $P = 0.0003$) or less abundant (stand 1: $F_{[1,59]} = 9.21$, $P = 0.004$; stand 7: $F_{[1,59]} = 10.9$, $P = 0.002$) in the same stands in 2001 (Table 2). In 2001, we observed some paper birch stems and twigs in the 25- to 75-cm substratum in stand 20, although paper birch was absent from that stand in 1975. However, the difference was not significant ($F_{[1,49]} = 0.66$, $P = 0.42$). The decline in numbers of paper birch stems was generally associated with a decrease of twig availability (in 8 out of 15 comparisons; Table 3), except from the 125- to 225-cm substratum of stands 1 ($F_{[1,59]} = 2.08$, $P = 0.15$) and 14 ($F_{[1,59]} = 2.01$, $P = 0.16$), where the observed decline was not significant.

Deciduous species other than paper birch were already found at low stem and twig densities in 7 and 5 stands, respectively, during the 1975 survey (Tables 2, 3). Most

Table 1. Characteristics of the forest stands surveyed from 1975 to 1978 and from 2001 to 2002 on Anticosti Island.

Stand No.	Habitat type (1975–1978)	Origin (1975–1978)	Stand composition		Stems/ha ^{a,b}	Canopy closure >4 m (%) ^c			Shrub closure ≤4 m in 2001–2002 (%) ^c
			1975–1978	2001–2002		1975–1978	2001–2002	2001–2002	
1	Mixed regeneration, logged	20-year clearcut	Balsam fir ^d	Balsam fir	1190 (180)	20 (20)	75 (10)	8.6 (1.6)	
3	Second-growth conifer	35-year white spruce	White spruce	White spruce ^e	560 (100)				
6	Mature irregular balsam fir	Light outbreak of hemlock looper (<i>Lambdina fuscicornis</i>) in 1929 (Guenee)) in 1929	Balsam fir, white spruce, paper birch ^f	White spruce	826 (77)	50 (30)	64 (16)	4.3 (1.1)	
7	Mixed regeneration, logged	20-year clearcut	Balsam fir	Balsam fir	468 (83)	70 (20)	60 (28)	10 (2)	
10	Second-growth conifer	50-year white spruce	White spruce	White spruce	1270 (190)	20 (20)	76 (11)	2.2 (0.7)	
11	Irregular black spruce ^g	—	Black spruce, balsam fir	Black spruce	284 (83)	50 (30)	69 (10)	2.5 (1.0)	
12	Mixed regeneration, logged	20-year clearcut	Balsam fir	White spruce	770 (120)	40 (20)	66 (15)	19.2 (2.8)	
13	Uneven-aged conifer, logged	40- to 120-year partial cut	Balsam fir	Black spruce	377 (83)	20 (20)	70 (16)	6.8 (1.5)	
14	Mixed regeneration, logged	20-year clearcut	Balsam fir	Balsam fir	1360 (180)	60 (30)	64 (16)	3 (1)	
16	Mature irregular balsam fir	Hemlock looper in 1929–1934	Balsam fir, white spruce, paper birch	White spruce	133 (55)				
20	Regeneration following insect outbreak	Outbreak of hemlock looper in 1969–1972	Balsam fir, white spruce	Balsam fir	116 (31)	50 (30)	38 (16)	45.2 (2.3)	
30	Open hardwood, conifer	30- to 100-year partial cut	Paper birch, balsam fir, white spruce	White spruce	491 (60)	50 (30)	87 (9)	1.7 (0.5)	
33	Irregular black spruce, balsam fir	—	Black spruce, balsam fir	Black spruce	160 (40)	40 (20)	47 (16)	40.2 (3.7)	
				Balsam fir	1240 (140)	70 (20)	46 (26)	17.8 (2.8)	
				White spruce	210 (36)				
				Balsam fir	132 (33)				
				White spruce	16 (10)				
				Black spruce	122 (30)				
				White spruce	119 (37)				
				Balsam fir	920 (110)				
				Black spruce	131 (18)				
				Balsam fir	695 (95)				
				Black spruce	420 (72)				

^aValues in parentheses show the standard error.^bFor dominant species with diameter at breast height ≥9 cm.^cValues in parentheses show the standard deviation.^d*Abies balsamea*.^e*Picea glauca*.^f*Betula papyrifera*.^g*Picea mariana*.

Table 2. Density of stems with at least one available twig of balsam fir, paper birch, and other deciduous browse species between 25 and 225 cm in surveys conducted in forest stands on Anticosti Island during the periods 1975–1978 (referred to as 1975) and 2001–2002 (referred to as 2001) ($n = 30$ plots per stand, except $n = 20$ for stand 20 in 1975).

Stand No.	Period	Stems/ha $\times 1000^a$					
		Balsam fir		Paper birch	Other deciduous species ^b		
1	1975	12.4 (3.7)	*	6.8 (2.2)	**	0.3 (0.2)	
	2001	1.4 (0.5)		0.1 (0.1)		0	
3	1975	0		0.3 (0.3)		0.1 (0.1)	
	2001	0		0		0	
6	1975	0.7 (0.7)		0		0	
	2001	0		0		0	
7	1975	3.9 (1.3)	**	4.7 (1.4)	**	0.3 (0.2)	
	2001	0		0.1 (0.1)		0	
11	1975	0.4 (0.3)		0		0.1 (0.1)	
	2001	0		0		0.1 (0.1)	
12	1975	4.0 (1.7)	**	4.7 (2.0)	**	0.3 (0.3)	
	2001	0		0		0	
13	1975	0.9 (0.4)	*	0		0	
	2001	0		0		0	
14	1975	0.3 (0.3)		7.0 (1.8)	**	4.6 (1.9)	**
	2001	0		0		0	
16	1975	1.8 (0.6)	**	0		0	
	2001	0		0		0	
20	1975	1.3 (0.7)		0		4.7 (2.4)	*
	2001	0.2 (0.1)		<0.1 (< 0.1)		<0.1 (<0.1)	
33	1975	13.8 (4.2)	*	0		0	
	2001	2.2 (0.6)		0		0	

Note: Stands 10 and 30 are omitted, since no stems of fir or any deciduous browse species were available during both surveys. Asterisks show significant differences between 1975 and 2001 periods among stands (*, $P \leq 0.05$; **, $P \leq 0.005$).

^aValues in parentheses show the standard error.

^bServiceberries (*Amelanchier* spp.), northern bush honeysuckle (*Diervilla lonicera*), balsam poplar (*Populus balsamifera*), quaking aspen (*Populus tremuloides*), pin cherry (*Prunus pensylvanica*), chokecherry (*Prunus virginiana*), willows (*Salix* spp.), American mountain ash (*Sorbus americana*), and squashberry (*Viburnum edule*).

species were not found in our sampling plots in 2001, namely serviceberries, northern bush honeysuckle, balsam poplar, pin cherry, chokecherry, willows, American mountain ash, and squashberry. The only deciduous species, other than paper birch, that was observed in the 2001 survey was quaking aspen, which still occurred at low density in stand 11 (stems: $F_{[1,59]} = 0.09$, $P = 0.76$; twigs, 25- to 75-cm substratum: $F_{[1,39]} = 0.33$, $P = 0.57$) and decreased in abundance in stand 20 (stems: $F_{[1,49]} = 5.54$, $P = 0.02$; twigs, 25- to 75-cm substratum: $F_{[1,49]} = 6.60$, $P = 0.01$; Tables 2, 3). The apparent increase in twig density in the 125- to 225-cm substratum of stand 20 was not significant ($F_{[1,49]} = 0.66$, $P = 0.42$; Table 3).

Use of balsam fir browse

Most stands did not contain enough plots with available balsam fir browse in 2001 to allow statistical inference con-

cerning changes in the rate of deer browsing. In stand 33, the rate of deer browsing on balsam fir twigs was much higher in the 2001 survey than in the 1975 survey (25- to 75-cm substratum: 39.7 ± 5.6 ($n = 16$) vs. 2.3 ± 2.3 ($n = 17$), $\chi^2_1 = 23.37$, $P < 0.0001$; 75- to 125-cm substratum: 44.1 ± 9.2 ($n = 11$) vs. 0.1 ± 0.1 ($n = 11$), $\chi^2_1 = 17.40$, $P < 0.0001$; 125- to 225-cm substratum: 36.5 ± 8.3 ($n = 12$) vs. 0.1 ± 0.1 ($n = 10$), $\chi^2_1 = 16.79$, $P < 0.0001$).

Browse and lichen abundance in the litterfall

Univariate and multivariate analyses yielded similar results, so only the former are presented. Total litterfall biomass was high (22–37 kg/ha) and stable among years ($F_{[2,12]} = 1.93$, $P = 0.20$; Table 4). The relative importance of fruticose arboreal lichens and balsam fir twigs to the winter litterfall did not vary ($F_{[1,6]} = 3.61$, $P = 0.11$) during each year (litterfall component \times sampling period: $F_{[2,12]} = 1.33$,

Table 3. Density of twigs of balsam fir, paper birch, and other deciduous browse species in forest stands on Anticosti Island surveyed during the periods 1975–1978 (referred to as 1975) and 2001–2002 (referred to as 2001).

Stand No.	Period	n	Twigs/ha × 1000 ^a													
			Balsam fir			Paper birch			Other deciduous browse species ^b							
			25–75 cm	75–125 cm	125–225 cm	25–75 cm	75–125 cm	125–225 cm	25–75 cm	75–125 cm	125–225 cm					
1	1975	30	680 (300)	**	980 (520)	*	1340 (550)	*	28 (12)	**	14 (6)	*	10 (7)	0.3 (0.3)	0	0
	2001	30	47 (47)		0	59 (59)		3 (3)		1 (1)		0.3 (0.3)		0	0	0
3	1975	10	0		0	0	0	0	0	0	0	0	0	4 (4)	0	0
	2001	30	0		0	0	0	0	0	0	0	0	0	0	0	0
7	1975	10	114 (49)	**	0	0	0	61 (26)	**	7 (6)	*	0	0	0.9 (0.9)	0	0
	2001	30	0		0	0	0	0		<0.1 (<0.1)		0	0	0	0	0
11	1975	10	0		0	0	0	0	0	0	0	0	0	0	0	0
	2001	30	0		0	0	0	0	0	0	0	0	0	<0.1 (<0.1)	0	0
12	1975	10	118 (79)	**	23 (23)	0	0	14 (10)	**	4 (4)	*	0	0	0	0	0
	2001	30	0		0	0	0	0		0		0	0	0	0	0
14	1975	30	1.3 (1.3)		0	0	0	37 (12)	**	9 (5)	*	2 (1)	16 (8)	**	11 (7)	32 (26)
	2001	30	0		0	0	0	0		0		0	0	0	0	0
16	1975	10	1.3 (1.3)		19 (19)	360 (250)	*	0	0	0	0	0	0	0	0	0
	2001	30	0		0	0	0	0	0	0	0	0	0	0	0	0
20	1975	20	1.8 (1.4)		0.2 (0.2)	170 (170)		0	0	0	0	0	12 (6)	*	1.6 (1.1)	0
	2001	30	5.7 (3.3)		0	0	0	<0.1 (<0.1)		0		0	0	0	0	<0.1 (<0.1)
33	1975	30	610 (230)		320 (120)	900 (360)		0	0	0	0	0	0	0	0	0
	2001	30	143 (44)		94 (34)	172 (66)		0	0	0	0	0	0	0	0	0

Note: Stands 6, 10, 13, and 30 are omitted, since no twigs were available during both surveys. Asterisks show significant differences between 1975 and 2001 periods among stands (*, $P \leq 0.05$; **, $P \leq 0.005$).

^aValues in parentheses show the standard error.

^bServiceberries, northern bush honeysuckle, balsam poplar, quaking aspen, pin cherry, chokecherry, willows, American mountain ash, and squashberry.

Table 4. Average biomass of fruticose arboreal lichens and balsam fir in the winter litterfall of balsam fir stands during three consecutive winters on Anticosti Island.

	Biomass (kg/ha) ^a		
	2001–2002	2002–2003	2003–2004
Lichen genera			
<i>Alectoria</i> + <i>Bryoria</i>	6.4±1.3	9.7±2.7	9.6±2.1
<i>Ramalina</i>	3.3±0.8	2.6±0.6	3.2±0.9
Total	9.7±1.7	12.3±3.0	12.8±2.2
Balsam fir browse	11.9±4.1	24.9±6.2	12.7±4.1

Note: Values are given as the mean ± SE.

$P = 0.30$; Table 4). The abundance of the different fruticose lichens did not vary among species ($F_{[2,12]} = 0.55$, $P = 0.51$) or with year ($F_{[2,12]} = 0.95$, $P = 0.38$; Table 4).

Discussion

Our analysis of changes in browse availability over a 25-year time interval on Anticosti Island revealed that white-tailed deer continued to modify their environment almost a century following their introduction, and that the changes are important enough to be measurable within a relatively short time period. The decline in browse availability for white-tailed deer began before the 1975 survey period (Leopold et al. 1947; Pimlott 1963; Marie-Victorin and Rolland-Germain 1969). Deciduous browse species, including serviceberries, northern bush honeysuckle, balsam poplar, pin cherry, chokecherry, willows, American mountain ash, and squashberry were already scarce in 1975 and continued to decline until they were almost completely eradicated by 2001. Balsam fir, paper birch, and quaking aspen, three common species in the canopy of boreal forests (Grondin et al. 1996), are now either absent or at very low density in the winter feeding stratum of most stands where they were more abundant 25 years ago and before. Such strong negative impacts of deer browsing that led to the suppression of preferred, less tolerant, or less resistant trees and shrubs have been reported elsewhere, particularly for Canada yew (Alverson et al. 1988), Canada hemlock (*Tsuga canadensis* (L.) Carr.) (Anderson and Katz 1993; Alverson and Waller 1997; Rooney et al. 2000), eastern white cedar (*Thuja occidentalis* L.) (Van Deelen 1999; Rooney et al. 2002), oaks (species of *Quercus* L.) (Healy et al. 1997), and other deciduous species (Stewart and Burrows 1989; Horsley et al. 2003) but was much less predictable for balsam fir (but see Michael 1992), paper birch, and trembling aspen. This suggests that equilibrium between deer and their food resources has not been reached on Anticosti Island notwithstanding the apparent stability in the deer population between the two surveys. Also, in view of the very low availability of woody browse, an alternative food source is called for that could contribute to sustaining a high deer density.

The strong dependence of deer on balsam fir on Anticosti Island is quite exceptional. Previous feeding experiments have shown that this forage alone cannot sustain deer in winter (Ullrey et al. 1968). Berteaux et al. (1998) suggested that energy content is the main factor governing winter food se-

lection by white-tailed deer. The metabolizable energy content of common deciduous browse species is lower than that of balsam fir (Mautz et al. 1976; Dumont 2004), but the concentration of plant secondary compounds, such as terpenes, is usually greater in conifers and this reduces the digestive capacity of ruminants (Danell et al. 1990; Robbins 1993). The energy content of the urine excreted by wild ruminants fed with coniferous browse has been shown to be higher than in the urine of those fed with deciduous browse (Robbins 1993). This loss would increase the amount of energy that individuals need to acquire to meet their needs.

The observed decline in browse availability could also be partially explained by mechanisms other than deer browsing, including canopy closure during the stem-exclusion phase of forest succession (Table 1). Browse species that are intolerant of low light levels, such as paper birch and quaking aspen, are expected to be less abundant under the canopy of closed forests (Burns and Honkala 1990). Conversely, they should be more abundant during the understory reinitiation phase, a phenomenon that we did not observe on Anticosti Island (e.g., stands 6, 16, and 20 in Table 1). Self-pruning of lower branches could reduce the availability of balsam fir browse during the stem-exclusion phase (Smith et al. 1997), as is seen for stands that were at the regeneration stage in 1975–1978 but showed higher canopy closure 25 years later (e.g., stands 1, 7, 12 and 14 in Table 1). However, this could be compensated for by the presence of a seedling bank in the understory of mature stands, which would produce browse in the 25- to 75-cm winter feeding substratum. This was obviously not the case and canopy closure cannot explain the absence of balsam fir browse in overmature stands with good shrub stocking (e.g., stands 16 and 20 in Table 1; see also McLaren and Janke 1996). We conclude that the observed decline in browse availability is a direct result of chronic heavy browsing pressure by white-tailed deer.

We agree with Gray and Servello (1995) and Ditchkoff and Servello (1998) that the winter litterfall may constitute a significant, and frequently overlooked, alternative source of food. We estimated the average annual biomass of lichens and balsam fir twigs in the winter litterfall of balsam fir stands on Anticosti Island at 11.6 ± 1.3 and 16.5 ± 3.1 kg/ha, respectively. At the scale of the winter home range of a doe (67 ha; Potvin and Dussault 2004), litterfall may provide a potential input of 777 ± 87 kg of lichens and 1110 ± 210 kg of balsam fir browse per winter. The metabolizable energy content of lichens and balsam fir is estimated at 10 700 kJ/kg (Säkinen et al. 1999) and 8164 kJ/kg (Mautz et al. 1976), respectively. Assuming that the litterfall would be completely available to deer over the entire winter period, we can estimate a potential daily input of $54\,700 \pm 6100$ kJ/day for lichens and $59\,000 \pm 11\,000$ kJ/day for balsam fir browse from December to April (152 days) in the home range of a doe. During winter, however, the litter is frequently covered with snow and thus is not always available. However, Ditchkoff and Servello (1998) noted that it periodically resurfaces during thaw periods in winter, and even more in spring, a critical period for deer survival. The daily maintenance requirement of an adult doe during February–March on Anticosti Island has been estimated at 13 295 kJ ($58 \text{ kg} \times 632.6 \text{ kJ/kg}^{0.75}$; Huot 1982). If we make the simple assumption that the total litterfall is available

once it is on the ground, then the winter litterfall (estimated from the lower and upper 95% confidence interval limits for balsam fir browse and lichens) could theoretically sustain from 8.5 to 17.2 does/km². This is probably an overestimate because of our assumption of total availability, but it is consistent with the observation that individual energy requirements are not met during winter (up to 30% of body reserves can be used, according to Huot 1982), since deer density in mature balsam fir stands can reach over 40 individuals/km² (Potvin et al. 1991). Although based on simplified assumptions, these calculations clearly highlight the potential importance of the winter litterfall for the energy budget of deer. Moreover, our results indicate that this food source does not vary significantly from one year to the other, making its availability relatively predictable.

Litterfall in mature balsam fir stands may thus constitute a resource subsidy for overwintering deer. This input of resource is independent of browsing for a long period; it therefore contributes to sustaining high deer populations and introduces a temporal uncoupling between the impact of deer on seedlings and the negative feedback of recruitment failure of mature balsam fir stands on deer survival and reproduction. While deer browsing induces seedling mortality on a yearly time scale, the reduction in the availability of mature trees is a process that involves a scale of almost twice this order of magnitude. Hence, under the current browsing pressure on seedlings, the eradication of balsam fir is expected to occur within a 50-year time frame (Potvin et al. 2003). Resource subsidy and spatial or temporal uncoupling of grazing/browsing and plant regeneration can lead grazed ecosystems into alternative stable states (Scheffer et al. 2001; Mayer and Rietkerk 2004). For example, a regime shift from salt marsh to mud flat has occurred in the arctic breeding grounds of the lesser snow goose (*Chen caerulescens caerulescens* (L., 1758)) because of food subsidies and the spatial uncoupling of agricultural crops that contribute to sustaining a large goose population (Handa et al. 2002). Similarly, in large parts of the white-tailed deer distribution range, alternative foods from agricultural lands contribute to maintaining deer at high density, causing overbrowsing on adjacent forests (Alverson et al. 1988). Factors such as selective browsing, resource subsidies, and spatiotemporal uncoupling make deer prone to act as biological switches that move forest communities toward alternative successional pathways and alternative stable states (for a review see Côté et al. 2004). Regime shifts could occur on Anticosti Island, where balsam fir advance regeneration is inhibited by deer browsing (Potvin et al. 2003), causing white spruce to gain an apparent competitive advantage (sensu Holt 1977). Following a disturbance, positive feedbacks (Scheffer et al. 2001) continue to force the system away from its previous state as balsam fir seed trees become sparse, or early establishment success is reduced following site preemption by browse-tolerant grass. Depending on the status of white spruce advance regeneration, the compositional state of this alternative regime could be dominated by white spruce or turn into a savanna-like system with sparse white spruce (Moore et al. 2000). An ongoing disturbance–disturbance removal experiment should allow us to verify these predictions and assess the reversibility of the observed compositional shifts.

Without large-scale active management of forest and deer populations, balsam fir is expected to disappear as a major component of the forest on Anticosti Island and, concurrently, a decline in abundance of balsam fir and lichens in the litterfall is anticipated. Many lichens, including *Alectoria sarmentosa*, *Bryoria* spp., *Lobaria pulmonaria*, and *Ramalina roesleri*, are abundant in old-growth forests and tend to decline following forest disturbances (Lesica et al. 1991; Esseen et al. 1996). A reduction of the abundance of balsam fir and arboreal lichens will likely cause a decrease in deer abundance on the island, but the magnitude of the decline is hard to forecast because deer have the capacity to survive winter starvation when the body reserves accumulated during late summer and autumn are sufficient (Huot 1982). The future of the deer population on Anticosti Island will depend not only on the capacity of individuals to store body reserves in late summer and autumn and to take advantage of the winter litterfall in old balsam fir stands, but also on their capacity to survive winter in habitats with a lower cover of balsam fir (Potvin and Boots 2004). Results from an experiment with captive wild-caught fawns from Anticosti Island suggest that deer could tolerate a twofold increase in the proportion of white spruce in their diet (Sauvé 2005; Taillon 2005). However, fawns had to compensate for the diminution of the quality of their diet by increasing food intake. The long-term sustainability of the deer population thus hinges on intensive deer- and forest-management initiatives such as the recently adopted Anticosti Island forest resources integrated management plan, which seeks to maintain balsam fir in the landscape using a combination of forest harvesting, fencing, sport hunting, and controlled culling (Beaupré et al. 2004).

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