Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of their distribution range[1]

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Abstract: Interspersion of dense coniferous stands that offer cover and more open mixedwood stands providing food resources has been recommended for the management of white-tailed deer (*Odocoileus virginianus*) wintering yards in northeastern North America. On Anticosti Island, at the northeastern limit of this deer's distribution range, previous studies have shown continuous decline of deciduous browse. As native balsam fir (*Abies balsamea*) stands progressively shift to white spruce (*Picea glauca*), the persistence of the deer population will increasingly depends on its capacity to use white spruce stands. To provide insights into deer responses to long-term changes in their habitat, we investigated resource use along a gradient of expected habitat quality for deer. Stand use increased with the proportion of balsam fir, reaching an asymptote when > 40% of the stand's basal area was composed of fir. Stand use did not appear to be related to snow interception since sinking depth was lower in white spruce forests. Deer using white spruce stands mainly consumed balsam fir (72%), whereas spruce represented only 17% of their diet. The consumption of arboreal lichens increased from 6% in January to 21% in March. The observed patterns of habitat use and the composition of the winter diet confirm the dependence of deer on balsam fir in winter and give additional support to the hypothesis that litterfall from balsam fir provides an alternate food source sustaining high deer density in a boreal forest without predators.

Keywords: boreal forest, ecological subsidy, habitat use, lichens, overbrowsing, plant–herbivore interactions.

Résumé : L'entremêlement de peuplements forestiers offrant abri et nourriture constitue un paysage optimal dans les aires d'hivernage du cerf de Virginie (*Odocoileus virginianus*). Sur l'île d'Anticosti, à la limite nord-est de l'aire de répartition de cette espèce, des études antérieures ont démontré le déclin continu de la majorité des espèces décidues à la base du régime alimentaire hivernal du cerf et la conversion des peuplements de sapin baumier (*Abies balsamea*) vers l'épinette blanche (*Picea glauca*). Afin d'évaluer les réponses des cerfs aux changements s'opérant dans leur habitat, nous avons étudié l'utilisation des ressources le long d'un gradient de qualité d'habitat. Nous avons observé que la fréquentation par les cerfs augmente avec la proportion de sapin baumier jusqu'à l'atteinte d'une asymptote lorsque la surface terrière en sapin excède 40%. L'utilisation des peuplements forestiers n'est pas corrélée à leur potentiel d'interception de la neige dans les peuplements d'épinette blanche. La proportion de sapin baumier dans le régime alimentaire des cerfs atteint 72 % alors que l'épinette blanche ne compte que pour 17 %. La consommation de lichens arboricoles passe de 6 % en janvier à 21 % en mars. Les patrons d'utilisation des ressources en hiver confirment la dépendance du cerf au sapin baumier et appuie l'hypothèse que la chute de lichens et de ramilles de sapins matures permet de soutenir de fortes densités de cerfs en forêt boréale dépourvue de prédateurs.

Mots-clés : contribution de l'écosystème, forêt boréale, interactions plante-herbivore, lichens, surbroutement, utilisation de l'habitat.

Nomenclature: Anonymous, 2005.

Introduction

The use of conifer stands by wintering deer at the northern limit of their range is generally associated to their need for shelter and thus represents a compromise between energy acquisition from browse and energy allocation to locomotion in snow and thermoregulation (Huot, 1974; Hanley & Rose, 1987; Dumont *et al.,* 1998). We generally assume that the use of coniferous stands by deer in winter is not an optimal strategy because food availability and quality is generally lower in coniferous than in deciduous stands (Pauley, Peek & Zager, 1993), although the accumulation of snow is also greater in the latter, making travel in these stands more energetically expensive. Most coniferous species are regarded as starvation food for deer (Ullrey *et al.,* 1968; Crête & Courtois, 1997), even though eastern white cedar (*Thuja occidentalis*) and eastern hemlock (*Tsuga canadensis*) may sometimes be important sources of food for wintering deer (Mautz *et al.,* 1976; Gray & Servello, 1995; Ditchkoff & Servello, 1998). Deer also reduce their energy losses during winter by using forest stands that offer the best thermal advantage, such as wind protection (Boulet, 1980; Huot, Potvin & Bélanger, 1984; Dumont *et al.,* 1998). Past studies have shown that use of dense forest cover by deer increases as ambient temperature drops (Ozaga & Gysel, 1972; Drolet, 1976). Conifer stands do offer a thermal advantage, but more importantly dense forest cover reduces the accumulation of snow on the ground (Hanley & Rose, 1987). It has been suggested that snow depth could be the most important factor explaining the use of conifer stands by deer during the winter months (Potvin, 1979; Boulet, 1980; D'Eon, 2001; Sakuragi *et al.,* 2003). Interspersion of dense coniferous stands offering cover and more open mixedwood stands providing food resources has been recommended for the management of white-tailed deer (*Odocoileus virginianus*) wintering yards in northeastern North America (Dumont *et al.,* 1998; Morrison, Forbes & Young, 2002).

On Anticosti Island, at the northeastern limit of the species' distribution range, the highest deer densities were found in forest stands where balsam fir (*Abies balsamea*) accounts for > 40–60% of the total basal area based on data from aerial surveys (Potvin, Boots & Dempster, 2003; Potvin & Boots, 2004). Recently, Tremblay *et al.* (2005) proposed that an ecological subsidy from arboreal lichens and balsam fir twigs falling from mature trees could enhance white-tailed deer winter survival independently of the browsing pressure. Ecological subsidies can dramatically change competitive and consumptive interactions in ecosystems (Jefferies, 2000; Croll *et al.,* 2005). The uncoupling of resource availability and population density has led to the eradication of most deciduous browse species on Anticosti (Pimlott, 1963; Marie-Victorin & Rolland-Germain, 1969; Potvin, **Beaupré & Laprise, 2003**; **Tremblay** *et al.,* 2005). Although balsam fir is basically the only currently available browse species, excluding white spruce (*Picea glauca*) and black spruce (*Picea mariana*), its availability has declined by 78% to 100% in the feeding layer of the stands where it was present 25 y ago (Tremblay *et al.,* 2005). The direct impact of deer browsing on advance fir regeneration (Chouinard & Filion, 2001; Potvin, Beaupré &

Laprise, 2003a; Tremblay, Huot & Potvin, in press) and the indirect impact of selective browsing on competitive interactions between plants (Tremblay, Huot & Potvin, 2006) are causing balsam fir stands to be converted progressively to white spruce or park forest landscapes. Under the present conditions, Potvin, Beaupré, and Laprise (2003) predicted that balsam fir could be eradicated from the island in approximately 50 y.

Although balsam fir is by far the main source of winter food for deer on Anticosti, results from experimental feeding trials with captive fawns suggest that they could cope with a diet composed of up to 40% of white spruce (Taillon, Sauvé & Côté, 2006). Thus, a legitimate question emerges from our current knowledge of this system and from its predicted trend: What is the contribution of white spruce stands to the carrying capacity of the habitat in terms of cover and food resources? To provide insights into this question, we studied resource use by deer along a gradient ranging from relatively high-quality balsam fir stands to presumably lower-quality young white spruce stands. Based on the hypothesis that deer are highly dependent on balsam fir to provide both cover and food from fallen twigs and arboreal lichens in winter, we predicted a higher occurrence of deer in balsam fir stands, a higher proportion of balsam fir in the diet of these deer, and lower snow accumulation and sinking depth in balsam fir stands.

Methods

STUDY AREA

Anticosti Island (49° 28' N, 63° 00' W) is a 7 943 km^2 limestone plateau located in the Gulf of St. Lawrence, Québec, Canada. Its vegetation belongs to the eastern balsam fir–paper birch (*Betula papyrifera*) bioclimatic region (Saucier *et al.,* 2003). Mean temperature in January is –11 °C (Environment Canada, 2005), and mean annual snowfall is 328 cm (Environment Canada, 1982). Our study area (~1 420 km^2) is representative of the western area of the island, where forest logging has interacted with deer since the early 1900s to shape forest composition. Mires, lakes, and other non-forested land cover 28% of the study area, while 46% of the productive forest is dominated by balsam fir, 32% by white spruce, and 19% by black spruce. Approximately 200 white-tailed deer were introduced on the island at the end of the 19th century; in the absence of natural predators, the population peaked in the 1930s and has remained high thereafter (~20 deer·km^{-2}; Potvin & Breton, 2005).

FIELD SURVEY DESIGN

A decreasing gradient of presumed habitat quality from > 90-y-old balsam fir stands (BF 90) to 70-y-old white spruce (WS 70), 50-y-old white spruce (WS 50), and 30-y-old white spruce (WS 30) was used to test predictions relative to deer responses to long-term change in their habitats. Three replicates within each stand type, for a total of 12 units were selected. Younger fir stands were not sampled because they cover < 1% of the study area. Stands were chosen from forest cover maps (1:20 000) according to their age and composition (Ordre des ingénieurs forestiers du Québec, 1996) as well as accessibility by snowmobile.

FOREST TYPE ATTRIBUTES

Sampling plots were placed at 40-m intervals along 2 parallel transects separated by 40 m, offset by 20 m and starting at least 20 m from stand edges (10 plots·stand⁻¹) within the 12 forest stands. For each plot, basal area by species with a factor 2 metric wedge prism was estimated. Forest overstory cover was assessed by noting the presence or absence of cover above 20 vertical equidistant points along a 1-m calibrated rope (Vales & Bunnell, 1988). Arboreal lichens falling from trees were collected in 1-m² litter traps (10 traps·stand⁻¹), which consisted of fine-mesh textile netting mounted on a wooden frame. Traps were set up in late October and contents were harvested in late May after complete snowmelt. Trap contents were air-dried and sorted according to lichen categories and genus (fruticose: *Alectoria* spp. + *Bryoria* spp. and *Ramalina* spp.; foliose: *Lobaria* spp.). Samples were air-dried for 24 h at 55 °C before being weighed (± 0.0001 g).

Snow accumulation was measured every 15 d at stations located in one stand per forest type (2 in BF 90). Each station consisted of 3-m graduated rulers ($n = 10$) spaced equidistantly every 5 m. A penetrometer was used to assess sinking depth of deer paired with each snow accumulation measurement (Verme, 1968). The number of days with sinking depth exceeding 50 cm is correlated to winter mortality of deer in northeastern North America (Severinghaus, 1947; Cantin & Pichette, 1989). This index is influenced by our 15-d sampling interval, but this should not affect comparison between stand types.

USE OF FOREST TYPES BY DEER

Winter use of forest types by deer was determined by counting tracks and pellet groups along a permanent 1-km by 2-m strip transect a each stand. Deer tracks in fresh snow were classified as 1 or 2 individuals, a path, or a network. Networks of tracks were discriminated from single paths when the number of tracks and direction of travel could not be assessed. Each transect was sampled once every 3 weeks between January and March 1999 within 24 h of a fresh snowfall (minimum of 5 cm), for a total of 4 sampling periods per transect.

WINTER DIET

Winter diet of deer was determined from fecal analyses. Our objective was to collect 5 fecal pellet groups along each transect, for a total of 15 samples per forest type (5 fecal samples per transect × 3 stands per forest type; Holecheck, Vavra & Pieper, 1982), and to repeat this procedure for each sampling period. The objective of 15 samples per forest type for each sampling period could not be met in white spruce stands because of their low use by deer. Samples were stored frozen prior to analyses. Fecal samples were analyzed by microhistology (Holecheck, Vavra & Pieper, 1982). Each fecal sample was thawed, hydrated for 3–4 d, and then sequentially passed through a series of sieves (2 mm, 1 mm, 500 μm, and 250 μm). A subsample of fecal material from the 1-mm sieve was suspended in a thin layer of water in a 6-×10-cm Plexiglas coil to evaluate the relative contribution of lichens and trees. The number of fruticose lichen fragments in the subsample was counted with a dissection microscope at 16× and the proportion of fruticose lichen was expressed as:

$$\text{proportion lichen in diet} = \frac{n_{lichen} \text{ fragments observed}}{n_{total} \text{ fragments observed}} \times 100 \quad [1]$$

The absolute proportion of lichens in the diet is most likely underestimated because of the higher digestibility of lichens compared to the other main components of the diet (Ditchkoff & Servello, 1998). These data should thus be regarded as the relative contribution of lichens to the winter diet between forest types and sampling periods.

Trees were further partitioned between fir and spruce using a subsample of particles retained on the 250-μm screen. These particles were suspended in 7 mL potassium hydroxide solution (KOH 10%) and boiled for 60 min. Fragments were then washed with tap water, put into 3 mL of hydrogen peroxide solution (H_2O_2) for 15 min, and finally washed again with tap water. A subset of the fragments was mounted on a microscope slide for microhistological analysis. The slide was examined under a microscope at 100×, and the fragments of balsam fir, white spruce, and black spruce stomata along 2 linear transects were identified to species and counted. Only the fragments of those tree species were counted because they represent the bulk of vegetation eaten by white-tailed deer on Anticosti Island (Huot, 1982), and also because other species are very rare (Tremblay *et al.,* 2005). Two slides per fecal sample were examined, for a total of 4 transects per sample. We were able to distinguish among tree species based on the shape of their stomata (Hansen, 1995). It was difficult to differentiate between spruce species, but black spruce was rare in the forest stands we sampled, and its presence in the deer diet is minimal (Huot, 1982). The proportion of balsam fir or spruce in the diet of deer was determined by dividing the number of fragments of a particular food item (fir or spruce) by the total number of fragments observed on the slide:

$$\text{proportion in diet} = \frac{n_{dietary\ item} \text{ fragments observed}}{n_{total} \text{ fragments observed}} \times 100 \quad [2]$$

The higher fibre content and concentration of secondary compounds in spruce than in balsam fir may reduce its digestibility (Von Rudloff, 1972; Sauvé & Côté, in press) and thus lead to overestimation of the proportion of spruce, but bias in detection of these forages in fecal pellets is assumed to be low (Huot, 1982).

STATISTICAL ANALYSES

Forest type attributes and the biomass of fallen arboreal lichens was compared using one-way ANOVAs or Kruskal–Wallis tests when the assumptions of parametric analyses could not be met. The influence of forest type and sampling period on winter use of forest stands was analyzed with mixed model ANOVAs with stand nested within each forest type as a random factor and period as a repeated measure. We assumed compound symmetry or first-order autoregressive structure of the covariance matrix and chose among those alternatives using the Akaike information criterion (AIC). Dependent variables were transformed when they did not meet normality and homoscedasticity criteria (logarithmic or square root transformation), and least-square

means were used for multiple comparisons. WS 30 stands were not included in the analyses of winter use by deer because only one fecal sample was found in those stands during our study. The relationships between the proportion of the basal area of a stand composed of balsam fir and deer occurrence was quantified using nonlinear mixed models with stand as a random factor. Results are presented as mean ± 1 SD, and a significance threshold $\alpha = 0.05$ was used. All statistical analyses were performed with SAS (SAS Institute Inc., 1996).

Results

Forest type attributes

Not surprisingly, the basal area of balsam fir was much higher in BF 90 than in other forest types ($F_{3,8} = 9.0$, $P = 0.006$; Table I), whereas it was highest for white spruce in WS 70 and lowest in BF 90 ($F_{3,8} = 10.0$, $P = 0.005$; Table I). The basal area of black spruce, trembling aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*) was low and did not vary among forest types. Basal area was slightly higher for white birch, especially in BF 90 ($F_{3,8} = 8.1$, $P = 0.008$; Table I). The total basal area was highest in WS 70 ($\chi_3^2 = 8.7$, $P = 0.03$; Table I). BF 90 stands were mixed stands composed mainly of balsam fir and white spruce (Table I). In comparison, white spruce stands were almost monospecific ($\geq 80\%$ white spruce), with little balsam fir or black spruce. Overstory cover did not differ among stands ($F_{3,8} = 1.2$, $P = 0.4$; Table I). The area covered by these 4 forest types totalled 52% of our study area (Table I).

The biomass$^{-0.5}$ of fruticose lichens falling from trees, although not statistically significant ($F_{3,8} = 3.6$, $P = 0.07$), tends to be lower in WS 30 than in older stands, especially BF 90 and WS 70 (Table I).

The maximum accumulation of snow during the winter of 1999–2000 ranged between 105 and 139 cm in February, with snow depth being 30% lower in BF 90 and WS 70 stands than in younger white spruce stands (Figure 1a). Maximum sinking depth varied between 56 and 81 cm among stand types in late January, and the greatest depths were recorded in 30-y-old white spruce stands (Figure 1b). The period during which the sinking depth exceeded 50 cm was shorter in WS 70 (28 d) than in BF 90 (47 d) or WS 30 and WS 50 (53 d).

Use of forest types by deer

White-tailed deer visited all forest stand types during winter, but differences were noticeable in the number of individual tracks, track networks, and number of pellet groups found in the different stands (individual tracks, $F_{3,8} = 14.5$, $P = 0.001$; track networks, $F_{3,8} = 4.4$, $P = 0.04$; pellet groups, $F_{3,8} = 5.8$, $P = 0.02$; Figure 2). Individual tracks were by far the most common index of deer presence, but all indices indicated a higher use of BF 90. Apart from individual tracks ($F_{3,24} = 3.3$, $P = 0.04$), which increased at the end of winter inde-

TABLE I. Attributes of the studied forest types on Anticosti Island, Québec, Canada. Values are presented as mean ± 1 SD. Values with the same letter on a row are not significantly different ($\alpha = 0.05$).

Attributes	BF 90* (n = 3)	WS 70 (n = 3)	WS 50 (n = 3)	WS 30 (n = 3)
Basal area ($m^2 \cdot ha^{-1}$)				
Balsam fir	15.8 ± 7.1^a	0.8 ± 1.4^b	4.6 ± 4.0^b	0^b
White spruce	15.7 ± 10.4^a	44.3 ± 4.7^c	30.3 ± 1.3^b	26.9 ± 6.0^{ab}
Black spruce	1.2 ± 0.9^a	0.5 ± 0.6^a	2.0 ± 3.3^a	1.4 ± 1.1^a
White birch	0.9 ± 0.3^a	0^b	0.4 ± 0.3^b	0.2 ± 0.1^b
Trembling aspen	0^a	0^a	0^a	1.2 ± 1.7^a
Balsam poplar	0^a	0^a	0^a	0.3 ± 0.3^a
Total	33.6 ± 5.0^{bc}	45.6 ± 6.1^a	37.3 ± 2.4^b	30.0 ± 3.2^c
Overstory cover (%)	66 ± 20^a	77 ± 17^a	79 ± 18^a	74 ± 18^a
Area (ha [% study area])	35 057 [25]	10 400 [7]	10 708 [8]	4158 [3]
Fallen lichen biomass (kg·ha^{-1})†	13.8 ± 6.1	13.5 ± 9.3	4.9 ± 1.5	3.1 ± 2.8

* BF 90: 90-y-old balsam fir stand; WS 70: 70-y-old white spruce stand; WS 50: 50-y-old white spruce stand; WS 30: 30-y-old white spruce stand.

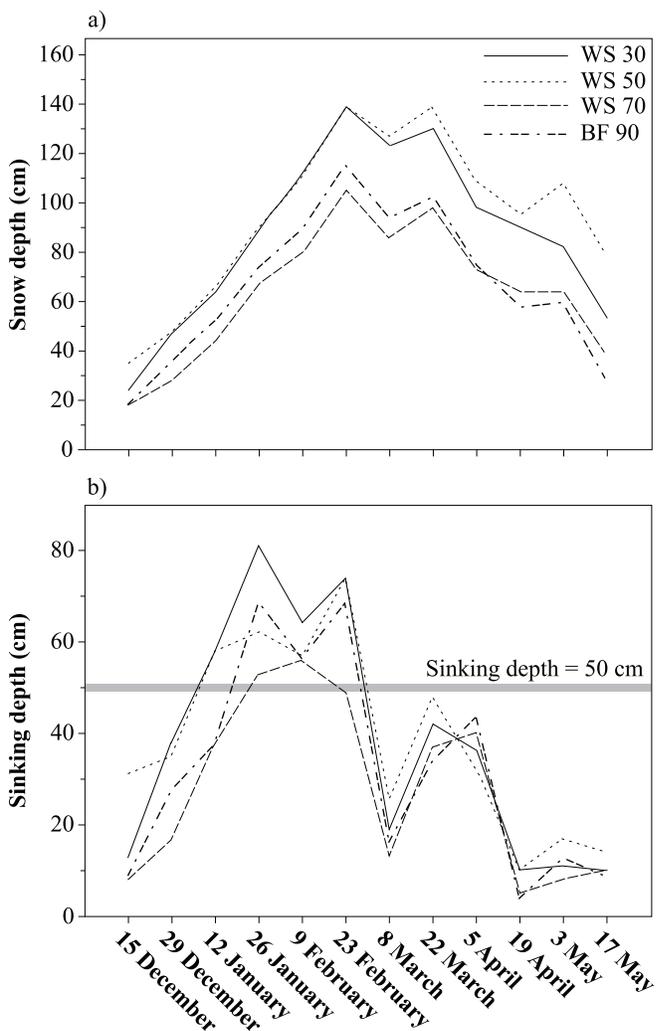† Fruticose lichens of the genera *Alectoria*, *Bryoria*, and *Ramalina*.

FIGURE 1. Snow and sinking depth recorded on Anticosti Island at 15-d intervals at stations located in 4 different forest types. In b), the shaded solid line represents the sinking depth threshold of 50 cm. Winter mortality of deer in northeastern North America is correlated to the number of days with sinking depth exceeding this threshold (Severinghaus, 1947; Cantin & Pichette, 1989).
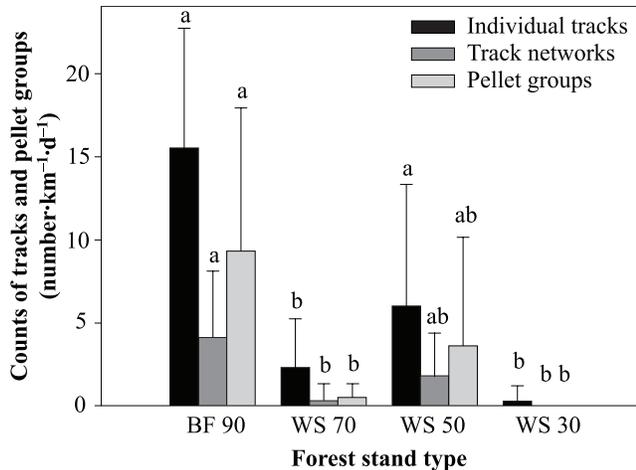
FIGURE 2. Counts of tracks and pellet groups (number·km⁻¹·d⁻¹) according to forest type. Data represent all 4 sampling periods grouped together. Bars representing the same variable and surmounted by the same letter do not differ significantly ($\alpha = 0.05$). Data are presented as mean + 1 SD.
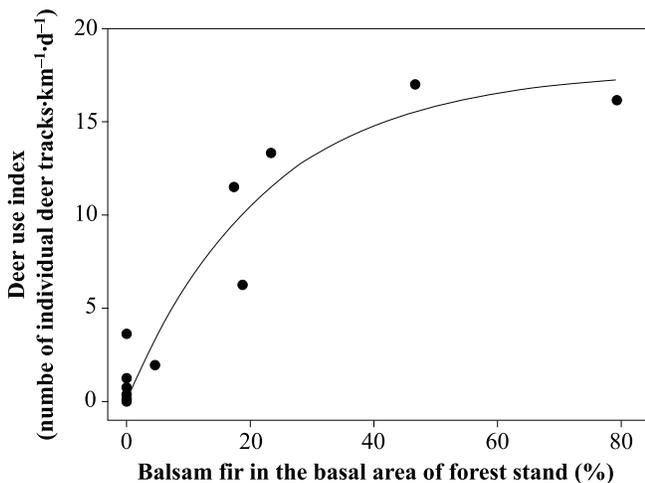

FIGURE 3. Relationship between the proportion of balsam fir in the basal area of forest stand and deer use index (number of individual deer tracks·km⁻¹·d⁻¹). Each data point represents one of the 12 forests stands surveyed. The line represents the best fit through the data, as determined by nonlinear regression ($y = 17.7(1 - e^{-0.044x})$; pseudo-$R^2 = 0.94$).

pendently of forest type, no other indices of occurrence changed with winter progression ($F_{3, 24} < 0.5$, $P > 0.5$). Neither was there any interaction between stand type and sampling period ($F_{9, 24} < 0.8$, $P > 0.6$). The use of forest stands by deer increased logarithmically as the proportion of balsam fir increased to an asymptote of approximately 40% of a the total basal area (Figure 3).

WINTER DIET

The composition of the winter diet did not differ among stand types ($F_{2, 5} = 0.19$, $P = 0.83$; $F_{2, 5} = 0.27$, $P = 0.77$; and $F_{2, 5} = 0.35$, $P = 0.72$ for % balsam fir$^{-0.5}$, % white spruce$^{-0.5}$, and % lichens$^{-0.5}$, respectively; Table II), either among sampling periods ($F_{3, 9} = 0.96$, $P = 0.45$ and $F_{3, 9} = 1.49$, $P = 0.28$), except for the proportion of lichens, which increased at the end of winter ($F_{3, 9} = 13.78$, $P = 0.001$; Table II). There was no interaction between for-

est types and periods ($F_{6, 9} = 1.19$, $P = 0.39$; $F_{6, 9} = 1.42$, $P > 0.3$; and $F_{6, 9} = 1.24$, $P > 0.37$; for balsam fir$^{-0.5}$, white spruce$^{-0.5}$ and lichen$^{-0.5}$, respectively) The main item in the white-tailed deer's winter diet on Anticosti Island was balsam fir (Table II). The consumption of lichens increased significantly at the end of winter; deer ate 3 times as many lichens during the period of 11–12 March as they did during any of the 3 previous sampling periods.

Discussion

Our study of resource use by deer in winter along a gradient of habitat suitability in the boreal forest demonstrates the dependence of deer on balsam fir after depletion of deciduous browse by chronic heavy browsing. As predicted, most indices of deer occurrence indicate greater use of old balsam fir stands compared to white spruce stands. Furthermore, the use of white spruce stands is modulated by their balsam fir content: use rises as the proportion of balsam fir area in a stand increases to an asymptote of approximately 40% of the total basal area. Using independent data sets from aerial surveys of deer and forest vegetation maps, Potvin and Boots (2004) and Potvin, Boots, and Dempster (2003) previously reported a plateau in deer use of forest stands when balsam fir accounted for > 50% of a stand. Our results validate these conclusions and provide ecological explanations for the observed pattern of winter habitat use by deer facing harsh winter conditions and a long-term decline in their browse supply (Tremblay *et al.,* 2005).

The higher use of balsam fir stands was not related to better snow interception properties as predicted. The sinking depth was in fact lower in mature white spruce stands where the total basal area was also higher. Nevertheless, deer continue to concentrate their activity in balsam fir stands even though fir availability has declined by more than 50% over the last century (Potvin, Beaupré & Laprise, 2003). Currently, BF 90 stands cover 25% of the forested area in the western part of Anticosti Island but are rapidly declining at the island scale as stands submitted to the natural regime of disturbance fail to regenerate (Potvin, Beaupré & Laprise, 2003). Younger stands with ≥ 25% of balsam fir stems account for only 12% of our study area. Apparently, the higher use of mature balsam fir stands is related not only to the shelter they provide against harsh climatic conditions, but also to food resources availability, as revealed by the importance of fir in the winter diet (more than two-thirds of the diet over the whole winter). The fact that wintering deer in mixed boreal forest on the southern shores of the St. Lawrence River hardly ever include balsam fir as part of their winter diet even in mild winters (Dumont *et al.,* 2005) indicates how poor winter food resources have become on Anticosti Island (see also Tremblay *et al.,* 2005). In fact, balsam fir is generally considered as a starvation food for white-tailed deer because of the presence of secondary compounds that reduce digestibility (Ullrey *et al.,* 1968; Mautz *et al.,* 1976; Sauvé & Côté, in press). Heavy consumption of balsam fir has been hypothesized to negatively affect the energy balance of moose (Crête & Courtois, 1997). The diet seems unrelated to the forest type where pellet groups are harvested, suggesting that deer can maintain a high proportion of balsam fir in their diet even in 50- to 70-y-old

Table II. Winter diet of white-tailed deer according to forest stand types (3 stands per type) and sampling periods. Values represent the percentage of fragments of dietary items ± 1 SD in fecal pellet groups.

Dietary item and sampling period	BF 90 $n = 60$*	WS 70 $n = 23$	WS 50 $n = 35$	WS 30 $n = 1$	Cumulative
Balsam fir					
January 17–24	67.8 ± 20.0	71.1 ± 14.2	83.6 ± 8.4	0	71.5 ± 16.0
February 4–13	65.2 ± 27.9	75.6 ± 11.3	80.3 ± 10.1	0	72.0 ± 20.2
February 25–27	69.7 ± 19.5	74.2 ± 5.0	85.8 ± 9.5	91.7	75.9 ± 14.1
March 11–12	64.1 ± 17.6	56.1 ± 20.2	53.6 ± 22.9	0	58.5 ± 16.0
Spruce					
January 17–24	23.8 ± 18.3	23.3 ± 13.4	15.2 ± 8.3	0	22.2 ± 16.0
February 4–13	26.4 ± 25.8	22.8 ± 11.1	12.5 ± 9.4	0	21.2 ± 20.2
February 25–27	19.5 ± 17.2	15.4 ± 4.5	11.4 ± 9.2	5.9	17.4 ± 14.1
March 11–12	15.9 ± 14.1	21.9 ± 15.8	26.8 ± 18.4	0	20.5 ± 16.0
Arboreal lichens					
January 17–24	8.4 ± 8.4	5.6 ± 3.5	1.2 ± 1.2	0	6.3 ± 7.3[a†]
February 4–13	8.4 ± 13.6	1.6 ± 0.5	7.2 ± 14.4	0	6.8 ± 13.0[a]
February 25–27	10.8 ± 11.9	10.4 ± 11.9	2.8 ± 3.1	2.4	8.1 ± 10.4[a]
March 11–12	20.0 ± 11.0	22.0 ± 20.7	19.6 ± 18.3	0	20.9 ± 15.5[b]

* Number of fecal pellet groups.

[†] Values with the same letter in a column are not significantly different.

white spruce stands. We cannot exclude the possibility that consumption and defecation are spatially distinct processes. However, insights into the foraging strategy of overwintering deer suggest that this is unlikely to be the main factor explaining our results. When foraging in snow at low ambient temperature, deer have to make a compromise between energy acquisition from food and energy allocation to locomotion and thermoregulation (Lesage *et al.*, 2001; Dumont *et al.*, 2005). At the northern limit of the distribution range of deer, the energy budget is usually negative (Huot, 1982) and deer must limit their movements to reduce energetic costs (Parker *et al.*, 1984; Dumont *et al.*, 2005). On Anticosti Island, the movement rate drops from 64 ± 4 m·h^{-1} in summer ($n = 19$) to 30 ± 1 m·h^{-1} in February to March ($n = 15$; A. Massé, pers. comm.), and the average winter home range is very small (51 ± 11 ha, $n = 20$; A. Massé, pers. comm.). The radius of a generic circular home range (approximately 200 m) is smaller than the distance between the transects we surveyed in white spruce stands and the closest balsam fir stands (mean = 400 ± 200 m excluding one WS 50 site that was adjacent to a balsam fir stand). We therefore assume that the contents of pellet groups deposited in a stand were representative of the food consumption in that stand.

The dominance of balsam fir in the winter diet contrasted with its availability in the browse layer. The number of balsam fir stems with twigs available within reach of deer did not exceed $2\,200 \pm 600$ stems·ha^{-1} (a 78% to 100% decline since 1975 in 13 representative stands; Huot, 1982; Tremblay *et al.*, 2005). On the other hand, the number of white spruce stems reached up to $10\,600 \pm 1\,200$ stems·ha^{-1} (Thibault *et al.*, 2005). Considering the very low availability of balsam fir in the browse layer, we suggest that balsam fir twigs falling from mature trees, as well as occasional windblown trees, represented the main source of food for deer in winter. Lower concentration of secondary compounds in small twigs at the top of conifer trees relative to shaded branches near the ground (Dawson, Armleder & Waterhouse, 1990) may increase the energetic value of this forage. Although lichens represent a small fraction of the diet, they nonetheless constitute a source of easily digestible energy (Robbins, 1987) and could also enhance dry matter digestibility (Jenks & Leslie, 1989).

The observed patterns of habitat use and the diet composition provided additional support for the hypothesis that litterfall from balsam fir provides an alternate food source sustaining high deer density on Anticosti Island (Tremblay *et al.*, 2005). Consumption of litterfall by ungulates has been reported for white-tailed deer in Maine (Ditchkoff & Servello, 1998), mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) in Montana (Ward & Marcum, 2005), black-tailed deer (*O. h. columbianus*) in Alaska (Stevenson & Rochelle, 1984), and sika deer (*C. nippon*) in Japan (Miyaki & Kaji, 2004). Although deer, balsam fir, and lichens are all components of the ecosystem of Anticosti Island, there is a disconnection between them because the input of litterfall is independent of browsing over a long time period. Independent flow of resources, or ecological subsidies, has not received much attention in terrestrial ecosystems (Menge *et al.*, 2003; but see Jefferies, 2000). The contribution of ecological subsidies to the carrying capacities of northern ungulate habitats should be considered by wildlife and forest managers seeking to achieve ecosystem-based management of natural resources. But whether the capacity of white-tailed deer on Anticosti Island to consume a high proportion of balsam fir is an adaptation to harsh environmental conditions, an expression of the considerable phenotypic plasticity of deer, or a consequence of balsam fir evolving in the absence of browsing is still an open question.

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