Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare[1]

Sonia de Bellefeuille, Louis Bélanger, Jean Huot, and Agathe Cimon

Abstract: We compared utilization by the snowshoe hare (*Lepus americanus* Erxleben) of recent clearcuts subjected to three regeneration scenarios commonly used in boreal forest: natural regeneration, plantation with herbicide release (glyphosate), and plantation with manual release (brushsaw). Refuges for snowshoe hare, on a landscape dominated by clearcuts, were also investigated. Colonization of regenerating sites by the hare comes late in the humid boreal forest because clear-cut stands take more than 10 years to reach the sapling stage. Our sites were in the seedling stage 7–9 years after cutting, and hares avoided them year round because of an inadequate protective cover. Therefore, regeneration treatments did not affect habitat use by the hare on a short-term basis. During the seedling stage, the snowshoe hare were found in the remaining forest which occupied at least 25% of the area of each home range. The preservation of residual forests is thus essential to maintain local populations on an area dominated by commercial clearcuts.

Résumé : Nous avons comparé l'utilisation par le lièvre d'Amérique (*Lepus americanus* Erxleben) d'aires de coupe récentes, soumises à trois scénarios de régénération couramment employés en forêt boréale, soit : la régénération naturelle, la plantation dégagée chimiquement (glyphosate) et la plantation dégagée mécaniquement (débroussaillage). Nous avons aussi étudié, à l'échelle du paysage, les refuges utilisés par le lièvre sur un territoire exploité. La recolonisation d'aires de coupe par le lièvre est tardive en sapinière boréale humide parce qu'il faut plus de 10 ans à la régénération pour atteindre le stade de gaulis. Nos sites étaient au stade de fourré 7–9 ans après coupe et étaient évités par le lièvre en raison d'un couvert de protection déficient en toutes saisons. À court terme, les traitements de régénération n'ont donc pas modifié l'utilisation de l'habitat par cette espèce. Pendant la période d'évitement des coupes, le lièvre s'est réfugié là où il y avait de la forêt résiduelle, celle-ci occupant au moins 25% de la superficie de chaque domaine vital. La conservation de parcelles de forêt résiduelle est donc indispensable au maintien de populations locales sur un territoire dominé par la coupe totale.

Introduction

Quebec's forest renewal policy emphasizes natural regeneration (Gouvernement du Québec 1994). Since 1995, clear-cutting with protection of regeneration and soil (CPRS), an approach intended to preserve some features of preharvest stand composition and structure (Gouvernement du Québec 1996), has replaced conventional clear-cutting in the boreal forest. With CPRS, all the merchantable trees are removed, but special care is taken to protect advance regeneration and soil in restricting machinery to parallel trails 5 m wide and 10 m apart. When regeneration is insufficient to ensure forest renewal, clearcuts are scarified and spruce are planted. To ensure survival and growth of planted seedlings, these plantations are usually released (herbicides or cutting) from angiosperm competition 1–5 years after planting. However, in the last two decades, the public has become increasingly concerned about herbicide release, which they associate with extensive monocultures and potentially hazardous chemicals in the environment (BAPE 1991, 1997; Lautenschlager 1993). Those concerns have led to environmental studies comparing standard herbicide release techniques and more publicly acceptable cutting treatments designed to control competing vegetation (Lautenschlager et al. 1998).

Few of those studies, however, have examined the effects of forest regeneration practices on snowshoe hare (*Lepus americanus* Erxleben) (Hjeljord et al. 1988; Sullivan 1994). This potential keystone species (Koehler 1990; Keith and Cary 1991; Boutin et al. 1995) was selected for our study because of its close association with regenerating boreal and boreal mixedwood areas (Wolff 1980; Litvaitis et al. 1985) and its considerable ecological, recreational, and economic value. Although commonly associated with early successional boreal forests, snowshoe hare avoids clearcuts during the

Received October 8, 1999. Accepted June 23, 2000. Published on the NRC Research Press website on December 16, 2000.

S. de Bellefeuille[2] and L. Bélanger. Département des sciences du bois et de la forêt, Faculté de foresterie et de géomatique, Université Laval, Sainte-Foy, QC G1K 7P4, Canada.
J. Huot. Département de biologie, Faculté des sciences et de génie, Université Laval, Sainte-Foy, QC G1K 7P4, Canada.
A. Cimon. Ministère des Ressources naturelles, 880 chemin Sainte-Foy, Québec, QC G1S 4X4, Canada.

[1]Results of this study come from the thesis of the first author.

[2]Corresponding author. Present address: Ministère des Ressources naturelles, Direction de l'environnement forestier, 880 chemin Sainte-Foy (5th floor), Québec, QC G1S 4X4, Canada. e-mail: sonia.debellefeuille@mrn.gouv.qc.ca

DOI: 10.1139-cjfr-31-1-41

seedling stage, when the average height of the woody vegetation is less than 2 m (Conroy et al. 1979; Scott and Yahner 1989; Ferron et al. 1994). During the sapling stage, when the average height of woody vegetation is between 2 and 5 m and vegetation structure is more complex (Titterington et al. 1979; Thompson 1988), snowshoe hare becomes more common (Ansseau et al. 1996).

CPRS is a technique well suited for regenerating even-aged forests, but when applied over large areas, its potential effects on wildlife raise many concerns, especially for game species users and native people (BAPE 1991; Morel 1996; Potvin et al. 1999). Silvicultural systems that can hasten the sapling stage may then be useful to sustain the wildlife values found during that stage and facilitate social acceptance of clearcuts.

This study was designed to test the hypothesis that conifer release would advance stand regeneration and provide habitat for snowshoe hare. We compared the effects of three regeneration methods commonly used in Quebec's boreal balsam fir forest: (*i*) natural regeneration, (*ii*) planting followed by herbicide (glyphosate) release, and (*iii*) planting followed by manual (brushsaw) release on the length of spruce and fir seedling stage. We also describe snowshoe hare use of a clear-cut area at stand and landscape scales.

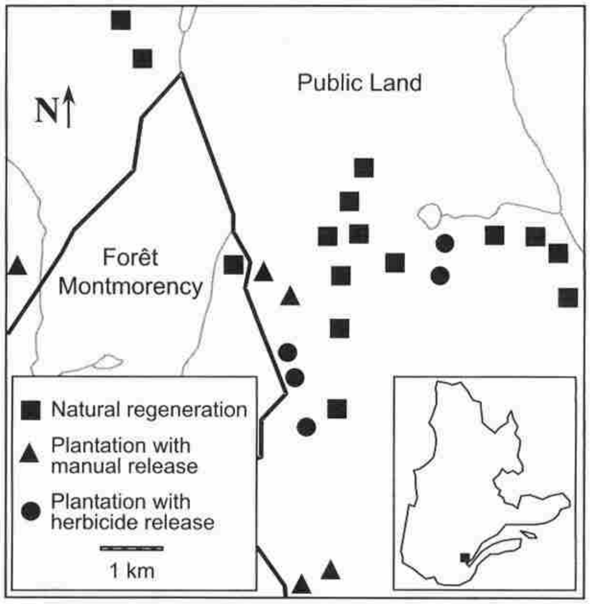
Study area

The study was conducted from 1991 to 1996 in south-central Quebec, on public land located approximately 80 km north of Québec city, Canada (47°18′–47°20′N, 71°01′–71°08′W). This forest region is part of the balsam fir (*Abies balsamea* (L.) Mill.) – white birch (*Betula papyrifera* March.) bioclimatic domain (Germain et al. 1996) and has a low boreal per-humid climate characterized by cold temperatures and high precipitation (Ecoregions Working Group 1989). Mean annual temperature is 0.3°C, and mean annual precipitation is 1527 mm, one-third of precipitation falls as snow, which covers the ground from late October to mid-May (Environment Canada 1993). The landscape is hilly, with elevations ranging from 600 to 1100 m and is covered with acidic glacial tills.

The study area was clear-cut between 1941 and 1945 and again starting in 1987. Balsam fir dominates second growth mature forest stands, but black spruce (*Picea mariana* (Mill.) BSP.), white birch, and white spruce (*Picea glauca* (Moench) Voss) are also common. Clearcuts are colonized by raspberry (*Rubus idaeus* L.), balsam fir, and white birch. Natural disturbances include recurrent spruce budworm (*Choristoneura fumiferana* (Clem)) outbreaks and windfalls. Because these forests are continuously wet during common fire periods, fire frequencies are low.

Whole-tree harvesting with roadside delimbing and protection of regeneration is common in the area. When advance conifer regeneration is lacking, clearcuts are scarified with a powered disk trencher and planted with black spruce. The landscape is characterized by recent clearcuts separated by blocks of residual forest, riparian forest strips and roads. Forest practices at the time of harvest included 20 m wide riparian forest strips and uncut forest blocks (3–10 ha), covering at least 4% of the logged area, which are preserved for moose (*Alces alces*) habitat (Gouvernement du Québec 1986). The size of a cut area was limited to 250 ha and forest strips 60–100 m wide were maintained between two adjacent clearcuts. Residual conifer forests occupy less than 18% of the study area (Gagné et al. 1999).

Fig. 1. Location of the 25 experimental blocks (6–9 ha) on the study area in a boreal balsam fir forest, south-central Quebec. Ten blocks were clear-cut in 1987, scarified in 1989, planted with black spruce in 1990, and released in 1992. Half of these planted blocks were released manually with brushsaws, whereas the five others were released with an aerial application of herbicide (Vision®). Fifteen naturally regenerated blocks clear-cut between 1987 and 1989 served as controls.



Methods

Experimental design

The experimental design is composed of 25 sites (6–9 ha each) originating from recent clearcuts. Ten sites were clear-cut in 1987, scarified in autumn 1989, planted with black spruce in spring 1990, and released in August 1992. Half of these plantations were released manually with brushsaws, whereas the five others were released chemically with aerial application of a solution containing Vision® (a.i. glyphosate) herbicide (5 L/ha). Fifteen naturally regenerated sites clear-cut between 1987 and 1989 served as controls (Fig. 1). In each site, thirty 1 × 5 m permanent plots were systematically spaced each 50 m (40 m in sites <7.5 ha) along adjacent transects 50 m apart.

Vegetation description

From 1991 to 1995, vegetation sampling was conducted annually in summer in all control and treated sites. In each permanent plots, stems of tree species were counted within a 1 × 4 m subplot, whereas stems of shrubs species were counted in a 1 × 1 m subplot. Average height and ground cover of trees and shrubs, and ground cover of herbs and logging debris were evaluated within the 4-m^2 subplot.

Food and cover

We evaluated food availability each summer from 1991 to 1995 in 20 of the permanent plots of each site. Woody stems having twigs between 25 and 225 cm above ground were counted in the 5-m^2 area. Twigs from woody deciduous species were also counted and sorted by height class (25–75, 76–125, 126–225 cm). Finally, browsing intensity was evaluated based on proportion of browsed twigs. Because snowshoes hares rarely feed on balsam fir and black spruce, we excluded those species from our browse sampling as suggested by Carreker (1985) and Guay (1994).

Ground cover was estimated visually during vegetation sampling, whereas lateral foliage density was evaluated with a 2.5-m vegetation profile board (Nudds 1977). Lateral foliage density was measured in 1995 at 10 permanent points when deciduous leaves were present and absent. The board was held on the ground and observed from two points 15 m distant at 0° and 90°.

Pellet counts

Hare use of clearcuts was estimated annually from 1991 to 1996 by pellet counts within twenty 1 × 5 m plots, adjacent to browse sampling plots. Pellets were counted and cleared twice a year, in June and September.

Hare trapping and telemetry

In 1994 and 1995, trapping grids (90 × 120 m) were established in 11 of the 25 sites: 3 herbicide-release plantations, 3 manually released plantations, and 5 naturally regenerated clearcuts. Each grid equally overlapped a clearcut and a mature stand. In each grid, 20 live traps (23 × 23 × 80 cm) were placed at 30-m intervals.

Collar-mounted transmitters (MI-2 Holohil, 38 g) were attached to adult hares only. The locations were determined by triangulation using a portable tracking system. Each hare was located once or twice a day. The home range size was estimated with McPAAL 1.21 (Stüwe and Blohowiak 1985), using the minimum convex polygon (95% closest locations) and the harmonic mean (95%, 75%, and 50% probabilities). A plot of the home range size against the number of cumulated successive locations was made for each hare, and only animals having an asymptotic curve were retained for statistical analyses (Ferron et al. 1994).

Refuges

Habitats used by radiotracked hares were described using 115 circular plots (5-m radius) established at 50-m intervals along transects crossing each of them. A visual estimate of ground cover was made for trees, shrubs, and herbs ≤50 cm tall and for logging debris. The percentage of the ground covered by the 126–250 cm vegetation stratum, the closure of the canopy, and the lateral foliage density were also visually estimated.

For data analysis, plots were sorted into four habitat types: recent clearcuts (6–10 years old), mature forest – clearcut edges, mature forest stands (>1 ha), and residual tree thickets (<1 ha). The oldest clear-cut areas used by radiotracked hares (10 years old) were located on an experimental forest adjacent to public land. Forest–clearcut edge was defined as a 30-m strip, overlapping equally uncut mature forest and recent clearcuts. Residual tree thickets were composed of a group of living trees left on the site at the time of harvest or of a group of trees killed by spruce budworm. In both cases, those thickets had a dense low understory of balsam fir.

To examine if habitat use differed among cover types, we computed a selection index (R_h) for each habitat type (h):

$$R_h = \frac{\text{\% of the locations in habitat } h}{\text{\% of the area of habitat } h \text{ with in the home range}}$$

Statistical analysis

Vegetation characteristics, lateral foliage density, and availability of browse were compared among treatments using a one-way ANOVA and multiple comparisons among means were done using Sheffé's F test. Differences in vegetation characteristics and availability of browse between years were examined with a t test for paired samples. A Mann–Whitney U test was performed to compare home range sizes and utilization of different habitat types between males and females. Also, to determine if the expected number of hare locations differed significantly from the occurrence of habitat types, we performed a goodness-of-fit test for each animal with the R index. When the null hypothesis was rejected and that sample size was considered sufficiently large, we used the Bonferonni normal statistics to test for preference of individual habitats (P = 0.05) (Neu et al. 1974).

Results

Vegetation control effectiveness

Before treatments (1992), the stem density of the most common competing species differed between plantations and naturally regenerated clearcuts. White birch density (stems/ha) was higher (P = 0.03) in naturally regenerated clearcuts than in plantations, while raspberry shrubs were more abundant (P = 0.03) in plantations (Fig. 2). These differences were probably caused by the scarification that can kill advance hardwood regeneration and enhance germination of buried seeds for species like raspberry (Gouvernement du Québec 1996; Lautenschlager 1997).

The herbicide release effectively reduced angiosperm competition. By the third growing season after release, herbicide-treated plantations still differed clearly from the two other regeneration scenarios with respect to hardwood competition; white birch density on those sites was six and eight times lower than in manually treated plantations and naturally regenerated clearcuts, respectively (P < 0.001) (Fig. 2). The average height and the percentage of ground cover of white birch were also significantly lower in herbicide-treated plantations (P < 0.001) (Fig. 2).

The manual release was less effective than the herbicide release in reducing competition because of the sprouting of hardwoods so that treatment had nearly no effect on stem density. White birch ground cover was reduced by 50% the first growing season as compared with pre-treatment, but this reduction was no longer perceptible after 3 years. The third year post-treatment, white birch was as tall as the softwood species on manually treated plots (Fig. 2).

Despite apparent differences in the effects of the two release methods, it is still too soon to know if the growth of the planted spruce will differ significantly among treatments, but other authors suggest that they will, with the highest growth observed on herbicide-treated sites and the lowest on controls (Lautenschlager et al. 1998).

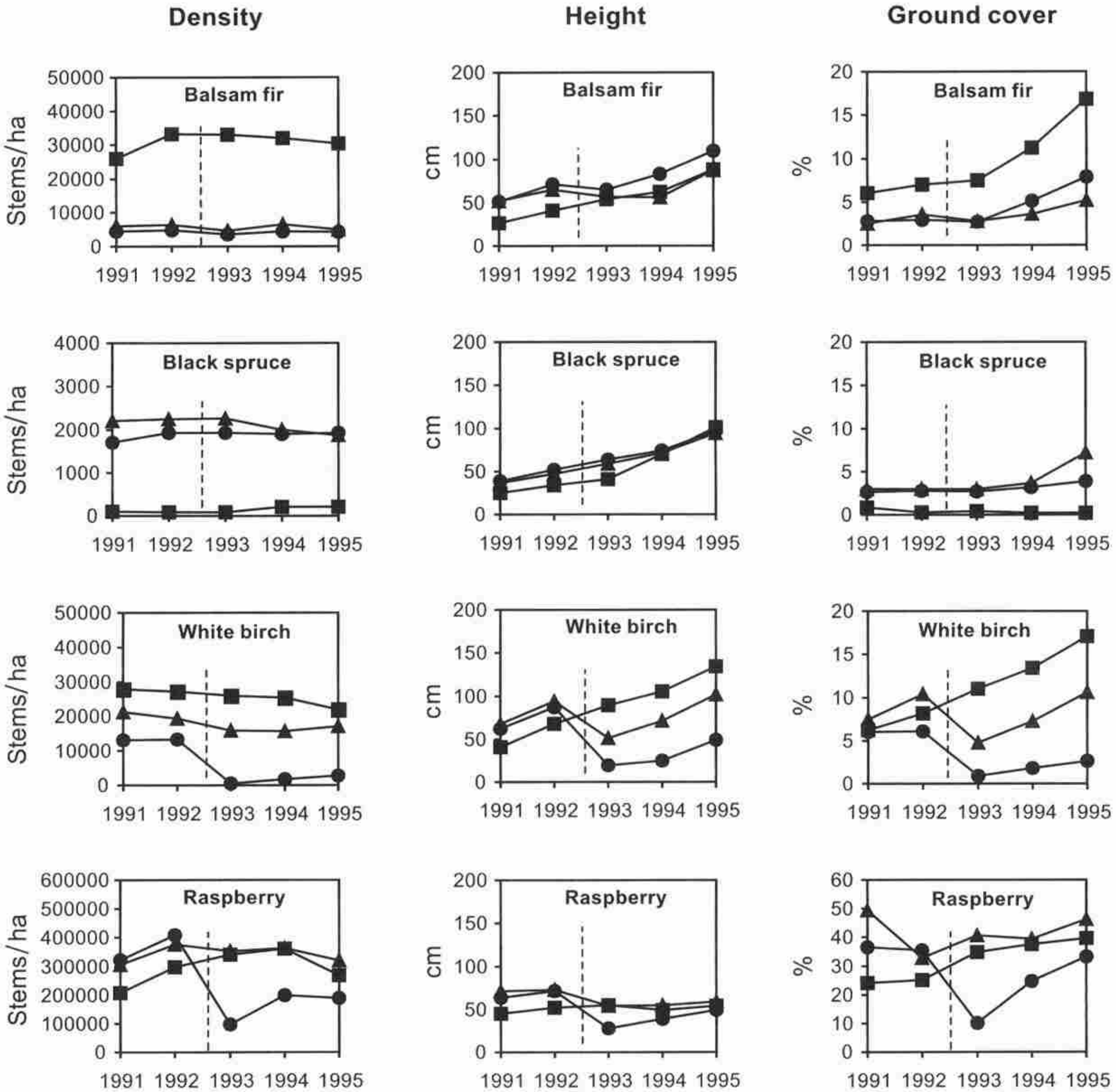
Habitat use

Fecal pellet counts showed that hare rarely used our experimental sites, 7–9 years after clear-cutting. Since the summer of 1992, pellets have been found in only 5% of the plots of each treatment for any season. In 1996, the greatest density of pellets (216 pellets/ha per month) was found in winter in naturally regenerated clearcuts. This same year, pellet densities in both types of plantations were lower than 44 per hectare per month in any season. In comparison, Darveau et al. (1998) observed a density of 800 pellets/ha per month in mature forest strips (>300 m wide) located on our study area during the winter of 1996.

Browse availability and use

In all our control and treated sites, hares never fed on softwood twigs and browsed less than 1% of all deciduous twigs

Fig. 2. Mean density (stems/ha), height (cm), and ground cover (%) of the most common competitive species, white birch and raspberry, and of the coniferous species, balsam fir and black spruce, in naturally regenerated clear-cut sites (■, n = 15), manually released plantations (▲, n = 5), and herbicide-released plantations (●, n = 5) in a boreal balsam fir forest, south-central Quebec, 1991–1995. Naturally regenerated sites were clear-cut between 1987 and 1989. Plantations were clear-cut in 1987, planted with black spruce in 1990, and released in August of 1992 (---).



available each year. This observation, added to the pellet index, confirms a very low utilization of our sites by hares.

The density of deciduous stems decreased after treatment in manually treated plantations but was comparable with that of the naturally regenerated clearcuts after 3 years (~25 000 stems/ha) (Fig. 3). The density of twigs in the 76–125 cm layer remained significantly lower in the former ($P < 0.001$) (Fig. 4). Very little browse was available in herbicide-released plantations, even after 3 years (Figs. 3 and 4).

Cover

In winter, conifer ground cover (126–250 cm) was less than 10%, and the overall lateral foliage density (0–250 cm) was lower than 50% for all regeneration methods (Table 1, Fig. 5). In the three higher classes (101–250 cm), lateral foliage density in naturally regenerated clearcuts was significantly greater than in plantations ($P < 0.001$) (Fig. 5). In summer, average visual obstruction in naturally regenerated clearcuts was 60%, which was significantly greater than that measured in plantations ($P < 0.001$) (Fig. 5).

Trapping and telemetry

A total of 12 adult hares were trapped during the summers of 1994 and 1995. Two individuals were caught at the periphery of one of the three herbicide-treated plantations (PL3), whereas none could be trapped in the three manually treated plantation. Three hares were captured at the edge of a naturally regenerated site clear-cut in 1988 (NR3), whereas the seven others were trapped in a naturally regenerated site clear-cut in 1987 (NR10). Nine hares (five males, four fe-

Table 1. Ground cover (%) of trees according to three height classes, in naturally regenerated sites (n = 15), manually (brushsaw) released plantations (n = 5), and herbicide-released plantations (n = 5) in a boreal balsam fir forest, south-central Quebec.

	Cover (%)			
Height classes	Naturally regenerated sites	Brushsaw-released plantations	Herbicide-released plantations	P
Coniferous trees				
0–25 cm	3.5±1.8*a*	1.0±0.5*b*	0.7±0.7*b*	0.001
26–125 cm	11.5±7.7	6.5±3.6	8.0±3.3	0.27
126–250 cm	6.6±5.0	2.0±1.2	4.7±2.5	0.12
Deciduous trees				
0–25 cm	2.1±1.1	2.2±0.4	1.7±0.4	0.60
26–125 cm	9.2±3.3*a*	11.2±3.0*a*	2.7±0.4*b*	<0.001
126–250 cm	12.7±5.3*a*	5.8±2.3*b*	0.4±0.5*b*	<0.001

Note: Values are means ± SE. Naturally regenerated sites were clear-cut between 1987 and 1989. Plantations were clear-cut in 1987, planted in 1990, and released in August of 1992. These data were gathered in 1995, three growing seasons after releases. One-way ANOVA was performed and multiple comparisons among means were done using Sheffé's F test. Values followed by the same letter or no letter are not statistically different.

Fig. 3. Mean density of deciduous stems (stems/ha) having twigs between 25 and 225 cm aboveground in naturally regenerated clear-cut sites (■, n = 15), manually released plantations (▲, n = 5), and herbicide-released plantations (●, n = 5) in a boreal balsam fir forest, south-central Quebec, 1991–1995. Naturally regenerated sites were clear-cut between 1987 and 1989. Plantations were clear-cut in 1987, planted with black spruce in 1990 and released in August of 1992 (---).

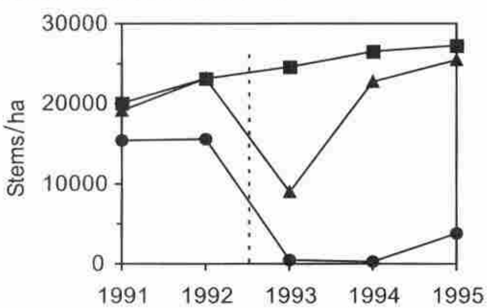
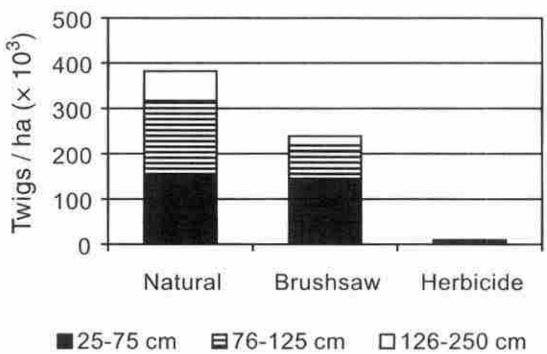


Fig. 4. Mean density of deciduous twigs (twigs/ha) for three height classes in naturally regenerated clear-cut sites (n = 15), manually (brushsaw) released plantations (n = 5) and herbicide-released plantations (n = 5) in a boreal balsam fir forest, south-central Quebec. Naturally regenerated sites were clear-cut between 1987 and 1989. Plantations were clear-cut in 1987, planted with black spruce in 1990, and released in August of 1992. These data were gathered in 1995, three growing seasons after releases.



males) were radiotracked for an entire summer. Mean home range size for males was large (19 ha) and significantly greater than that for females (5 ha) (Table 2).

Refuges

Every habitat type was used significantly more than expected by at least one hare (Table 3). However, in a landscape largely dominated by recent clearcuts, presence of hare was clearly linked with the presence of residual forest. Patches of residual forest (mature forest + forest tree thickets + half of the forest–clearcut edge area) occupied at least 25% of the area of the home range of each hare, except for one female (No. 4) (Table 3). This animal had the smallest home range (3 ha) and spent the summer in a very well regenerated clearcut surrounded by mature forest (NR 10) (Fig. 6). This site was used by five hares and had an exceptional growth compared with the 14 other naturally regenerated clearcuts studied. The proportion of residual forest found in the home range of the four hares living near the other sites ranged from 35 to 55% (Table 3).

The variables that appeared to be critical in the selection of a refuge by the snowshoe hare were the percentage of the ground covered by the 126–250 cm vegetation stratum and the percentage of lateral visual obstruction between 0 and 250 cm (Table 4). If edges, which have a very variable structure, are not taken into account, every type of habitat positively selected by hares had a 126–250 cm stratum ground cover >40% and a percentage of lateral obstruction >85% (Table 4). The composition of the understory and the amount of woody debris did not seem to influence the selection of a refuge.

Discussion

A seedling stage longer than expected

Clearcuts at the seedling stage are avoided by snowshoe hares (Conroy et al. 1979; Scott and Yahner 1989; Ferron et al. 1998). Many authors (Wolff 1980; Buehler and Keith

Table 2. Home range sizes (ha) of snowshoe hares radiotracked in 1994 or 1995 on the study area, in a boreal balsam fir forest, south-central Quebec.

					Home range size (ha)			
					Convex	Harmonic mean		
Hare No.	Sex	Capture site	Year	Locations	polygon 95%	95%	75%	50%
1	F	NR10	1994	61	6.6	8.1	2.4	1.1
2	F	NR10	1994	62	6.6	7.3	2.7	0.4
3	M	NR10	1994	63	34.0	37.9	8.9	1.5
4	F	NR10	1995	31	2.8	3.0	0.1	0.1
5	M	NR10	1995	11	—	—	—	—
6	F	NR3	1994	54	4.4	5.0	1.8	0.9
7	M	NR3	1994	59	19.4	18.8	11.1	4.5
8	M	NR3	1995	31	12.0	6.6	4.7	1.3
9	M	PL3	1994	59	12.0	15.9	3.5	1.2
Mean home range size (ha), ±SE					12.8±10.2	12.8±11.5	4.4±3.7	1.4±1.3
Male's mean home range size (ha), ±SE					19.4±10.4*a*	19.8±13.1	7.1±3.6*a*	2.1±1.6*a*
Female's mean home range size (ha), ±SE					5.1±1.9*b*	5.9±2.3	1.8±1.2*b*	0.6±0.4*b*
P					0.019	0.083	0.021	0.021

Note: The capture sites were two naturally regenerated stands, NR3 and NR10, clear-cut respectively in 1988 and 1987 and a plantation, PL3, clear-cut in 1987, planted with black spruce in 1990, and released with herbicide in 1992. To compare home range size between males and females, means and standard errors (SE) of the home range for each sex are also presented with their associated probability (P). Home range sizes were calculated with the convex polygon method using 95% of all locations and the harmonic mean method for which 95, 75, and 50% of the total number of points were included. For both methods, home range sizes for males and females were compared using a Mann–Whitney U test. Values followed by the same letter or no letter are not statistically different.

Table 3. Habitat selection ratios (R) of radiotracked snowshoe hares in four habitat types found in the surroundings of the three capture sites, in a boreal balsam fir forest, south-central Quebec.

				Habitat type												
Hare		Capture		Recent clearcut (6–10 years old)			Mature stand			Forest–clearcut edge			Thicket of residual trees			Total residual forest[e]
no.	Sex	site	N^a	U^b	A^c	R^d	U	A	R	U	A	R	U	A	R	A
1	F	NR10	61	88	62	1.4*	5	15	0.3	7	23	0.3	0	0	—	27
2	F	NR10	62	78	62	1.3*	6	8	0.8	16	30	0.5	0	0	—	23
3	M	NR10	63	30	9	3.3*	11	66	0.2	51	23	2.2*	8	2	4.0	80
4	F	NR10	31	94	86	1.1	0	4	0	6	10	0.6	0	0	—	9
5	M	NR10	11	82	—		9	—		9	—		0	—		—
6	F	NR3	54	4	11	0.4	13	21	0.6	83	68	1.2*	0	0	—	55
7	M	NR3	59	0	40	0.0	41	15	2.7*	51	32	1.6*	8	13	0.6	44
8	M	NR3	31	6	33	0.2	23	33	0.7	32	25	1.3	39	9	4.3*	55
9	M	PL3	59	20	62	0.3	5	13	0.4	4	4	1.0	71	21	3.4*	36

Note: The capture sites were two naturally regenerated stands, NR3 and NR10, clear-cut respectively in 1988 and 1987 and a plantation, PL3, clear-cut in 1987, planted with black spruce in 1990, and released with herbicide in 1992. The habitat selection ratio is the proportion of locations made in one habitat (use) on the proportion of the home range occupied by this type of habitat (availability).

[a]N, Number of locations.

[b]U, Use (percentage of the locations made in this type of habitat).

[c]A, Availability (percentage of the home range occupied by this type of habitat). Home range size was calculated with the convex polygon method using 95% of all locations.

[d]R, use/availability (ratio with an asterisk indicates that, according to the Bonferonni normal statistic, this type of habitat was used significantly more than expected ($\alpha = 0.05$)).

[e]The availability of residual forest within the home range was calculated by summing the percentage of availability of mature stands and residual tree thickets and half the percentage of availability of forest–clearcut edges.

1982; Wolfe et al. 1982; Parker 1984; Litvaitis et al. 1985; Monthey 1986; Sullivan and Moses 1986; Koehler 1991; Ferron et al. 1996), suggest that snowshoe hare abundance is strongly correlated with regenerating softwood stands 2–5 m tall, which provide plenty of food in winter and a good cover year round. In a spruce–fir forest of northern Maine, this vegetation structure corresponding to the sapling stage appeared 3–5 years after clear-cutting (Titterington et al. 1979). In the same study area, Burgason (1977) observed that hares began to colonize clearcuts 6 or 7 years after clear-cutting. In this study, contrary to our expectations, 7- to 9-year-old regenerating stands were still at the seedling stage and were avoided by snowshoe hare, regardless of time of year.

In Quebec, Guay (1994) found that a stand reaches maximum browse value for snowshoe hares when density of de-

Fig. 5. Means and standard errors (SE) of the lateral visual obstruction (%) for five height classes and the overall mean density during summer (*a*) and winter (*b*) in naturally regenerated clear-cut sites (n = 15), manually released plantations (n = 5), and herbicide-released plantations (n = 5) in a boreal balsam fir forest, south-central Quebec. Naturally regenerated sites were clear-cut between 1987 and 1989. Plantations were clear-cut in 1987, planted in 1990, and released in August of 1992. These data were gathered in 1995, three growing seasons after releases.

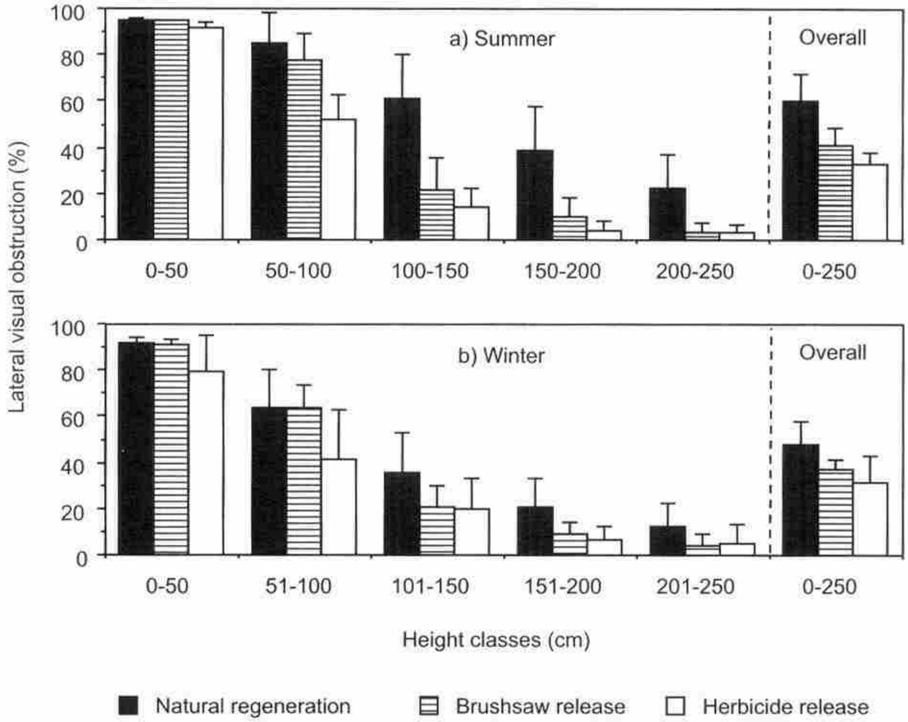


Fig. 6. Maps showing the spatial distribution of the four different habitat types around the three trapping grids where hares have been captured in 1994 and 1995 on the study area, in a boreal balsam fir forest, south-central Quebec. The home range of each individual is delimited by a convex polygon using 95% of all locations. Two other grids where no hares were trapped are also shown (NR1 and NR7).

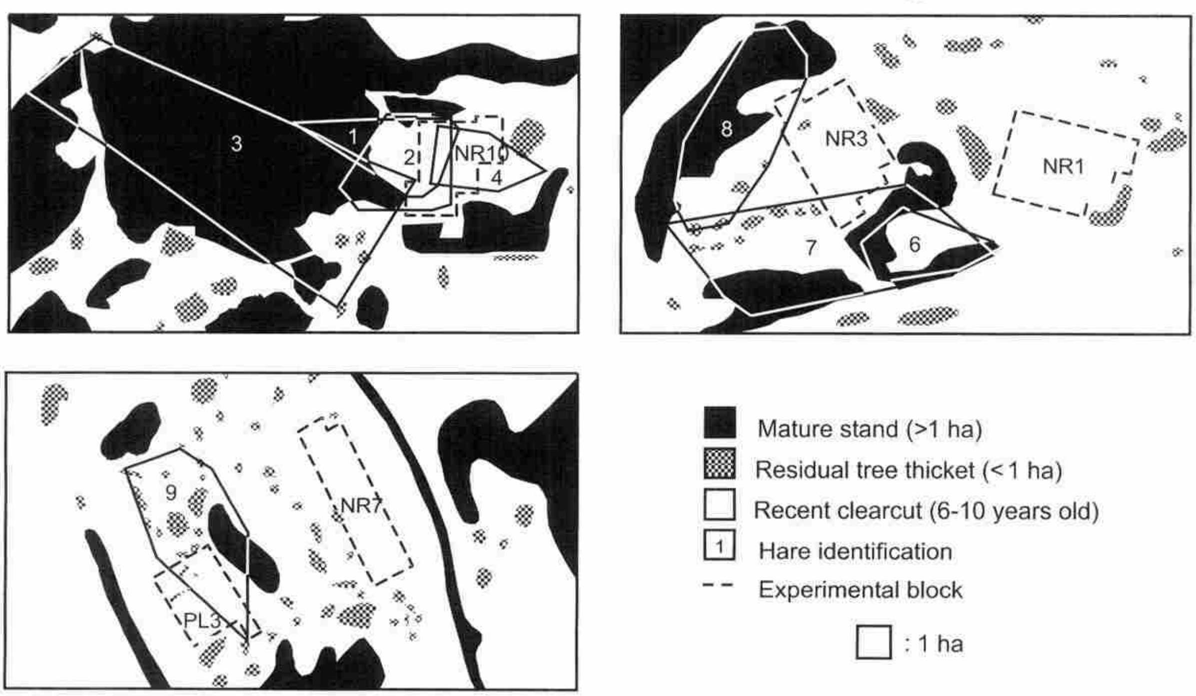


Table 4. Cover variables measured in four habitat types used in summer by radiotracked snowshoe hares in the surroundings of the three capture sites, in a balsam fir forest, south-central Quebec, 1994–1995.

Habitat type	Capture site	No. of plots	Slash debris cover (%)	Understory cover (126–250 cm) (%)	Canopy closure (%)	Lateral foliage density (0–250 cm) (%)
Recent clearcut	PL 3	11	11.0±6.9	6.4±3.0	0.0±0.0	64.3±18.7
(6–10 years old)	NR 3	13	17.8±10.1	7.0±3.8	0.0±0.0	61.6±14.3
	NR 10	13	11.7±8.7*	44.7±16.1*	0.0±0.0*	92.7±5.1*
Mature stand	PL 3	3	45.5±17.3	25.5±17.3	68.8±20.8	87.8±6.8
	NR 3	29	9.3±4.9*	46.9±16.8*	33.1±12.4*	87.8±10.8*
	NR 10	18	26.1±12.1	27.2±11.0	70.5±16.9	77.5±14.4
Forest–clearcut edge	PL 3	3	58.8±11.6	55.5±36.1	8.8±5.8	88.8±9.1
	NR 3	12	13.0±11.4*	22.2±17.8*	11.3±11.5*	66.0±25.9*
	NR 10	3	15.5±0.0*	35.5±17.3*	32.2±28.9*	91.2±7.5*
Residual trees thicket	PL 3	6	38.8±18.6*	63.8±19.4*	17.0±25.6*	94.3±2.4*
	NR 3	3	12.2±5.8*	38.8±20.8*	62.2±15.3*	84.8±5.0*
	NR 10	1	25.5	45.5	45.5	95.5

Note: The capture sites were two naturally regenerated stands, NR3 and NR10, clear-cut respectively in 1988 and 1987 and a plantation, PL3, clear-cut in 1987, planted with black spruce in 1990, and released with herbicide in 1992. The four cover variables estimated in 5-m radius circular plots (n = 115) were the ground cover (%) of slash debris, the ground cover (%) of the understory in the 126–250 cm layer, the canopy closure (%), and the lateral foliage density (%) between 0 and 250 cm aboveground. The values with asterisks are associated with a type of habitat that was used significantly more than expected (α = 0.05) according to the Bonferonni normal statistic (see Table 3).

ciduous stems with twigs between 0.5 and 3 m aboveground is greater than 14 000 stems/ha; stands with less than 4000 deciduous stems/ha are unattractive. Based on those criteria, woody food supply was lacking on our herbicide released plantations but would have been adequate to attract hare on controls and on manually released plantations. However, since snow depth on our study area can reach an average of 1.40 m for a 4-month period, most of the browse available may have been inaccessible for several months anyway (Fig. 5).

Our experimental sites were also avoided by hares in summer, even though there was plenty of forage available. The critical variable influencing habitat use would then be the lack of cover, as suggested by several authors (Bider 1961; Conroy et al. 1979; Wolff 1980; Buehler and Keith 1982; Wolfe et al. 1982; Litvaitis et al. 1985; Monthey 1986; Litvaitis 1990). According to the literature, snowshoe hare use habitats with lateral foliage density ranging from 69 to 90% in summer (0–2.5 m) (Ferron and Ouellet 1992; Ferron et al. 1994) and greater than 40% above the snow surface in winter (1–2.5 m) (Wolfe et al. 1982). Our sites did not reach these values and, therefore, still cannot provide suitable protective cover for snowshoe hares (Fig. 6).

Thus, despite the use of clear-cutting with regeneration and soil protection to shorten the time of rotation by protecting advance regeneration, our sites were still in the seedling stage 7–9 years after cutting. The severe climate conditions found in humid balsam fir boreal forests could explain this delay since the growing season is rather short, about 120 days. The fact that our sites originate from second-growth forests could also have lengthened the seedling stage. It seems that due to the relatively short rotation ages that are presently used, advance regeneration is often less abundant than in virgin forests (Déry 1995).

In boreal balsam fir ecosystems, it will take more than 10 years for a clear-cut patch to become suitable habitat for the snowshoe hare. Because snow cover in our study area can be very deep for several months, our sites may not begin to provide good cover in winter until conifers reach 4 m in height. It takes 15–22 years for balsam fir to reach this height (Zarnovican 1983), whereas 18–30 years are necessary for black spruce (Carpentier et al. 1993). A study conducted in Forêt Montmorency, Laval University's experimental forest adjacent to our study area, supports this hypothesis showing that hare density was significantly higher in 20- to 25-year-old stands than in those 10–15 or 50 years old, both in summer and winter (Alvarez 1996). The snowshoe hare can then be considered as a mid-successional species in the humid balsam fir boreal forest, where the age of rotation is about 50 years.

Comparison of regeneration scenarios

The three regeneration scenarios could not be compared as to their effects on the length of the seedling stage, because contrary to our expectations, the snowshoe hare was still avoiding our sites at the time of the study. However, the seedling stage could be lengthened in plantations because softwood density and cover were lower on scarified and reforested sites than in controls, and the planted species, black spruce, grows more slowly than balsam fir.

Importance of refuges

If clear-cut areas are avoided by the snowshoe hare for several years, it becomes obvious that maintaining a hare population on cutover forest land will depend essentially on the presence of refuges. These refuges will prevent local extinction and provide the stock for a subsequent population increase (Wolff 1980). The critical refuges for hares are the ones used in winter or when population densities are low (Keith 1966; Wolff 1980).

The absolute density of hares on the study area is unknown, but statistics of hunting success from the Saguenay –

Lac-St-Jean region, located 100 km north of our study area, suggest that populations were at a high level at the time of harvest (1987–1989) and at a low level at the time of the study (Courtois and Potvin 1994; F. Potvin, ministère de l'Environnement et de la Faune du Québec, unpublished data). Those indications, added to our poor trapping success, suggest that habitat utilization was not influenced by population densities and that refuges used by hares were the critical ones.

It is not clear, however, if the low population density observed during our study was caused by a cyclic fluctuation or by habitat alteration. Many authors have observed noncyclic populations of hares in fragmented areas where only scattered islands of suitable habitat were available (Dolbeer and Clark 1975; Wolff 1980; Buehler and Keith 1982; Keith et al. 1993), and perhaps, the population cycle of hares could be interrupted or altered by commercial clear-cutting.

In pristine boreal balsam fir forest, recurrent spruce budworm outbreaks and windfalls created a forest mosaic by naturally breaking up the landscape (Leblanc et al. 1995). Forest harvesting, however, leads to a much more homogeneous landscape. Even though the maximal size of a clearcut has been limited to 150 ha since 1996, clearcuts are still distributed in a clustered pattern and residual forest is present mostly as buffer strips. In such a landscape, hares were found only where there was residual forest, i.e., mature stands and groups of residual tree thickets. Mature stands served as shelters and corridors, whereas their edges were intensively used because of the presence of food. All hare refuges in summer had in common a good protective cover, with a ground cover of the 1.26–2.5 m layer higher than 40% and a lateral foliage density above 85%. This last result agrees with other studies mentioning that an optimal habitat for the snowshoe hare has a lateral foliage density higher than 85% (Ferron and Ouellet 1992; Carreker 1985). We can also point out that, with the exception of one hare, residual forest occupied more than one quarter of the summer home range of all individuals.

Management implications

In the humid boreal balsam fir forest, snowshoe hare avoid clear-cut areas for several years, no matter what regeneration method is used. In a landscape homogenized by clear-cutting, the only refuges available for at least 10 years after logging are the small islands of residual forest. We noticed that stands more than 25 years old can shelter hares all summer long, and a study conducted in the same area showed that they are also intensively used in winter (M. Whiteside, unpublished data).

Thus, the preservation of patches of residual forest in the humid boreal balsam fir forest region is essential to support local hare populations in a area dominated by clearcuts. Patch retention harvesting, as proposed by Coates and Stevenson (1994), would be in this context an appropriate silvicultural system. Our methodology does not allow the precise assessment of the proportion of forest and residual tree thickets that should be protected. However, our results indicate that summer habitat of the snowshoe hare during the seedling stage was composed of at least 25% of remaining coniferous forest while the proportion of residual forest left over the entire study area was less than 20%.

The ideal mitigation measure of a lengthened seedling stage would be the adoption of a silvicultural system that more closely emulates the natural disturbance pattern of balsam fir forests. This is the strategy that has been adopted in the Forêt Montmorency (Bélanger 1992). The principles guiding landscape management in this experimental forest are to maintain young successional stages (<20 years old) in a sub-dominant position within small landscape units (3–10 km^2) and to use a diversity of clearcut sizes.

Finally, because the snowshoe hare is an important link in the food chain, its habitat needs are well known, and its monitoring can be simple and inexpensive, we suggest that it could become an indicator species for the landscape management of the boreal balsam fir ecosystem.

Acknowledgments

This study was funded by the ministère des Ressources naturelles du Québec and the ministère de l'Environnement et de la Faune du Québec, with contributions from the Daishowa Company and Laval University. S. de B. benefited from a M.Sc. scholarship from the Fonds pour la formation de chercheurs et l'aide à la recherche. We are grateful to all the people who helped with the fieldwork: É. Alvarez, M. Bolduc, C. Bouliane, J. Bouliane, M.-C. Dansereau, S. Lamarre, S. Lauzier, D. Leblanc, S. Lemay, S. Marcotte, P. Matthieu, G. Parent, and F. Zwarts. We also thank J. Ferron, R.A. Lautenschlager, E. Board, and three anonymous reviewers for their helpful comments on earlier versions of this paper.

References

Alvarez, É. 1996. La forêt mosaïque: une alternative d'aménagement pour le maintien de la martre dans la sapinière boréale? M.Sc. thesis, Université Laval, Sainte-Foy, Que.

Ansseau, C., Bélanger, L., Bergeron, J.-F., Bergeron, Y., Bouchard, A., Brisson, J., DeGranpré, L., Gagnon, G., Grondin, P., Lavoie, C., Lessard, G., Payette, S., Richard, P.J.H., Saucier, J.-P., Sirois, L., and Vasseur, L. 1996. Écologie forestière. *In* Manuel de foresterie. Ordre des ingénieurs forestiers du Québec (O.I.F.Q), Presses de l'Université Laval, Sainte-Foy, Que. pp. 133–279.

Bélanger, L. 1992. La forêt mosaïque: une stratégie socialement acceptable pour la forêt boréale du Québec. Aubelle, **89**: 15–18.

Bider, J.R. 1961. An ecological study of the hare *Lepus americanus*. Can. J. Zool. **39**: 81–103.

Boutin, S., Krebs, C.J., Boonstra, R., Dale, M.R.T., Hannon, S.J., Martin, K., Sinclair, A.R.E., Smith, J.N.M., Turkington, R., Blower, M., Byrom, A., Doyle, F.I., Doyle, C., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D.L., Nams, V., O'Donoghue, M., Rohner, C., and Schweiger, S. 1995. Population changes of the vertebrate community during hare cycle in Canada's boreal forest. Oikos, **74**: 69–80.

Buehler, D.A., and Keith, L.B. 1982. Snowshoe hare distribution and habitat use in Wisconsin. Can. Field-Nat. **96**: 19–29.

Bureau d'audiences publiques sur l'environnement (BAPE). 1991. Des forêts en santé: rapport d'enquête et d'audience publique sur la Stratégie de protection des forêts. Commission sur la protection des forêts, Québec. Spec. Rep. 2.

Bureau d'audiences publiques sur l'environnement (BAPE). 1997. Programme de dégagement de la régénération forestière. Rapport d'enquête et d'audience publique n° 116. Commission sur la protection des forêts, Québec.

Burgason, B.N. 1977. Bird and mammal use of old commercial clearcuts. M.Sc. thesis, University of Maine, Orono.

Carpentier, J.-P., Lacombe, L., and Tardif, P. 1993. Modélisation de la croissance et du rendement des pessières noires au Québec. Ministère des Forêts, Direction de la recherche, Québec. Res. Rep. 108.

Carreker, R.G. 1985. Habitat suitability index models: snowshoe hare. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. Biol. Rep. 82 (10.101).

Coates, K.D., and Stevenson, J.D. 1994. Patch retention harvesting as a technique for maintaining stand level biodiversity in forests of north central British Columbia. *In* Innovative silvicultural systems in boreal forests. *Edited by* C.R. Bamsey. Canadian Forest Service, Edmonton, Alta. pp. 102–106.

Conroy, M.J., Gysel, L.W., and Dudderar, G.R. 1979. Habitat components of clear-cut areas for snowshoe hares in Michigan. J. Wild. Manage. **43**: 680–690.

Courtois, R., and Potvin, F. 1994. Résultats préliminaires sur l'impact à court terme de l'exploitation forestière sur la faune terrestre et ses utilisateurs en forêt boréale. Ministère de l'Environnement et de la Faune, Direction de la faune et des habitats, Service de la faune terrestre, Québec.

Darveau, M., Huot, J., and Bélanger, L. 1998. Riparian forest strips as habitat for snowshoe hare in a boreal balsam fir forest. Can. J. For. Res. **28**: 1494–1500.

Déry, S. 1995. Dynamique de l'enfeuillement après coupe de la sapinière boréale de seconde venue. M.Sc. thesis, Université Laval, Sainte-Foy, Que.

Dolbeer, R.A., and Clark, W.R. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. J. Wildl. Manage. **39**: 535–549.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Working Group of the Canada Committee on Ecological Land Classification. Environment Canada, Ottawa, Ont. Ecol. Land Classif. Ser. 23.

Environment Canada. 1993. Canadian climate normals, 1961–1990 (Quebec). Atmospheric Environment Service, Ottawa, Ont. Publ. Can. Climatol. Program 5.

Ferron, J., and Ouellet, J.P. 1992. Daily partitioning of summer habitat and use of space by the snowshoe hare in southern boreal forest. Can. J. Zool. **70**: 2178–2183.

Ferron, J., Potvin, F., and Dussault, C. 1994. Impact à court terme de l'exploitation forestière sur le lièvre d'Amérique en forêt boréale. Ministère de l'Environnement et de la Faune, Service de la faune terrestre, Québec.

Ferron, J., Couture, R., and Lemay, Y. 1996. Manuel d'aménagement des boisés privés pour la petite faune. Fondation de la faune du Québec, Sainte-Foy.

Ferron, J., Potvin, F., and Dussault, C. 1998. Short-term effects of logging on snowshoe hares in the boreal forest. Can. J. For. Res. **28**: 1335–1343.

Gagné, N., Bélanger, L., and Huot, J. 1999. Comparative responses of small mammals vegetation, and food sources to natural regeneration and conifer release treatments in boreal balsam fir stands of Quebec. Can. J. For. Res. **29**: 1128–1140.

Germain, G., Larue, P., Morasse, M., and Potvin, F. 1996. Aménagement de la faune et de ses habitats. *In* Manuel de foresterie. Ordre des ingénieurs forestiers du Québec (O.I.F.Q.), Presses de l'Université Laval, Sainte-Foy, Que. pp. 673–702.

Gouvernement du Québec. 1986. Guide des modalités d'intervention en milieu forestier. Ministère de l'Énergie et des Ressources, ministère de l'Environnement et ministère du Loisir de la Chasse et de la Pêche, Québec. Publ. 3214.

Gouvernement du Québec. 1994. Stratégie de protection des forêts. Ministère des Ressources naturelles, Québec.

Gouvernement du Québec. 1996. Biodiversité du mileu forestier: bilan et engagements du ministère des Ressources naturelles. Ministère des Ressources naturelles, Direction de l'environnement forestier, Québec. Publ. RN96-3045.

Guay, S. 1994. Modèle d'indice de qualité d'habitat pour le lièvre d'Amérique (*Lepus americanus*) au Québec. Ministère des Ressources naturelles, ministère de l'Environnement et de la Faune, Gestion intégrée des ressources, Québec. Tech. Doc. 93/6.

Hjeljord, O., Sahlgaard, V., Enge, E., Eggestad, M., and Grønvold S. 1988. Glyphosate application in forest—ecological aspects: VII. The effect on mountain hare (*Lepus timidus*) use of a forest plantation. Scand. J. For. Res. **3**: 123–127.

Keith, L.B. 1966. Habitat vacancy during a snowshoe hare decline. J. Wildl. Manage. **30**: 828–832.

Keith, L.B., and Cary, J.R. 1991. Mustelid, squirrel, and porcupine population trends during a snowshoe hare cycle. J. Mammal. **72**: 373–378.

Keith, L.B., Bloomer, S.E.M., and Willebrand, T. 1993. Dynamics of a snowshoe hare population in fragmented habitat. Can. J. Zool. **71**: 1385–1392.

Koehler, G.M. 1990. Population and habitat characteristics of lynx and snowshoe hare in north-central Washington. Can. J. Zool. **65**: 565–567.

Koehler, G.M. 1991. Snowshoe hare, *Lepus americanus*, use of forest successionnal stages and population changes during 1985–1989 in north-central Washington. Can. Field-Nat. **105**: 291–293.

Lautenschlager, R.A. 1993. Response of wildlife to forest herbicide applications in northern coniferous ecosystems. Can. J. For. Res. **23**: 2286–2299.

Lautenschlager, R.A. 1997. Effects of perturbations and stimulants on red raspberry (*Rubus idaeus* L.) seed germination. For. Chron. **73**: 453–457.

Lautenschlager, R.A., Belle, F.W., Wagner R.G., and Reynolds, P.E. 1998. The Fallingsnow Ecosystem Project: documenting the consequences of conifer release alternatives. J. For. **96**: 20–27.

Leblanc, M., Bégin, É., Bélanger, L., and Labbé, P. 1995. Paysages de la forêt primitive de la sapinière boréale humide. *In* Landscape ecology in land use planning. *Edited by* G. Domon and J. Falardeau. Polyscience Publications, Morin Heights, Que. pp. 221–227.

Litvaitis, J.A. 1990. Differential habitat use by sexes of snowshoe hares (*Lepus americanus*). J. Mammal. **71**: 520–523.

Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. J. Wildl. Manage. **49**: 866–873.

Monthey, R.W. 1986. Responses of snowshoe hares, *Lepus americanus*, to timber harvesting in northern Maine. Can. Field-Nat. **100**: 568–570.

Morel, S. 1996. L'intégration des préoccupations des trappeurs montagnais à l'aménagement des forêts du Québec. M.Sc. thesis, Université Laval, Sainte-Foy, Que.

Neu, C.W., Byers, C.R., and Peek, J.M. 1974. A technique for analysis of utilization–availability data. J. Wildl. Manage. **38**: 541–545

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. **5**: 113–117.

Parker, G.R. 1984. Use of spruce plantations by snowshoe hare in New Brunswick. For. Chron. **62**: 159–163.

Potvin, F., Courtois, R., and Bélanger, L. 1999. Short-term response of wildlife to clear-cutting in Quebec boreal forest : multiscale effects and management implications. Can. J. For. Res. **29** : 1120–1127.

Scott, D.P., and Yahner, R.H. 1989. Winter habitat and browse use by snowshoe hares, *Lepus americanus*, in a marginal habitat in Pennsylvania. Can. Field-Nat. **103**: 560–563.

Stüwe, M., and Blohowiak, C.E. 1985. McPAAL. Micro-computer programs for the analysis of animal locations. Mimeographed report. Conservation Research Center, Smithsonian Institute, Washington, D.C.

Sullivan, T.P. 1994. Influence of herbicide-induced habitat alteration on vegetation and snowshoe hare populations in sub-boreal spruce forest. J. Appl. Ecol. **31**: 717–730.

Sullivan, T.P., and Moses, R.S. 1986. Demographic and feeding responses of a snowshoe hare population to habitat alteration. J. Appl. Ecol. **23**: 53–63.

Thompson, I.D. 1988. Habitat needs of furbearers in relation to logging in boreal Ontario. For. Chron. **64**: 251–261.

Titterington, R.W., Crawford, H.S., and Burgason, B.N. 1979. Songbird responses to commercial clear-cutting in Maine spruce–fir forests. J. Wildl. Manage. **43**: 602–609.

Wolfe, M.L., Debyle, N.V., Winchell, C.S., and McCabe, T.R. 1982. Snowshoe hare cover relationships in northern Utah. J. Wildl. Manage. **46**: 662–670.

Wolff, J.O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecol. Monogr. **50**: 111–130.

Zarnovican, R. 1983. Production stationnelle dans les sapinières en Gaspésie, Québec. Env. Can. Serv. Can. For. Cent. Rech. For. Laurentides Inf. Rep. LAO-X-64.