Recovery time of snowshoe hare habitat after commercial thinning in boreal Quebec

Guylaine Bois, Louis Imbeau, and Marc J. Mazerolle

Abstract: As short-term effects of partial cuts generally decrease available cover for snowshoe hare (*Lepus americanus* Erxleben), most studies have shown negative effects of such treatments on this keystone species in boreal ecosystems. This study aims to determine the long-term impact of commercial thinning on snowshoe hare habitat, and we hypothesized that habitat quality, as well as habitat use, recovers with time since treatment. We selected stands aged 50–90 years dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) in Abitibi (Quebec). We used models of habitat parameters to explain the abundance of snowshoe hare tracks and pellets in 20 commercially thinned stands treated between 1989 and 1999 and 12 control stands. Lateral cover was the dominant parameter influencing snowshoe hare habitat use. On average, commercially thinned stands had a lower lateral cover than controls (–18%). We also found that snowshoe hare use of commercially thinned stands increases with time since treatment. However, 11–18 years are needed before commercially thinned stands return to the same level of lateral cover and snowshoe hare signs as control stands. Commercial thinning is generally followed by harvesting all merchantable stems 15 years after treatment. Thus, we suggest that commercial thinning as currently practiced should be avoided if the objective is to maintain quality habitat for snowshoe hare and its associated predators.

Résumé : Puisque les coupes partielles diminuent généralement à court terme le couvert latéral pour le lièvre d'Amérique (*Lepus americanus* Erxleben), la plupart des études récentes ont documenté les effets négatifs de ces traitements sur cette espèce-clé en milieu boréal. La présente étude visait à évaluer l'impact à moyen et à long terme des éclaircies commerciales sur l'habitat du lièvre d'Amérique en émettant l'hypothèse qu'il y a un rétablissement de la qualité d'habitat et des indices d'utilisation de celui-ci dans le temps. Dans des peuplements de 50 à 90 ans dominés par l'épinette noire (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) localisés en Abitibi (Québec), nous avons modélisé les indices de présence (crottins et pistes hivernales) de 20 sites éclaircis entre 1989 et 1999 et de 12 sites témoins selon différents paramètres d'habitat. Les résultats indiquent que le couvert latéral influence de façon prédominante l'utilisation des sites par le lièvre d'Amérique. Les sites éclaircis ont toutefois un couvert latéral moyen plus faible que les sites témoins (–18 %). Nous avons également observé que l'utilisation des éclaircies commerciales par le lièvre d'Amérique augmente avec le temps. Cependant, 11 à 18 ans sont nécessaires afin que le couvert latéral et les indices de présence du lièvre d'Amérique atteignent des niveaux équivalents à ceux des sites témoins. Comme l'éclaircie commerciale est suivie d'une coupe totale en moyenne 15 ans après l'intervention, nous considérons que l'éclaircie, telle qu'elle se pratique actuellement, ne devrait pas être utilisée si l'objectif principal est de maintenir des habitats de qualité pour le lièvre d'Amérique et ses prédateurs.

Introduction

Fire frequency, the primary natural disturbance in the North American boreal forest (Bergeron 1991; Johnson 1992; Payette 1992), has decreased since the beginning of the industrial era (Bergeron et al. 2001). As a consequence, the proportion of mature and overmature stands, including stands with an uneven structure, has increased (Bergeron et al. 2001; Bouchard et al. 2008). Under natural disturbance regimes, at least 50% of the boreal forest landscape in eastern Canada is made up of stands over 100 years old (Bergeron et al. 2001, 2006). Consequently, a forest management strategy that aims to reproduce the natural pattern of the boreal landscape should not only consist of clearcuts, which regenerate even-aged stands, but also contain a substantial proportion of partial cuts, which maintain or create uneven-aged stands (Bergeron 2004).

Partial cuts represented only 12% of harvested areas in 2009 in Canada, with selection cut, shelterwood harvest, and commercial thinning being the most common types of partial cuts (National Forestry Database Program 2009). The coniferous boreal forest of Quebec is a case in point, where 55% of the partially harvested area between 2000 and 2003 was commercially thinned (MRNF 2004). Despite the recent enthusiasm for commercial thinning, its impact on wildlife (especially game species) is still little understood (Bédard et al. 2003).

Received 19 July 2011. Accepted 5 November 2011. Published at www.nrcresearchpress.com/cjfr on 9 December 2011.

G. Bois and L. Imbeau. Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable et Centre d'étude de la Forêt, Département des sciences appliquées, Université du Québec en Abitibi-Témiscamingue, Centre d'Amos, 341 Principale Nord, Amos, QC J9T 2L8, Canada.
M.J. Mazerolle. Centre d'étude de la forêt, Département des sciences appliquées, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.

Corresponding author: Louis Imbeau (e-mail: louis.imbeau@uqat.ca).

The snowshoe hare (*Lepus americanus* Erxleben) occupies various habitats with dense lateral cover throughout the boreal forest, regardless of the plant species making up this cover (Litvaitis et al. 1985; Litvaitis 1990; Ferron and Ouellet 1992). As the abundance of snowshoe hares also influences the abundance of many predators (Boutin et al. 1995; Krebs et al. 2001), snowshoe hare is considered to be a keystone species in boreal forest ecosystems (Boutin et al. 1995; Krebs et al. 1995). Consequently, a silvicultural treatment that negatively affects snowshoe hare will also negatively affect many other species, including furbearing mammals (Etcheverry et al. 2005).

Studies in the mixed forests of Maine show that, in the short term, snowshoe hares are found in partial cut areas, but at lower densities than in control areas (Fuller and Harrison 2005). In contrast, studies in the coniferous forest of Quebec show that in the short term, snowshoe hares are nearly absent from areas where 45%–50% of the commercial volume has been harvested (Valois 2005). This can likely be explained by the significant reduction in lateral cover that follows partial harvest, as similar results are often reported following precommercial thinning in younger stands (Homyack et al. 2007; Sullivan et al. 2007).

Commercial thinning might have little impact on snowshoe hares if there is considerable residual cover after treatment. Partial cuts open up the canopy, resulting in increased levels of sunlight reaching the forest floor, which in turn generally increases the growth rate of the regeneration (Darveau et al. 1998; Fuller et al. 2004; Hanley 2005). Therefore, the initial negative effect of lateral cover reduction on snowshoe hares due to partial cutting should be reduced in the first years following harvest. However, this cannot currently be confirmed, as no studies have looked at the long-term effect of partial cuts on mammals (Thompson et al. 2003; Vanderwel et al. 2009).

To confirm that coniferous stands that have been commercially thinned maintain critical habitat components for snowshoe hare, we first compared habitat variables in commercially thinned and control stands. We also examined whether there were differences in snowshoe hare abundance (evaluated via pellets and snow tracks) between these two stand types. Finally, we hypothesized that habitat quality (vegetation cover) as well as abundance of snowshoe hares in the commercially thinned stands would increase over time.

Methods

Study area

This study took place in Abitibi-Témiscamingue in northwestern Quebec, Canada (48°34′N, 78°08′W) (Fig. 1), in the western white birch – fir bioregion (Thibault and Hotte 1985). Forest stands are composed of balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), jack pine (*Pinus banksiana* Lamb.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.) (Grondin 1996). Average annual snow precipitation is 300 cm (Environment Canada 2008). During the 10-year population cycle of snowshoe hare in the boreal forest, abundance can vary widely (Wolff 1980; Hodges 1999; Krebs et al. 2001). In Abitibi-Témiscamingue, the Department of Natural Resources and Wildlife has been systematically collecting data since 1998 and the results indicate that the last population maximum was in 2001–2002 (MRNF, unpublished results). Assuming a 10-year cycle, the snowshoe hare population was probably at its minimum or at the beginning of its recovery during our study in 2006–2007.

All study sites were dominated by black spruce, classified as 50–90 years old according to provincial forest maps and likely originated from forest fires. Treated stands had been commercially thinned between 1989 and 1999 (N = 20) (Fig. 2*a*). Commercial thinning in Quebec removes approximately 25%–35% of the merchantable basal area of a stand. It is applied to even-aged stands 15 years before they reach maturity, and the basal area removed in the skid trails must not exceed 15% of the initial basal area of the stand (MRNF 2005). Our study area was in public forest with different forestry companies carrying out commercial thinning operations. Control stands (N = 12) (Fig. 2*b*) had the characteristics of stands eligible for commercial thinning according to Quebec regulatory requirements. Stands were at least 500 m apart to minimize the probability that snowshoe hare home ranges (17 ha in coniferous boreal forest (Ferron et al. 1998)) would overlap more than one site. Because we were limited by winter access to certain sites, distribution of control and treated sites was not random.

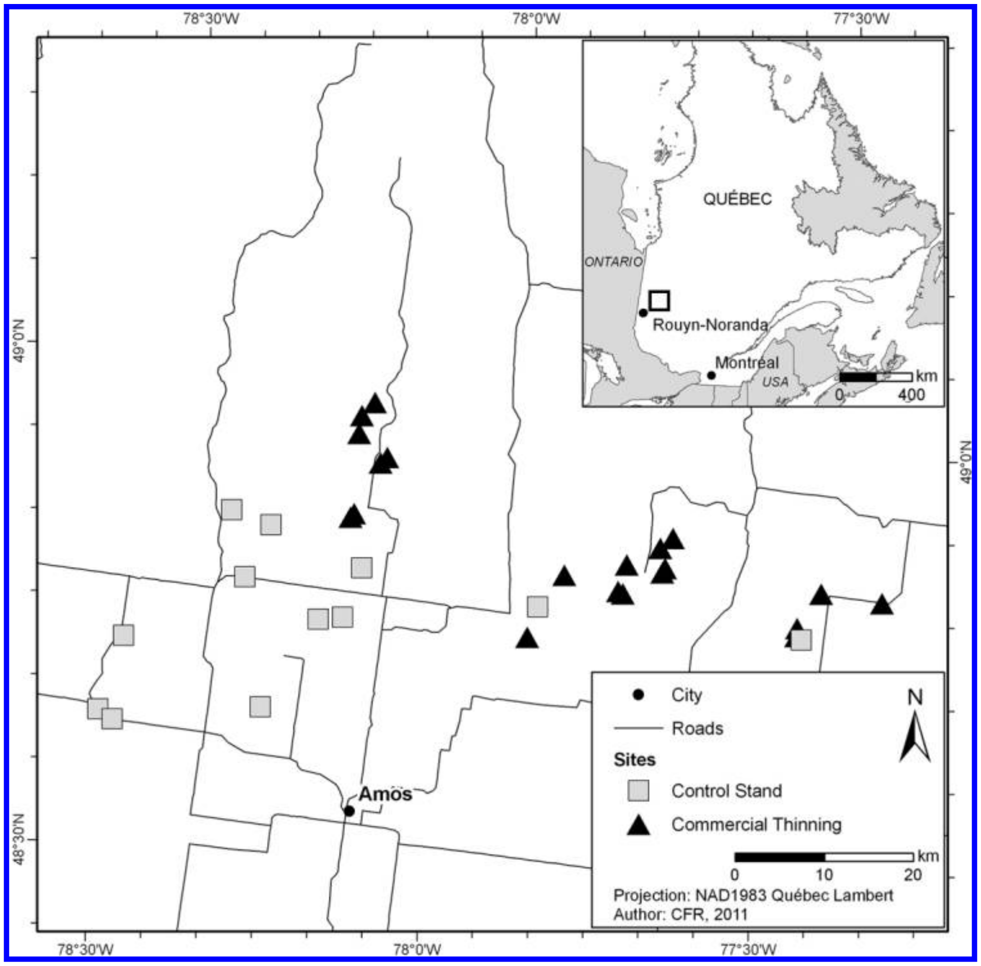
Habitat parameters

Inside each stand, six or seven sampling stations were established every 25 m along a single linear transect (Fig. 3*a*), or when the shape of the stand could not accommodate a single transect, we used two parallel transects spaced at least 50 m from one another (Fig. 3*b*) to minimize the probability that the same snowshoe hare trail would be counted twice (Ausband and Baty 2005). These transects were established perpendicular to skid trails and at least 50 m from the stand edge to reduce edge effects.

At each sampling station, basal area, lateral cover from 0 to 2 m, vertical shrub cover, and number of stems available for browsing were evaluated during the spring of 2006 after snowmelt and before the vegetation greened up (Fig. 3*c*). Basal area of each sampling station was determined with a prism (factor 2). Lateral cover was measured at 15 m from the sampling station with a vegetation cover board 2 m high and 30 cm wide divided into four sections, each 50 cm high with contrasting colors (Nudds 1977). The amount of each section obstructed was evaluated by 20% classes and the average of the four sections was used. The vertical canopy closure of trees (>4 m high) was evaluated visually with five interception points (3 m spacing) up to 15 m from the station (Potvin and Bertrand 2004). To provide an average measure accurately reflecting the local effects of skid trails on protective cover surrounding each sampling stations, lateral and vertical cover were measured four times at every station (every 90° starting from the axis of the transect (Fig. 3*c*)).

Potential browse stems were counted by species within a circular plot (3.14 m^2) centered on the sampling station. Browse stems were included in the tally if a stem had at least one twig more than 5 cm long and between 0 and 2 m in height (Bissonnette et al. 1997). A stem was considered unavailable if more than 50% of its twigs were browsed. Although some studies report that snowshoe hares browse

Fig. 1. Distribution of commercial thinnings and control sites in the study of site use by snowshoe hare (*Lepus americanus*) in Abitibi, Quebec, Canada, 2007.



conifer branches, the use of this food source varies by habitat type (St-Laurent et al. 2008). To determine which species of browse were preferred in our study sites, we also inventoried browsed stems.

Snow-tracking

We recorded snowshoe hare tracks during the winter of 2007 (from 13 January to 6 March) along single 200 m transects or, when the stand configuration did not permit it, we used two 100 m transects spaced at least 50 m from one another (Figs. 3*a* and 3*b*). These transects were established using the same rules as indicated above for sampling stations. All tracks within a 1 m band on either side of the transect were included. Tracks were inventoried between 24 and 72 h (one to three nights) after sufficiently abundant snowfall to cover old tracks (approximately 5 cm). We used the average hourly temperature between sunset and sunrise of the nights without snow preceding inventories (1–3 nights) because temperature affects snowshoe hare movement (Théau and Ferron 2000; Roy et al. 2010). Time since snowfall and temperature were used to account for track detectability in subsequent analyses.

Pellet inventory

Pellets were counted at the center of each sampling station in a circular plot (3.14 m^2). A circular plot was used to reduce the error associated with rectangular plots when populations are low, as was the case in our study (Murray et al. 2002). To ensure that only pellets produced over the winter were included in the sample, plots were cleared between 23 October and 16 November 2006. We conducted pellet surveys during the spring (7–16 May 2007) immediately after snowmelt and before vegetative growth (Ferron and Ouellet 1992).

Pellets can degrade within a year, influencing future counts (Murray et al. 2002; Prugh and Krebs 2004), so we compared the rate of pellet degradation between our two treatments. Specifically, we placed 10 fresh snowshoe hare pellets in each of the 20 stands during the spring of 2006 in circular wire cages 15 cm in diameter. We added mosquito netting over the cages to avoid deposition of new pellets. We determined the type of substrate under the cage (moss, lichen, mineral soil) and the canopy closure (by 25% classes) over the cages. The pellets were recounted in the fall of 2006 and the spring of 2007.

Data analysis

Habitat parameters

We compared the average values of habitat parameters between control and commercially thinned stands with *t* tests

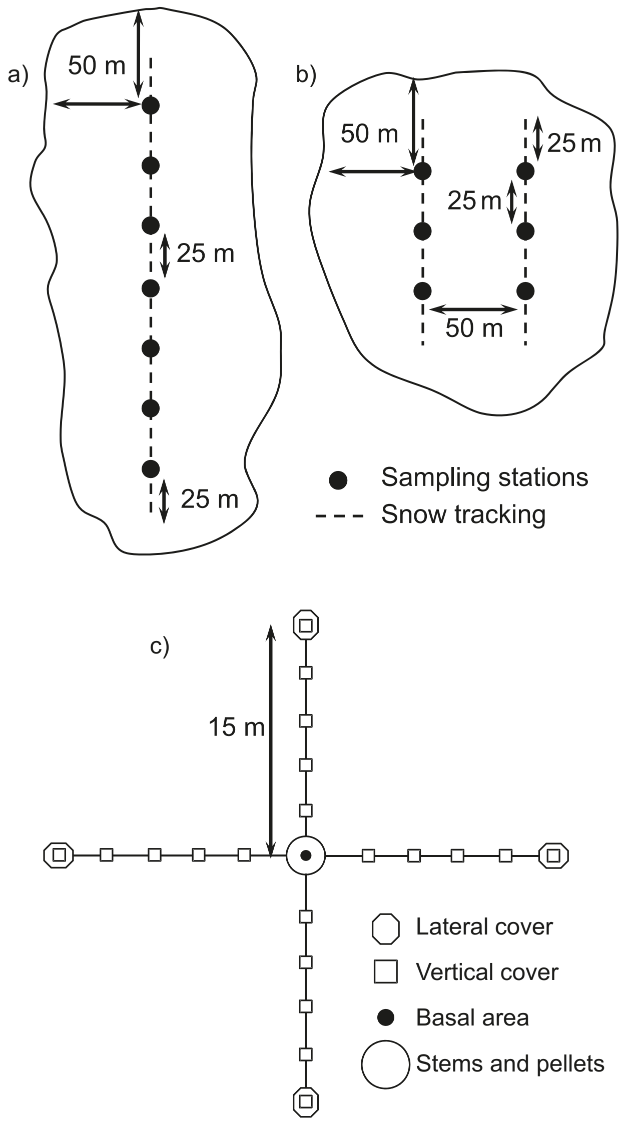
Fig. 2. Examples of stands visited in spring 2007 in Abitibi, Quebec: (*a*) commercially thinned in 1998 and (*b*) control stand.

(Welch *t* tests were used in cases of unequal variances). We investigated the level of correlation among habitat variables with Pearson correlations. All analyses were conducted in R version 2.13.2 (R Development Core Team 2011).

Snowshoe hare tracks

As each stand was visited three times during the same winter, we used *N*-mixture models to evaluate the number of tracks after accounting for detectability (Royle 2004*a*; Mazerolle et al. 2007). The *N*-mixture model estimates the abundance of a species (λ) at a collection of sites visited on many sampling occasions while considering the probability of detection (*p*). We modeled the total number of snowshoe hare tracks per 20 m based on a Poisson distribution. *N*-mixture models were fit in R using the unmarked package (Fiske et al. 2011). In our analyses, we centered continuous variables by subtracting the mean from each value. Six hypotheses on factors affecting hare track abundance were tested: (1) habitat structure (lateral and vertical cover), (2) food availability (browse), (3) habitat structure and food availability, (4) treatment effect, (5) food availability and treatment effect, and (6) a null model (Table 1). We compared the six hypotheses on track abundance on each of three scenarios of track detection: constant detection, detection varying with mean air temperature, or detection varying with number of nights since snowfall (Table 1). We did not consider a combination of stand type with either lateral or vertical cover, as both were strongly associated with stand type (Table 2). Similarly,

Fig. 3. Experimental design established in 12 control stands and 20 commercially thinned stands in Abitibi, Quebec, 2006–2007: (*a*) design in rectangle-shaped stands, (*b*) design in square-shaped stands, and (*c*) inventory design at each sampling station.



basal area was excluded from our model selection approach because this parameter does not directly affect snowshoe hare habitat and was correlated with lateral (r = –0.39) and vertical cover (r = 0.59). Because the stems of coniferous species were rarely consumed, we used only the number of deciduous browse stems in our analysis. The 18 models were ranked based on the second-order Akaike information criterion (AIC_c) and Akaike weights (w_i) using the AICcmodavg package (Burnham and Anderson 2002; Mazerolle 2006, 2011). When many models were equivalent ($\Delta AIC_c < 2$), we used multimodel inference to assess the effect of parameters occurring in these models (Burnham and Anderson 2002; Mazerolle 2006). Model fit was assessed using a parametric bootstrap approach on the most complex models with 1000 iterations (Royle 2004*b*).

To evaluate recovery time on the use of commercially thinned stands, we conducted a separate analysis for these sites using *N*-mixture models. We included the number of years since the commercial thinning. Because the number of stands was reduced for this analysis, our models included no more than one parameter associated with detection to avoid overfitting the data for a total of four models (one scenario on λ and three scenarios on p and a null model).

Pellets

We did not include pellet degradation in our analyses because 98% of the pellets placed in the wire cages were retrieved in excellent condition. Due to the nested structure of our data (i.e., several stations within a stand), we used Poisson regression with random intercepts to model the pellet number relative to habitat parameters as fixed effects (lateral and vertical cover, browse, treatment) and a random intercept for each site (Gelman and Hill 2007). Parameters were estimated with the Laplace approximation of the likelihood with the lme4 package (Bates et al. 2011). We compared six candidate models (Table 1) based on the AIC_c (with sample size based on the number of sites) and conducted multimodel inference with the AICcmodavg package. Plots of residuals against predicted values did not suggest systematic patterns and there were no indications of departure from the normality of random effects.

To evaluate our hypothesis that habitat use would increase with time since thinning in treated stands, a null model was compared with another including time since thinning (years). We used Poisson mixed models with the same random effects structure as in the preceding section.

Estimation of recovery time after thinning

We used a linear regression of lateral cover as a function of time since commercial thinning to determine whether lateral cover reestablished with time since treatment. Finally, to determine whether there was an increase in use of commercially thinned stands by snowshoe hares with time since thinning, we obtained model-averaged predictions of the number of tracks or the number of pellets as a function of years since commercial thinning from our modeling framework. For a given response variable, we calculated the predicted values for 7–17 years after commercial thinning based on the entire model set (Burnham and Anderson 2002; Mazerolle 2006). Unconditional SEs of the model-averaged estimates were calculated from the SEs obtained with the delta method (Williams et al. 2002).

Results

Habitat parameters

When commercially thinned stands were sampled in spring 2007, they were then 7–17 years old. Considering this time since treatment, there was no significant difference in total basal area ($t_{14.7}$ = –0.65, P = 0.526), black spruce basal area (t_{30} = –1.00, P = 0.326), jack pine basal area (t_{30} = 0.39, P = 0.698), or basal area of other species (t_{30} = 0.05, P = 0.964) between commercially thinned and control stands (Table 2). However, lateral cover (t_{30} = –3.58, P = 0.0012) and vertical tree cover (t_{30} = –3.46, P = 0.0016) were greater in control stands compared with commercially thinned stands. The density of deciduous and coniferous browse stems did not differ between the treatment types ($t_{29.4}$ = 1.12, P = 0.271 and t_{30} = –0.45, P = 0.2654, respectively) (Table 2).

Table 1. Candidate models explaining the abundance of snowshoe hare (*Lepus americanus*) tracks (λ, *N*-mixture models) during the winter of 2006–2007 and number of pellets (mixed models) during the spring of 2007 in 20 commercially thinned stands and 12 control stands in Abitibi, Quebec.

Model	Hypotheses on variables affecting habitat use
LC + VC	Habitat structure
BR	Food availability
LC + VC + BR	Habitat structure + food availability
TR	Treatment effect
BR + TR	Food availability and treatment effect
Intercept	Null model

Note: LC, lateral cover; VC, vertical cover; BR, deciduous stems available for browse; TR, treatment. In the case of snowshoe hare tracks, each *N*-mixture model was run according to three scenarios of track detection for a total of 18 models (constant detection, detection varying with mean air temperature, and number of nights since last snowfall).

Table 2. Habitat parameters collected in the spring of 2006 in 20 commercially thinned and 12 control stands in Abitibi, Quebec.

	Commercially thinned stands		Control stands	
Habitat parameter	Mean	SE	Mean	SE
Total basal area (m^2/ha)	31.02	1.61	33.79	3.96
Black spruce basal area (m^2/ha)	24.48	1.74	28.03	3.57
Jack pine basal area (m^2/ha)	3.96	0.88	3.17	2.18
Other basal area (m^2/ha)	2.62	0.59	2.57	1.12
Lateral cover 0–200 cm (%)*	66.14	3.15	84.41	3.99
Vertical cover over 4 m (%)†	47.75	2.52	61.54	2.95
Deciduous stems available for browse (stems/ha)	5786	1599	3640	1047
Coniferous stems available for browse (stems/ha)	28511	4659	31607	4163

*$t = 3.579$, df = 30, $P = 0.0012$.
†$t = 3.464$, df = 30, $P = 0.0016$.

Table 3. Model selection results for the number of snowshoe hare (*Lepus americanus*) tracks (λ) (*p*, probability of detection) inventoried in the winter of 2006–2007 and the number of pellets counted in the spring of 2007 in 20 commercially thinned and 12 control stands in Abitibi, Quebec.

Model	Log-likelihood	*K*	AIC_c	ΔAIC_c	w_i
Snowshoe hare tracks in all stands					
λ(LC+VC+BR) *p*(Temp)	–67.36	6	150.08	0	0.36
λ(LC+VC+BR) *p*(·)	–68.97	5	150.24	0.16	0.34
λ(LC+VC+BR) *p*(Delay)	–68.02	6	151.39	1.31	0.19
Snowshoe hare tracks in commercially thinned stands only					
λ(Years) *p*(·)	–33.28	3	74.06	0	0.48
λ(Years) *p*(Temp)	–32.02	4	74.72	0.66	0.35
λ(Years) *p*(Delay)	–32.78	4	76.23	2.17	0.16
Snowshoe hare pellets in all stands					
LC+VC+BR	–591.16	5	1194.63	0	0.53
LC+VC	–592.70	4	1194.88	0.25	0.47
Snowshoe hare pellets in commercially thinned stands only					
Years	–478.11	3	963.72	0	0.79
Null	–480.83	2	966.38	2.66	0.21

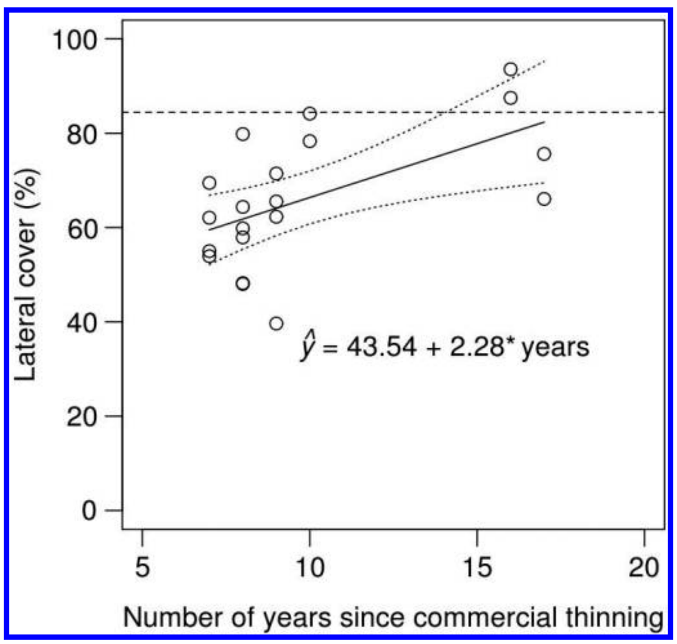
Note: LC, lateral cover; VC, vertical cover; BR, deciduous stems available for browse. Temp, detection varying with mean air temperature; Delay, detection varying with number of nights since snowfall. Only models with $\Delta AIC_c < 4$ are presented with the number of parameters included (*K*), the second-order Akaike information criterion (AIC_c), the distance from the best model (ΔAIC_c), and Akaike weight (w_i).

Table 4. Unconditional confidence intervals (95%) of parameters obtained from multimodel inference for models explaining the number of snowshoe hare (*Lepus americanus*) tracks (λ) (*p*, probability of detection) inventoried in the winter of 2006–2007 and the number of pellets counted in the spring of 2007 in 20 commercially thinned and 12 control stands in Abitibi, Quebec.

	Parameter	Model-averaged estimate	SE	Lower	Upper
Snowshoe hare tracks in all stands					
λ	LC	0.072	0.014	0.044	0.101
	BR	0.225	0.082	0.064	0.386
	VC	0.014	0.017	–0.020	0.047
p	Temp	–0.068	0.044	–0.154	0.018
	Delay	0.289	0.212	–0.130	0.702
Snowshoe hare tracks in commercially thinned stands only					
λ	Years	0.256	0.075	0.110	0.402
p	Temp	–0.083	0.058	–0.196	0.030
	Delay	0.470	0.487	–0.485	1.425
Snowshoe hare pellets in all stands					
	LC	0.034	0.002	0.029	0.038
	VC	0.011	0.002	0.007	0.015
	BR	–0.010	0.006	–0.021	0.001
Snowshoe hare pellets in commercially thinned stands only					
	Years	0.239	0.096	0.050	0.427

Note: LC, lateral cover; BR, deciduous stems available for browse; VC, vertical cover. Temp, detection varying with mean air temperature; Delay, detection varying with number of nights since snowfall.

Fig. 4. Relationship between lateral cover and time since commercial thinning (treated between 1989 and 1999) in Abitibi, Quebec. Dotted lines denote 95% confidence bands around predictions and the dashed line indicates the average of lateral cover for control stands.



Snowshoe hare tracks

The global submodels did not significantly lack fit, as shown by parametric bootstrap simulations ($P = 0.193$, $P = 0.197$, $P = 0.507$, and $P = 0.587$). Three models including cover and browse had a ΔAIC_c close to 2 and could be considered equally plausible (Burnham and Anderson 2002; Mazerolle 2006) (Table 3), whereas the models including the treatment variable all had ΔAIC_c greater than 15. Multimodel inference indicated that lateral cover at 0–2 m and the number of deciduous browse stems had a positive effect on track abundance, while vertical cover had no effect (Table 4). Temperature and the number of nights since snowfall did not influence track detection (Table 4).

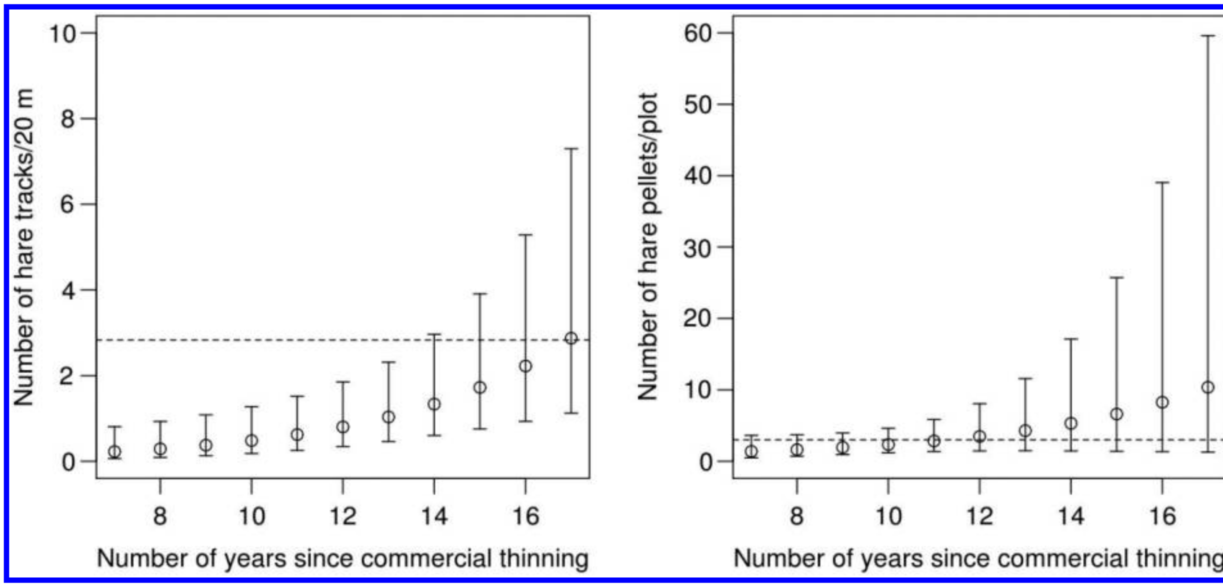
Pellets

The two most likely models included habitat structure (Table 3), with a difference in ΔAIC_c of only 0.25. Both lateral and vertical cover had a positive effect on pellet abundance, although the number of browse stems did not influence the number of pellets (Table 4).

Recovery time after thinning

The average lateral cover in commercially thinned stands did not meet the average value for control stands (mean ± SE: 84.41 ± 3.08%) 17 years after treatment (Fig. 4), although according to linear regression, this level would be reached shortly thereafter (18 years after thinning, $r^2 = 0.32$). When the upper boundary of the 95% confidence interval of predicted lateral cover is used, at least 14 years are necessary to meet the average value of control stands (Fig. 4). The number of both snowshoe hare tracks and snowshoe hare pellets in commercially thinned stands increased with the number of years following thinning (Tables 3 and 4; Fig. 5). The number of snowshoe hare tracks reached the levels of control stands 17 years after thinning (14 years when the upper boundary of the 95% confidence interval of snowshoe hare tracks is used), whereas the number of pellets reached the same levels as in control stands (i.e., mean ± unconditional SE: 3 ± 0.66) 11 years after commercial thinning (Fig. 5). However, even the youngest sites after treatment (7 years) included the mean of control stands when the upper

Fig. 5. Relationship between time since commercial thinning and the number of snowshoe hare (*Lepus americanus*) tracks (winter 2007) and pellets (counted in spring 2007) in 20 commercially thinned stands treated between 1989 and 1999 in Abitibi, Quebec. Note that 95% confidence bands around the predictions are shown and the dashed line indicates the model-averaged number of tracks and pellets for control stands.



boundary of the 95% confidence interval of hare pellets was used (Fig. 5). Taken together, these results indicate that 11–18 years are required after commercial thinning for mean lateral cover and snowshoe hare abundance to recover to the mean values in control stands. Considering the variability in our data, especially based on lateral cover and snowshoe hare pellets, at least some sites may be comparable with control stands only 7–8 years after treatment.

Discussion

Habitat parameters influencing snowshoe hare habitat use

Lateral cover was the only habitat parameter shown to have a positive effect in all analyses conducted to determine the abundance of snowshoe hare signs (pellets and snow tracks) in the sampled stands. This conclusion is similar to what has been found in other studies where density of the shrub layer was the most important parameter determining snowshoe hare habitat use (Wolff 1980; Litvaitis et al. 1985; Ferron and Ouellet 1992). Many investigators reported vertical cover as an important habitat parameter (Litvaitis 1990; Potvin et al. 2005), likely because a closed canopy allows snowshoe hare to hide from predators. However, our results show only a very weak effect as compared with lateral cover. Very dense vertical cover reduces the density of the shrub layer (Fuller and Harrison 2000) and this could explain this apparent discrepancy in our coniferous stands.

At least 4000 stems/ha of browse are generally considered necessary for providing optimal snowshoe hare habitat (Guay 1994). Both of our treatment types were close to this value (mean ± SE: 5786 ± 1599 and 3640 ± 1047 for control and commercially thinned stands, respectively) and there was no significant difference between them, probably due to the high variability within each treatment type. Both methods used to examine winter habitat use (tracks and pellets) generally indicated that lateral cover was an important parameter influencing use of stands by snowshoe hare. Vertical cover is an important parameter when modeling pellets, but not for tracks. Conversely, the number of deciduous browse stems follows the opposite pattern. We suggest that these differences can be explained by the difference in scale at which the two indicators were applied: tracks describe site use at the stand level (200 m transects), while pellet counts describe site use at the microhabitat level (3.14 m^2 plots) (Krebs et al. 1987).

Parameters affecting hare track detectability

Snowshoe hare activity in winter is reportedly influenced by extreme cold (Gray 1993; Théau and Ferron 2000), although we did not observe an influence of temperature on track detection in our study. This result could be due to the rarity of extreme cold events preceding track inventories, as only one cold night occurred prior to our surveys (–28 °C). Surprisingly, we did not observe an influence on the number of nights since snowfall on track detection. This was probably due to the majority of inventories being carried out one night after snowfall, with only 34% and 15% on the second and third nights, respectively.

Commercial thinning effect

Lateral cover was a more important predictor of snowshoe hare stand use than treatment in our study. Lateral cover varied widely within both treatment types (mean ± SD: 66.14 ± 14.08 and 84.41 ± 13.81 for commercially thinned and control stands, respectively). However, as the commercially thinned stands had a lower level of lateral cover than controls, we can consider commercially thinned stands to be inferior snowshoe hare habitat relative to controls. Variability within the commercially thinned stands can be partially explained by the variation in time since thinning (7–17 years), while variation in both commercially thinned and control stands can be explained by natural variation within stands (Hanley 2005).

The few studies documenting the effect of commercial thinning on biodiversity are not very applicable to forest ecosystems in Quebec (Bédard et al. 2003). However, Darveau et al. (1998) examined riparian zones and determined that snowshoe hares used thinned riparian zones as much as nonthinned riparian zones. In this case, thinning in riparian zones is done by harvesting the largest stems, while commercial thinning removes small, repressed stems (MRN 2000). Furthermore, skid trails are not needed to remove the harvested trees in riparian zones, as these strips are only 20 m wide (MRN 2000). In the skid trails, all of the tree cover is removed and the shrub cover is damaged by the passage of machinery. Consequently, skid trails have much lower vegetation (tree and browse) cover than the rest of the stand, creating a heterogeneous environment with discontinuous cover. This suggests that the reduction in lateral cover in commercially thinned sites, and consequently reduced snowshoe hare habitat use, could be due to the presence of skid trails increasing the effect of the removal of stems on residual protective cover.

Snowshoe hares are only found in suboptimal habitat when the density of individuals is high (Fuller and Harrison 2005). That our study occurred during the low point in the population cycle and the fact that commercially thinned stands were used at all suggests that these are real and not marginal habitats. The average lateral cover observed within commercially thinned stands (66.14%) is above the limit generally required in winter (40%) (Wolfe et al. 1982; Ferron and Ouellet 1992), which possibly explains this pattern.

Recovery time

Use of commercially thinned stands by snowshoe hare increases with time since treatment, as indicated by multimodel inference. Parameter estimates for number of years since commercial thinning were quite similar for both response variables (0.256 and 0.239 for tracks and pellets, respectively). This increase can be explained by the increase in lateral cover with time since commercial thinning. The average lateral cover in thinned stands will equal that of the control 18 years after treatment (Fig. 4). Estimated snowshoe hare abundance values based on pellets and tracks converge close to this value 11–17 years following thinning (Fig. 5). Based on these estimates, we can assume that, on average, commercially thinned stands will become equivalent snowshoe hare habitat to the control not earlier than ≥11 years after treatment. However, we acknowledge that these results should be interpreted with some caution. Indeed, we had a limited range of values for recently thinned stands and our study is based on a chronosequence approach rather than a long-term monitoring of study sites. Therefore, we based our main interpretations relating to recovery time on the average predicted values after thinning, especially since the levels prior to treatment were unknown.

It is difficult to compare our results with the literature, as no study has yet examined the long-term response of mammals to partial harvests (Thompson et al. 2003). However, Hanley (2005) reported that the understory cover had a biomass 10 times greater than the control 13–14 years after commercial thinning in Alaska, suggesting that recovery time in such sites could be shorter than our own estimates. In contrast, inventories 5 years after a partial harvest (50% harvested) in mixed forest indicated that there was still no significant growth in the shrub layer compared with the control (MacDonald and Thompson 2003). Nevertheless, the importance of protective cover in the reestablishment of snowshoe hares on treated stands is consistent with similar studies conducted on sites subjected to precommercial thinning (Homyack et al. 2007; Sullivan et al. 2007).

Conclusions

Commercial thinning as currently applied in Quebec should not be seen as an alternative to clearcutting that has less impact on snowshoe hares. A similar conclusion was reached for spruce grouse (*Falcipennis canadensis* (Linnaeus)) in a concurrent study (Lycke et al. 2011). Commercially thinned stands will recover to a level of habitat quality equivalent to untreated stands 11–18 years after thinning. Harvest of all merchantable stems with protection of the soil and regeneration generally takes place 15 years after commercial thinning. In northern spruce forests, snowshoe hare populations recover only 13–27 years after harvest of all merchantable stems (Jacqmain et al. 2007). From this perspective, commercial thinning followed by harvest of all merchantable stems would have a negative impact on snowshoe hare populations for a minimum of 24 to a maximum of 42 years.

To limit the impact of commercial thinning on snowshoe hare, it should be applied in stands where there is already significant regeneration or where the lateral cover is over 60% (Potvin et al. 2005). In most cases, our results suggest that the harvest of all merchantable stems is currently planned close to or slightly before recovery time for snowshoe hare, increasing the number of years in which habitat quality for this species is poor on a complete forest rotation.

Acknowledgements

We thank M. Renée, V. Lafrance-Rivard, S. Boucher, and L. Villeneuve, who provided invaluable field assistance. M. Desrochers helped us with ArcGis analyses and produced a map of our study sites. Comments from L. Bélanger and P. Drapeau greatly improved an earlier version of this manuscript. Funding for this project was provided by the Natural Sciences and Engineering Research Council of Canada and Canada Economic Development. Commission Scolaire Haricana, Kruger, Scierie Landrienne, Tembec, Matériaux Blanchette, and Abitibi-Consolidated supplied additional logistic support and maps. Finally, we sincerely thank N. Fenton for translating an earlier French version of this manuscript.

References

Ausband, D.E., and Baty, G.R. 2005. Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests. Can. J. For. Res. **35**(1): 206–210. doi:10.1139/x04-152.

Bates, D., Maechler, M., and Bolker, B. 2011. lme4: linear mixed-effects models using S4 classes. R package version 0.999375-39. http://CRAN.R-project.org/web/packages/lme4/index.html.

Bédard, S., De Grandpré, L., Duchesne, L., Grondin, P., Jetté, J.-P., Jobidon, R., et al. 2003. Éclaircie commerciale pour le groupe de production prioritaire SEPM — avis scientifique. Ministère des Ressources naturelles, Direction de la recherche forestière, Comité consultatif scientifique du manuel d'aménagement forestier, Québec, Qué.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**(6): 1980–1992. doi:10.2307/1941553.

Bergeron, Y. 2004. Is regulated even-aged management the right strategy for the Canadian boreal forest? For. Chron. **80**(4): 458–462.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. **31**(3): 384–391. doi:10.1139/x00-178.

Bergeron, Y., Cyr, D., Drever, C.R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, E., Leduc, A., Le Goff, H., Lesieur, D., and Logan, K. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can. J. For. Res. **36**(11): 2737–2744. doi:10.1139/x06-177.

Bissonnette, J., Bélanger, L., Larue, P., Marchand, S., and Huot, J. 1997. L'inventaire forestier multiressource: les variables critiques de l'habitat faunique. For. Chron. **73**(2): 241–247.

Bouchard, M., Pothier, D., and Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can. J. For. Res. **38**(6): 1621–1633. doi:10.1139/X07-201.

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 a snowshoe hare cycle in Canada boreal forest. Oikos, **74**(1): 69–80. doi:10.2307/3545676.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

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**(10): 1494–1500. doi:10.1139/x98-110.

Environment Canada. 2008. Canadian climate normals. Environment Canada, Atmospheric Environment Service, Canadian Climate Program, Ottawa, Ont.

Etcheverry, P., Crête, M., Ouellet, J.-P., Rivest, L.P., Richer, M.C., and Beaudoin, C. 2005. Population dynamics of snowshoe hares in relation to furbearer harvest. J. Wildl. Manage. **69**(2): 771–781. doi:10.2193/0022-541X(2005)069[0771:PDOSHI]2.0.CO;2.

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**(11): 2178–2183. doi:10.1139/z92-294.

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**(9): 1335–1343. doi:10.1139/x98-113.

Fiske, I., Chandler, R.B., and Royle, J.A. 2011. unmarked: models for data from unmarked animals. R package version 0.9-0. http://CRAN.R-project.org/web/packages/unmarked/index.html.

Fuller, A.K., and Harrison, D.J. 2000. Influence of partial timber harvesting on American marten and their primary prey in northcentral Maine. Maine Cooperative Forestry Research Unit and Maine Department of Inland Fisheries and Wildlife.

Fuller, A.K., and Harrison, D.J. 2005. Influence of partial timber harvesting on american martens in north-central Maine. J. Wildl. Manage. **69**(2): 710–722. doi:10.2193/0022-541X(2005)069[0710:IOPTHO]2.0.CO;2.

Fuller, A.K., Harrison, D.J., and Lachowski, H.J. 2004. Stand scale effects of partial harvesting and clearcutting on small mammals and forest structure. For. Ecol. Manage. **191**(1–3): 373–386. doi:10.1016/j.foreco.2004.01.014.

Gelman, A., and Hill, J. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York.

Gray, D.R. 1993. Behavioural adaptations to Arctic winter: shelter seeking by Arctic hare (*Lepus arcticus*). Arctic, **46**(4): 340–353.

Grondin, P. 1996. Écologie forestière. *In* Manuel de foresterie. *Edited by* Les Presses de l'Université Laval et Ordre des ingénieurs forestiers du Québec, Québec. pp. 133–279.

Guay, S. 1994. Modèle d'indice de qualité d'habitat pour le lièvre d'Amérique (*Lepus americanus*) au Québec. Ministère des ressources naturelles et Ministère de l'Environnement et de la Faune, Québec, Qué.

Hanley, T.A. 2005. Potential management of young-growth stands for understory vegetation and wildlife habitat in southeastern Alaska. Landsc. Urban Plan. **72**(1–3): 95–112. doi:10.1016/j.landurbplan.2004.09.015.

Hodges, K.E. 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. Ecoscience, **6**(4): 487–496.

Homyack, J.A., Harrison, D.J., and Krohn, W.B. 2007. Effects of precommercial thinning on snowshoe hare in Maine. J. Wildl. Manage. **71**(1): 4–13. doi:10.2193/2005-481.

Jacqmain, H., Bélanger, L., Hilton, S., and Bouthillier, L. 2007. Bridging native and scientific observations of snowshoe hare habitat restoration after clearcutting to set wildlife habitat management guidelines on Waswanipi Cree land. Can. J. For. Res. **37**(3): 530–539. doi:10.1139/X06-252.

Johnson, E.A. 1992. Fire and vegetation dynamics — studies from the North American boreal forest. Cambridge studies in ecology. Cambridge University Press, Cambridge, U.K.

Krebs, C.J., Gilbert, B.S., Boutin, S., and Boonstra, R. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. **65**(3): 565–567. doi:10.1139/z87-087.

Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K., and Turkington, R. 1995. Impact of food and predation on the snowshoe hare cycle. Science, **269**(5227): 1112–1115. doi:10.1126/science.269.5227.1112. PMID: 17755536.

Krebs, C.J., Boonstra, R., Boutin, S., and Sinclair, A.R.E. 2001. What drives the 10-year cycle of snowshoe hares? Bioscience, **51**(1): 25–35. doi:10.1641/0006-3568(2001)051[0025:WDTYCO]2.0.CO;2.

Litvaitis, J.A. 1990. Differential habitat use by sexes of snowshoe hares (*Lepus americanus*). J. Mammal. **71**(4): 520–523. doi:10.2307/1381790.

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**(4): 866–873. doi:10.2307/3801359.

Lycke, A., Imbeau, L., and Drapeau, P. 2011. Effects of commercial thinning on site occupancy and habitat use by spruce grouse in boreal Quebec. Can. J. For. Res. **41**(3): 501–508. doi:10.1139/X10-226.

MacDonald, G.B., and Thompson, D.J. 2003. Responses of planted conifers and natural hardwood regeneration to harvesting, scalping, and weeding on a boreal mixedwood site. For. Ecol. Manage. **182**(1–3): 213–230. doi:10.1016/S0378-1127(03)00047-1.

Mazerolle, M.J. 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. Amphib.-Reptilia, **27**(2): 169–180. doi:10.1163/156853806777239922.

Mazerolle, M.J. 2011. AICcmodavg: model selection and multimodel inference based on (Q)AIC(*c*). R package version 1.17. http://CRAN.R-project.org/web/packages/AICcmodavg/index.html.

Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royle, J.A., Converse, S.J., and Nichols, J.D. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. J. Herpetol. **41**(4): 672–689. doi:10.1670/07-061.1.

MRN. 2000. Modalités d'intervention dans le milieu forestier — fondements et applications. Ministère des Ressources naturelles, Québec, Qué.

MRNF. 2004. Ressources et industries forestières — portrait statistique édition 2004. Ministère des Ressources naturelles et de la Faune, Québec, Qué.

MRNF. 2005. Instructions relatives à l'application du règlement sur les valeurs des traitements sylvicoles admissibles en paiement des droits (Exercice 2005–2006). Ministère des Ressources naturelles et de la Faune, Québec, Qué.

Murray, D.L., Roth, J.D., Ellsworth, E., Wirsing, A.J., and Steury, T. D. 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. Can. J. Zool. **80**(4): 771–781. doi:10.1139/z02-027.

National Forestry Database. 2009. The Canadian compendium of forest statistics [online]. Canadian Council of Forest Ministers, Ottawa, Ont. Available from http://nfdp.ccfm.org [accessed 23 March 2011].

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. **5**(3): 113–117.

Payette, S. 1992. Fire as controlling process in the North American boreal forest. *In* A systems analysis of the boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, Cambridge, U.K. pp 144–169.

Potvin, F., and Bertrand, N. 2004. Leaving forest strips in large clearcut landscapes of boreal forest: a management scenario suitable for wildlife? For. Chron. **80**(1): 44–53.

Potvin, F., Breton, L., and Courtois, R. 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. Can. J. For. Res. **35**(1): 151–160. doi:10.1139/x04-151.

Prugh, L.R., and Krebs, C.J. 2004. Snowshoe hare pellet-decay rates and aging in different habitats. Wildl. Soc. Bull. **32**(2): 386–393. doi:10.2193/0091-7648(2004)32[386:SHPRAA]2.0.CO;2.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Roy, C., Imbeau, L., and Mazerolle, M.J. 2010. Transformation of abandoned farm fields into coniferous plantations: is there enough vegetation structure left to maintain winter habitat of snowshoe hares? Can. J. Zool. **88**(6): 579–588. doi:10.1139/Z10-037.

Royle, J.A. 2004*a*. *N*-mixture models for estimating population size from spatially replicated counts. Biometrics, **60**(1): 108–115. doi:10.1111/j.0006-341X.2004.00142.x. PMID:15032780.

Royle, J.A. 2004*b*. Modeling abundance index data from anuran calling surveys. Conserv. Biol. **18**(5): 1378–1385. doi:10.1111/j.1523-1739.2004.00147.x.

St-Laurent, M.-H., Cusson, M., Ferron, J., and Caron, A. 2008. Use of residual forest by snowshoe hare in a clear-cut boreal landscape. Northeast. Nat. **15**(4): 497–514. doi:10.1656/1092-6194-15.4.497.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., and Ransome, D.B. 2007. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: IV. Relative habitat use by mammalian herbivores. For. Ecol. Manage. **240**(1–3): 32–41. doi:10.1016/j.foreco.2006.11.020.

Théau, J., and Ferron, J. 2000. Influence des conditions climatiques sur le comportement du Lièvre d'Amérique (*Lepus americanus*) en semi-liberté. Can. J. Zool. **78**(7): 1126–1136.

Thibault, M., and Hotte, D. 1985. Les régions écologiques du Québec méridional. Ministère de l'Énergie et des Ressources du Québec, Direction de la recherche et du développement, Québec, Qué.

Thompson, I.D., Baker, J.A., and Ter-Mikaelian, M. 2003. A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. For. Ecol. Manage. **177**(1–3): 441–469. doi:10.1016/S0378-1127(02)00453-X.

Valois, S. 2005. Influence à court terme de la coupe partielle sur des mammifères de la forêt boréale. M.Sc. thesis, Université du Québec à Rimouski, Rimouski, Qué.

Vanderwel, M.C., Mills, S.C., and Malcom, J.R. 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. For. Chron. **85**(1): 91–104.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations. Academic Press, New York.

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**(3): 662–670. doi:10.2307/3808557.

Wolff, J.O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecol. Monogr. **50**(1): 111–130. doi:10.2307/2937249.