Transformation of abandoned farm fields into coniferous plantations: Is there enough vegetation structure left to maintain winter habitat of snowshoe hares?

C. Roy, L. Imbeau, and M.J. Mazerolle

Abstract: Natural forests will likely be unable to sustainably fulfill society needs for wood fibers and intensively managed plantations could be an alternative source of timber in the future. Abandoned farm fields are often targeted for conversion, as they are already disturbed sites; however, they also represent high-quality habitat for species such as snowshoe hares (*Lepus americanus* Erxleben 1777), a keystone mammal in the boreal forest. We evaluated the effect of converting abandoned farm fields (n = 22) to conifer plantations (n = 19) on habitat use by snowshoe hares, using pellet counts and snow-tracking surveys. Both survey techniques yielded similar results: winter habitat use by hares is mostly affected by vegetation cover rather than habitat type. In the short term, plantations do not offer less protective cover than the one found in abandoned farm fields. However, upon reaching a certain height (≥7 m), plantations are mechanically pruned and lose their protective quality. Promoting silvicultural techniques that maintain lateral cover beyond a critical threshold (70%) could preserve the quality of hare habitat for an extended proportion of rotation time of the plantation.

Résumé : Il est vraisemblable que les forêts naturelles ne puissent pas combler de façon durable les besoins de la société pour les fibres de bois et que des plantations intensives servent alors de sources de replacement de bois dans le futur. Les champs de ferme abandonnés sont souvent visés pour la conversion en plantation, car ce sont des sites déjà perturbés; ils représentent toutefois un habitat de grande qualité pour des espèces comme le lièvre d'Amérique (*Lepus americanus* Erxleben, 1777), un mammifère clé de la forêt boréale. Nous avons évalué l'effet de la conversion de champs de ferme abandonnés (n = 22) en plantations de conifères (n = 19) sur l'utilisation de l'habitat par le lièvre d'Amérique en utilisant le décompte de fèces et les inventaires de pistes sur la neige. Les deux techniques d'inventaire donnent des résultats similaires : l'utilisation de l'habitat en hiver par les lièvres est plus affectée par le couvert protecteur que par le type d'habitat. À court terme, les plantations n'offrent pas moins de couvert protecteur que les champs de ferme abandonnés. Cependant, lorsqu'elles ont atteint une certaine taille (≥7 m), les plantations sont émondées mécaniquement et perdent leur propriété protectrice. La promotion de techniques de sylviculture qui laisseraient la couverture latérale au-delà d'un seuil critique (70 %) pourrait préserver la qualité de l'habitat du lièvre pendant une portion étendue de la période de rotation de la plantation.

[Traduit par la Rédaction]

Introduction

Forest managers must now consider both an increasing number of alternative forest objectives and an increasing pressure to use the forest resources more efficiently (Seymour and Hunter 1999). Consequently, industrial wood production in natural forests is unlikely to increase because of limitations to sustainable harvests and environmental concerns (Sedjo 1999). Meanwhile, the trade in forest products continues to expand (FAO 2007), which leads some to question whether natural forests will be able to sustain our needs in the near future (Sedjo and Botkin 1997; South 1999; Fenning and Gershenzon 2002). As growth rates in extensively managed natural forests might not be sufficient to sustainably produce the amount of wood and fiber required by society (Fox 2000), we may soon have to rely on intensively managed plantations to supply the increasing demand for wood products (Binkley 1997; Sedjo 2001; Fenning and Gershenzon 2002).

The use of plantations offers many potential advantages, but there is a common belief that an increase in fiber yield decreases biodiversity. As a result, plantations are often viewed unfavorably both by the public and by conservation biologists (Hartley 2002). This perception is supported, in

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C. Roy[1,2] and L. Imbeau. Chaire industrielle CRSNG–UQAT–UQAM en aménagement forestier durable, Département des sciences appliquées, Université du Québec en Abitibi-Témiscamingue, Centre d'Amos, 341 Principale Nord, Amos, QC J9T 2L8, Canada.
M. Mazerolle. Centre d'étude de la forêt, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.

[1]Corresponding author (e-mail: christian.roy.22@ulaval.ca).
[2]Present address: Université Laval and Ducks Unlimited Canada, 710 rue Bouvier, Bureau 260, Quebec City, QC G2J 1C2, Canada.

part, by the scientific literature available. For instance, negative effects have been shown on both abundance and diversity of forest birds (Gjerde and Saetersdal 1997; Moore and Allen 1999; Twedt et al. 1999), small mammals, amphibians (Moore and Allen 1999; Waldick et al. 1999), and arthropods (Magura et al. 2000; Cunningham et al. 2005). Because plantations are considered low-quality habitat for a wide range of taxa, it has been proposed that plantations be established on already degraded lands rather than on natural or near-natural sites to reduce their negative impacts (Seymour and Hunter 1999). Whereas the types of degraded lands that are available vary across regions, abandoned agricultural fields are the most frequently converted to plantations (Sedjo 1999). The establishment of plantations on these fields is appealing because such sites are generally close to mills, and their transformation allows field owners to benefit financially from otherwise unproductive land.

In contrast to plantations, early successional forests or shrub-dominated habitats, like those found on abandoned farm fields, are intensively used by some species of mammals such as the snowshoe hares (*Lepus americanus* Erxleben, 1777) (Litvaitis 2001; Fuller and DeStefano 2003), which is a game species providing an important socio-economic benefit in several regions (Bittner and Rongstad 1982; de Bellefeuille et al. 2001). Thus, the rapid transformation of heterogeneous abandoned farmland into homogenous habitats, such as monospecific plantations, could be negative for populations of snowshoe hares. Because of its significant impact on both vegetation and predators, snowshoe hare is considered a keystone species in the boreal forest of North America (Keith 1990; Boutin et al. 2003). Consequently, management decisions affecting snowshoe hares (hereafter hares) may have important effects on several fur-bearing predators.

Our main objective in this study was to evaluate the effect of converting abandoned farm fields to conifer plantations on habitat use by hares. Because protective cover is an important factor for hares (Wolfe et al. 1982; Litvaitis et al. 1985; Ferron et al. 1998), we predicted that habitat use by hares would increase with lateral cover independently of habitat types, but that this species would use the edges of plantations more intensively than the interior since deciduous browse would be limited in that habitat.

Materials and methods

Study area

We conducted this study in the Abitibi region, which is part of the northern Clay Belt of northwestern Quebec, Canada (Vincent and Hardy 1977). Although many old fields have already been converted to plantations in Quebec, approximately 100 000 ha of abandoned farm fields occur in Abitibi. As a result, this region offered a good opportunity to study the effects of converting farm fields to plantations on hares.

Our study area was located at the southern limit of the boreal forest and vegetation was characterized by a mixedwood composition dominated by balsam fir (*Abies balsamea* (L.) P. Mill.), black spruce (*Picea mariana* (P. Mill.) B.S.P.), and paper birch (*Betula papyrifera* Marsh.), with white spruce (*Picea glauca* (Moench) Voss) and quaking aspen (*Populus tremuloides* Michx.) as codominants (Rowe 1972). In the agricultural part of the landscape, the forest consisted mainly of second-growth stands dominated by aspen because of overexploitation and repeated uncontrolled slash fires during colonization in the 1930s (Vincent 1995). The climate was continental with a mean annual temperature of 0.6 °C (Environment Canada 1982). Total snowfall varies between 200 and 250 cm, although accumulation on the ground seldom exceeds 100 cm (Vincent 1995).

Site selection

The study sites were old fields that had been abandoned (ABF) or planted with conifers (PL). Plantations consisted of jack pine (*Pinus banksiana* Lamb.) ($n = 14$), or less frequently, white spruce ($n = 5$). All fields had at least one forested edge to make sure that hares could access them. Because we wanted to investigate edge effects, distance between our sampling stations and the other edges had to be at least 150 m. Although most fields were ≥9 ha (300 m × 300 m), seven fields of 6–9 ha (300 m × ≥200 m) were used if the field was constrained on the opposite end from the main edge by an area not suitable for wildlife use (e.g., farm field, grazing field, major road). To be considered statistically independent, each site was ≥1 km apart from the nearest neighboring site.

To investigate habitat use during all stages of development in both ABF and PL, we tried to diversify the sites selected for our study by stratifying them. Age could not be included as a stratification variable for either type of site: colonization of ABF by species of the family Poaceae induced a pattern of woody vegetation succession that was inconsistent across time, and growth within PL varied greatly across species and soil types. Instead, we used an index based on the developmental stage of the woody vegetation to represent the succession of ABF and PL through time. Stages for ABF were as follows: ≥25% and <50% of the ground covered by woody vegetation (stage 1), >50% of the ground was covered by woody vegetation (stage 2), and young shade intolerant trees established across most of the field (stage 3). Stages for PL were as follows: 1–3 m tall (stage 1), 3–7 m tall (stage 2), and >7 m tall (stage 3).

Fecal pellet and vegetation inventory

We established seven permanent sampling stations along a 70 m transect that was located in the middle of each site, perpendicular to the forested edge. The first station was placed 10 m from the edge and subsequent stations were spaced 10 m apart. We estimated lateral cover by placing a 0.3 m × 2.0 m profile board (Nudds 1977) at 15 m on each side of the station. We evaluated the vertical canopy closure of trees (>4 m high) and shrubs (1.5–4.0 m) with five interception points (3 m spacing) on each side of the station with ocular estimation (Bertrand and Potvin 2003). We repeated the cover measures in line with the site transect at 10 and 20 m in the forested edge. Vegetation measures were made in either 2004 or 2005 during station establishment.

We estimated habitat use by hares by counting fecal pellets in a circular 1 m radius plot at each station in spring, shortly after snow melt and before the onset of vegetation outburst (Krebs et al. 1987, 2001; Murray et al. 2002). Populations of hares were at the lowest point of their cycle during our study (Assels et al. 2007). In such situations, 1 m radius circular plots are more appropriate (Murray et al.

2002). We repeated fecal pellet counts in 2004, 2005, and 2006. Because the use of uncleared plots can lead to biased estimates (Prugh and Krebs 2004; Murray et al. 2005), we only used data from cleared plots for 2005 and 2006 in our analyses. We also counted all available browse stems (0.3–2.0 m from the ground) present in the 1 m plot and browsed stems were identified.

Snow-tracking surveys

We conducted snow-track counts in each site from December 2004 to March 2005, as well as from December 2005 to March 2006, to evaluate habitat use by hares during winter. Counts were conducted by an observer 24–72 h after a snowfall that was important enough to easily discriminate fresh tracks from older ones (≥5 cm). On a 1 m band extending on either side of every transect used for pellet inventories, we identified each track that crossed our path and its distance relative to the forest. Signs of hare presence were classified as tracks (single track), trails (multiple tracks), or networks (overlapping tracks with no clear direction and impossible to count) following Potvin et al. (2005). We recorded the number of days since the last snowfall for each visit and we calculated the mean temperature for nights since the last snowfall using data obtained from the closest Environment Canada weather station.

Fecal pellet degradation

Prugh and Krebs (2004) and Murray et al. (2005) reported different degradation rates for fecal pellets in different habitat types. We therefore designed an experiment to assess the influence of habitat type and pellet origin on pellet degradation. We constructed 30 pellet cages (30 cm diameter × 20 cm height) out of 6.3 mm mesh hardware cloth. We sewed a plastic screen mesh at the bottom of our cages to prevent the deposition of new pellets during winter, while at the same time allowing leaves to come into contact with fecal pellets. We placed a cage in the center of 15 ABF and 15 PL during spring 2005. Each cage received 15 fecal pellets collected in an ABF and 15 from a PL after removing any pre-existing pellets. Cages were inspected in spring 2006: 27 cages were still intact and 3 damaged cages (all in ABF) were discarded. For each cage, we recorded whether the remaining pellets looked "new" or "old" based on criteria similar to those presented by Prugh and Krebs (2004). For each cage, we categorized fallen leaf cover in four different classes (0%–25%; 26%–50%; 51%–75%; and 76%–100%) and recorded whether the drainage of the ground on which the cage rested was considered good or poor.

Statistical analyses

Vegetation cover

We calculated mean lateral cover and vertical cover for each site and we analyzed differences in cover using an analysis of variance (ANOVA) in the GLM procedure of SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA). We used vegetation stage, habitat type, and their interaction as explanatory variables.

Browse inventory

We summarized browse data for each site and each stem was reclassified into one of three possible classes: deciduous, conifer, and Rosaceae. The logarithm of the number of browsed stems in each class was analyzed as a multiple regression using the GLM procedure in SAS version 9.1, with habitat type and logarithm of available browse as explanatory variables. Each stem class was analyzed separately.

Fecal pellet inventory

We analyzed fecal pellet counts from the inventory with generalized estimating equations (GEEs) using the GENMOD procedure in SAS version 9.1. We used an autoregressive correlation structure between stations, as it was the most suitable working correlation matrix for our experimental design (Hardin and Hilbe 2003). Because our fecal pellet counts were substantially overdispersed, we used a negative binomial GEE model (McCullagh and Nelder 1989). Data were analyzed separately for 2005 and 2006.

We formulated six candidate models involving habitat variables corresponding to our biological hypotheses (Table 1). The explanatory variables we considered included habitat type (ABF or PL), logarithm of the distance from the edge (Conroy et al. 1979; Wolfe et al. 1982; Ferron and Ouellet 1992), lateral cover (Litvaitis et al. 1985; Ferron et al. 1998; de Bellefeuille et al. 2001), vertical cover (Wolfe et al. 1982; Potvin et al. 2005), and a quadratic effect of vertical cover (Orr and Dodds 1982). We tested the hypothesis that edge use by hare differs in plantations relative to abandoned farm fields by including an interactive effect between habitat type and distance from edge in all models that contained distance to edge. For each sampling station, we averaged the lateral cover measures into a single value and indices of vertical canopy closure for trees and shrubs were collapsed into a single index to avoid overfitting our models.

We based our model selection on Pan's (2001) modification of Akaike's information criterion (AIC) for generalized estimating equations, yielding the quasi-likelihood information criterion (QIC). We computed ΔQIC and Akaike weights (ω_i) following conventional procedures and assessed the effect of each variable using multimodel inference (Burnham and Anderson 2002).

Snow-tracking surveys

For each site, we calculated the sum of all hare tracks observed in the first 200 m of transect. Networks of more than two tracks were given an arbitrary value of 3, as by definition they were impossible to count. We then reported the number of observations by 20 m distance increments. We constructed different models that considered the effects of days since last snowfall and temperature on nights preceding each survey on the probability of detection (p) and the effects of habitat type, lateral cover, and vertical cover on abundance (λ) of tracks (Table 1), analyzed using repeated count models (Royle 2004*a*). As hares are nocturnal animals (Gilbert and Boutin 1991), we used the mean temperature of the previous nights since the last snowfall. For lateral cover and vertical cover, we used the mean of the seven stations for each site. Each model was subsequently run in PRESENCE version 2.0. We used Akaike's information criterion corrected for small sample size (AIC_c) to select the most parsimonious models, and performed multimodel inference to determine the effects of each parameter (Burnham and

Table 1. Candidate models for the analysis of fecal pellet inventories from snowshoe hares (*Lepus americanus*) conducted during spring 2005 and 2006 and snow-tracking inventories conducted during winter 2004–2005 in abandoned farm fields (ABF) and plantations (PL) in northwestern Quebec, Canada.

Method	Model name	Parameters[a]
Fecal pellet counts	1. Type	TY
	2. Cover	LC, VC
	3. Cover^2	LC, VC, VC^2
	4. Type + edge	TY, DE, DE × TY
	5. Type + cover + edge	TY, LC, VC, DE, DE × TY
	6. Global	TY, LC, VC, VC^2, DE, DE × TY
Snow-tracking inventories	1. Null	λ(.) *p*(.)
	2. Delay	λ(.) *p*(DL)
	3. Type	λ(TY) *p*(DL)
	4. Cover	λ(LC + VC) *p*(DL)
	5. Habitat	λ(TY + LC + VC) *p*(DL)
	6. Temperature	λ(.) *p*(DL + T)
	7. Type + temperature	λ(TY) *p*(DL + T)
	8. Cover + temperature	λ(LC + VC) *p*(DL + T)
	9. Global	λ(TY + LC + VC) *p*(DL + T)

[a]Models included the intercept, as well as the effects of habitat type (TY), lateral cover (LC), vertical cover (VC), quadratic effect of lateral cover (VC^2), distance from edge (DE) on abundance (λ), and the effects of temperature (T) and days since the last snowfall (DL) on probability of detection (*p*).

Anderson 2002). We assessed model fit of the global model with a parametric bootstrap procedure described by Royle (2004*b*), which we implemented in R version 2.6.0 (R Foundation for Statistical Computing, Vienna, Austria).

Pellet degradation

To characterize pellet degradation, we used a binomial response variable, the ratio of pellets with low degradation (i.e., those looking like "new" pellets) to the total number of pellets placed in a cage at the beginning of the experiment. We used a generalized linear mixed model (GLMM) for binomial responses that treated cage as a random effect. Data analysis was performed by adaptive Gaussian quadrature with function glmer of the lme4 package in R version 2.9.0 (Bates et al. 2008). We used the origin of pellets, habitat type, leaf cover (≤50% or >50%), drainage, and habitat × origin interaction as explanatory variables.

Results

Vegetation cover

The effect of vegetation stage on lateral cover varied across habitat types (vegetation stage × habitat type interaction: $F_{[2,2]}$ = 4.25, P = 0.022, R^2 = 0.390). Specifically, lateral cover gradually increased between stages for ABF, but there was a sharp decrease for stage 3 in PL (Fig. 1A). Vertical cover increased significantly with vegetation stage in both ABF and PL ($F_{[2,2]}$ = 29.018, P < 0.001, R^2 = 0.632), but cover was more developed in ABF than in PL ($F_{[2,1]}$ = 11.243, P = 0.002; Fig. 1B).

Browse

Overall, proportion of browsed deciduous stems in ABL did not differ from that in PL (β = 0.035, SE = 0.485, P = 0.943) and the same results held for conifer stems (β = 0.479, SE = 0.511, P = 0.349; Figs. 2A, 2B). However, Rosaceae were significantly less browsed in ABF than in PL (β = –0.851, SE = 0.321, P = 0.011).

Fecal pellet inventories

In 2005, 54.7% of the 203 plots contained pellets, and there were 10.64 ± 25.46 pellets/plot (mean ± SD). Only the global model stood out of the set of competing models (ω_i = 0.990; Table 2). Following multimodel inference, lateral cover and, to a lesser extent, vertical cover had a positive effect on habitat use by hares (Fig. 3). Hares avoided edges more strongly in PL than in ABF (interactive effect between habitat type and distance from edge; Fig. 3). Habitat type did not influence habitat use by hares (Table 3).

In 2006, 69.3% of the 287 plots contained pellets, and there were 19.97 ± 48.54 pellets/plot (mean ± SD). Two models stood out of the set of competing models with their ω_i values summing to 0.999 (Table 2). Here again, lateral cover, vertical cover, and in this case distance from edge had a positive effect on habitat use by hares in both habitats (Fig. 3). The habitat type and the interactive effect between habitat type and distance from edge did not influence the response variable (Table 3).

Snow-tracking surveys

Twenty sites were visited three times and 14 sites were visited twice during winter 2004–2005. Optimal snow-tracking conditions were more restrictive in 2005–2006 and few sites were visited twice. As models estimating detection probability require at least two visits, data collected during winter 2005–2006 were not considered for this analysis. Surveys were conducted on 18 different days in 2004–2005. Eight surveys were conducted the day following a snowfall, six were conducted 2 days after snowfall, and four were conducted 3 days after snowfall. Mean temperature on nights preceding surveys varied between –1.6 and –35.0 °C (–20.4 ± 5.8 °C; mean ± SD). We encountered snow tracks in 65 (32 in ABF and 33 in PL; 74%) of our 88 transects. Of

Fig. 1. (A) Mean lateral cover (LC) and (B) vertical cover (VC) measured in abandoned farm fields (ABF), plantations (PL), and adjacent forested edges (FE) in northwestern Quebec, Canada, during spring 2004–2005. Error bars are ±90% confidence intervals (CI). Stage 1 of ABF had ≥25% and <50% of the ground covered by woody vegetation, stage 2 had >50% of the ground covered by woody vegetation, and stage 3 had young shade-intolerant trees established on most of the area. PL classification was based on the height of dominant trees: 1–3 m high (stage 1), 3–7 m high (stage 2), and >7 m high (stage 3).

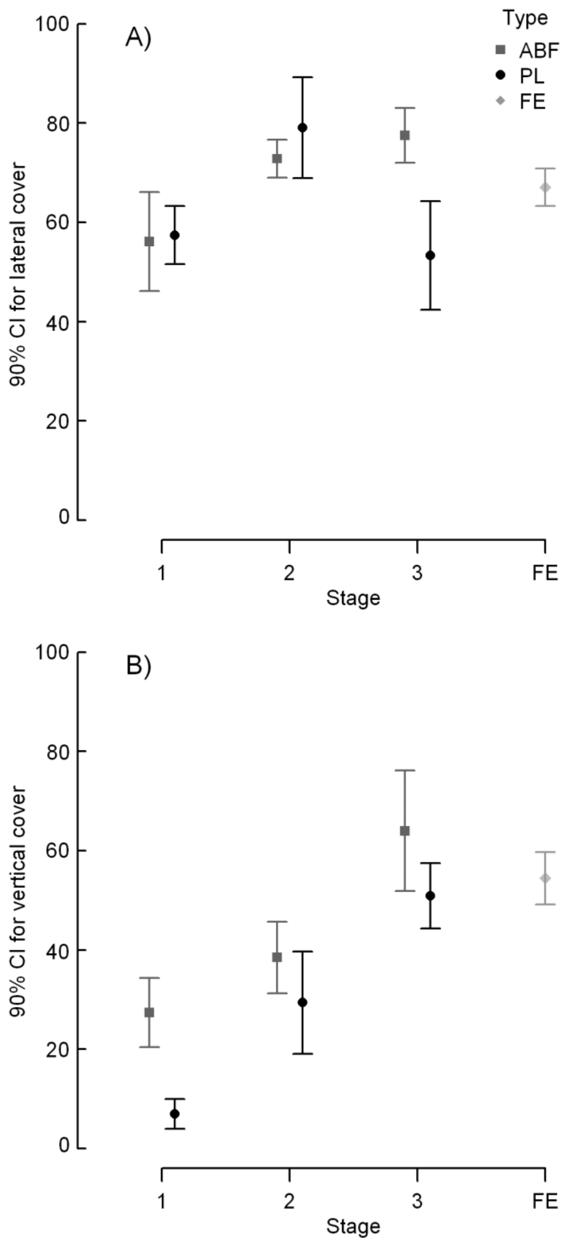
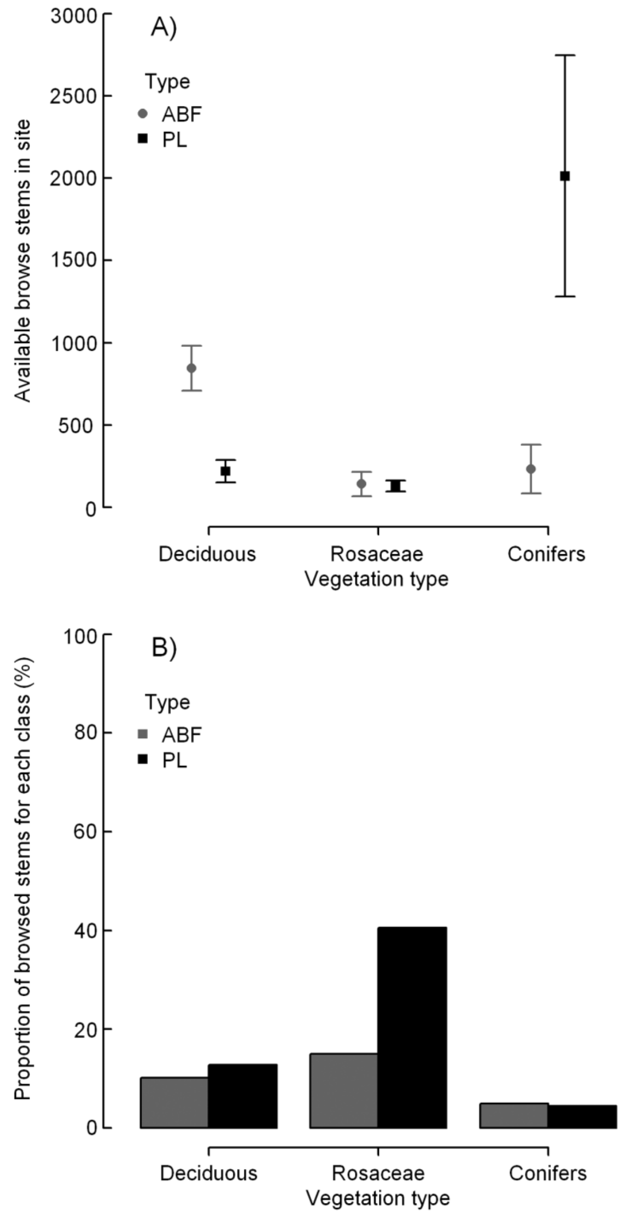


Fig. 2. (A) Available stems (mean± SE) and (B) proportion of browsed stems for three classes of browse available to snowshoe hares (*Lepus americanus*) measured in abandoned farm fields (ABF) and plantations (PL) in northwestern Quebec, Canada, during spring 2004–2005.



these tracks, 80.0% occurred as single tracks, 11.7% as multiple tracks (trails), and 8.3% occurred as networks (overlapping and indistinguishable tracks). We detected 13.76 ± 14.74 tracks/site (mean ± SD) in ABF and 14.86 ± 18.85 tracks/site (mean ± SD) in PL. The global model provided a good fit to the data (parametric bootstrap, $P = 0.946$, $n = 1000$ iterations). Four models stood out of the set of competing models (sum of $\omega_i = 0.926$). These models are, respectively, the cover, habitat, cover + temperature, and global models (Table 2). Temperature only slightly increased the detection of hare tracks, whereas days since the last snowfall did not influence the probability of detection (Table 4, Fig. 4B). Based on multimodel inference, habitat use by hares increased with lateral cover (Fig. 4A), but did not vary with the other explanatory variables (Table 4).

Fecal pellet degradation

Overall, 23.7% of all fecal pellets in the experimental cages were rated as "new", 24.9% were rated as "old", and 51.4% had disintegrated after 1 year. Leaf cover was highly

Table 2. Model selection results for the analysis of fecal pellet inventories from snowshoe hares (*Lepus americanus*) conducted during spring 2005 and 2006 and snow-tracking inventories conducted during winter 2004–2005 in abandoned farm fields (ABF) and plantations (PL) in northwestern Quebec, Canada.

Method	Model[a]	K^b	ΔAIC_c or ΔQIC_c[c]	ω_i
Fecal pellet counts (2005)	Global	8	0.00	0.990
Fecal pellet counts (2006)	Type + cover + edge	7	0.00	0.846
	Global	8	3.40	0.154
Snow-tracking inventories (2004–2005)	Cover	5	0.00	0.328
	Habitat	6	0.59	0.245
	Cover + temperature	6	0.62	0.241
	Global	7	2.16	0.112

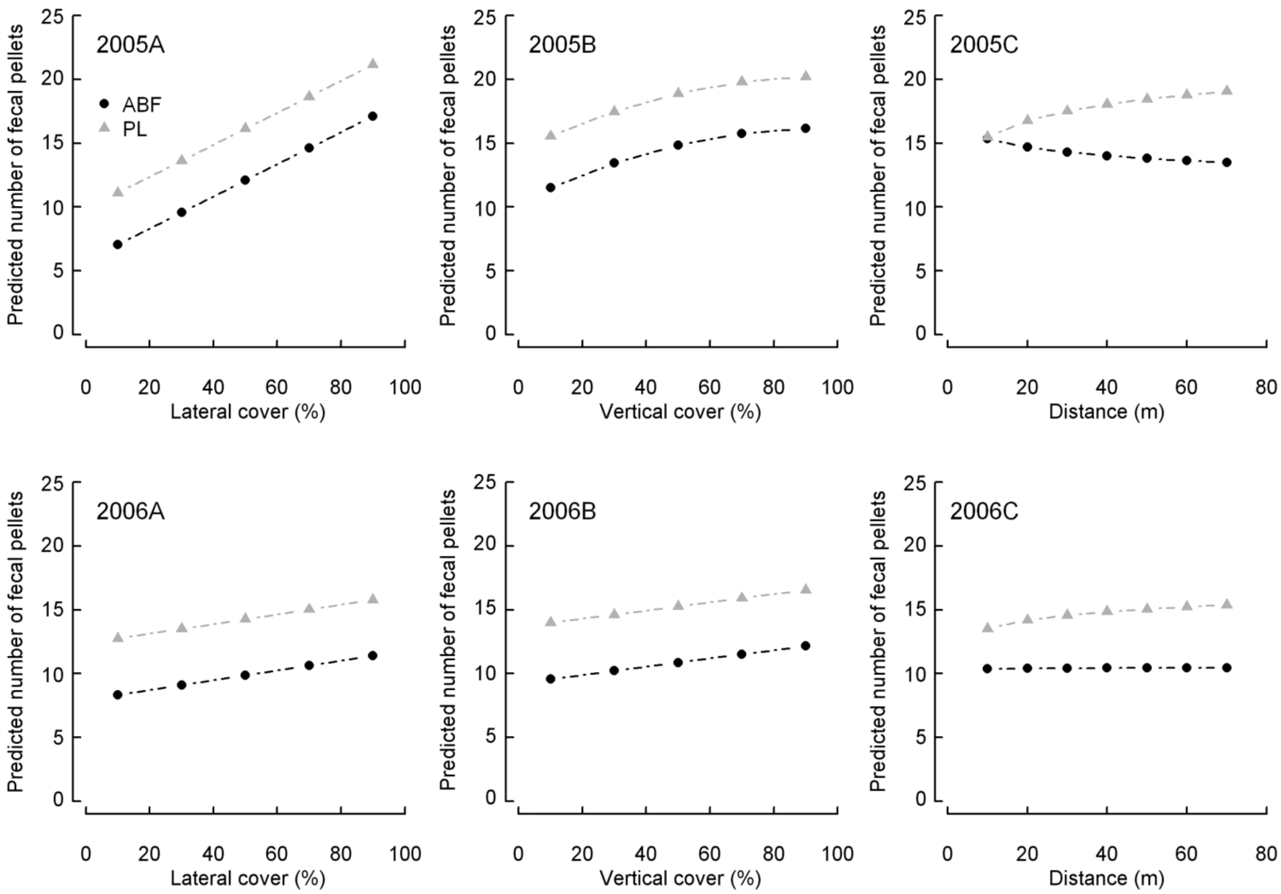
Note: Only models with $\omega_i > 0.100$ are shown for brevity.

[a]Models included the effects of habitat type (TY), lateral cover (LC), vertical cover (VC), quadratic effect of lateral cover (VC^2), distance from edge (DE), temperature (T), and days since the last snowfall (DL).

[b]Number of estimated parameters (K) in candidate model.

[c]Models involving fecal pellet counts used quasi-likelihood information criterion (QIC_c), whereas models involving snow-tracking inventories used Akaike's information criterion corrected for small sample size (AIC_c).

Fig. 3. Number of fecal pellets from snowshoe hares (*Lepus americanus*) in abandoned farm fields (ABF) and plantations (PL), according to model-averaged predictions, as a function of lateral cover (A), vertical cover (B), and distance to edge (C), during spring 2005 and 2006 in northwestern Quebec, Canada.



variable (42.78% ± 41.89%; mean ± SD); eight sites were well-drained, whereas the remainder of sites (n = 19) were poorly drained. Pellet degradation was not affected by habitat type, leaf cover, or drainage class, but the pellets collected from ABF degraded faster than those originating from PL (β = 0.438, SE = 0.220, P = 0.047).

Discussion

Habitat use by snowshoe hares

Habitat use by hares was more closely linked to the development of vegetative cover, especially lateral cover, rather than with habitat type (ABF vs. PL). The strong rela-

Table 3. Parameter estimates from multimodel inference on models of habitat use by snowshoe hares (*Lepus americanus*) determined from fecal pellet inventories conducted in abandoned farm fields (ABF) and plantations (PL) in northwestern Quebec, Canada, during spring 2005 and 2006.

Parameter	Model-averaged β estimate for spring 2005	90% CI for spring 2005 Lower	90% CI for spring 2005 Upper	Model-averaged β estimate for spring 2006	90% CI for spring 2006 Lower	90% CI for spring 2006 Upper
Type (ABF)	1.947	–0.049	3.943	–0.418	–2.025	1.189
Lateral cover	0.039	0.029	0.049	0.015	0.008	0.022
Vertical cover	0.018	0.004	0.033	0.013	0.007	0.019
Vertical cover^2	0.000	–0.001	0.000	0.000	–0.003	0.003
Distance	0.571	0.111	1.031	0.379	0.024	0.739
Distance × type	–0.868	–1.485	–0.251	–0.360	–0.849	0.130

Note: CI, confidence interval.

Table 4. Model-averaged parameter estimates of Royle count models used to estimate the number of tracks from snowshoe hares (*Lepus americanus*) per 20 m from snow-tracking inventories conducted in abandoned farm fields (ABF) and plantations (PL) in northwestern Quebec, Canada, during winter 2004–2005.

	Parameter	Model-averaged β estimate	90% CI Lower	90% CI Upper
Parameters on abundance (λ)	Type (ABF)	–0.525	–1.113	0.063
	Lateral cover	0.680	0.495	0.866
	Vertical cover	0.125	–0.156	0.405
Parameters on detectability (p)	Days since last snowfall	0.437	–0.368	1.242
	Temperature	0.368	0.051	0.685

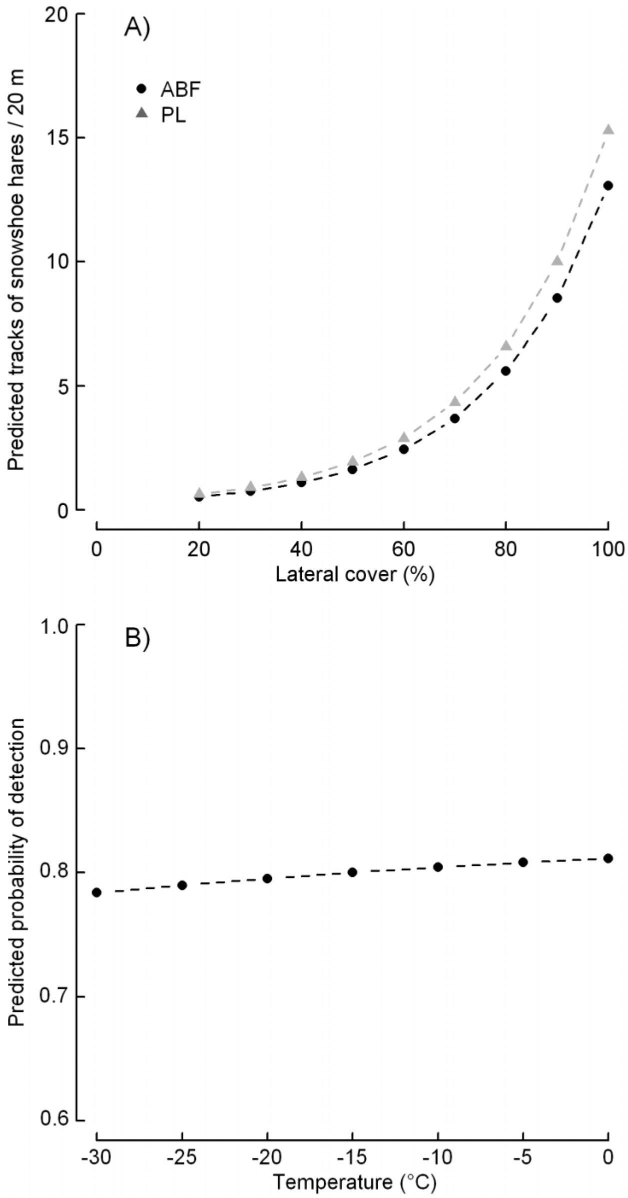
Note: CI, confidence interval.

tionship between lateral cover and hares has already been reported in the literature (Litvaitis et al. 1985; Ferron et al. 1998; de Bellefeuille et al. 2001). Our results show that conversion of abandoned fields to plantations in our region may have limited effects on populations of hares in the short term if adequate lateral cover is maintained. However, lateral cover in ABF and PL developed differently across time. Indeed, most plantations are pruned when they reach a height of ≥7 m (15–25 years after establishment) and canopy closure in mature plantations prevents the establishment of understory vegetation. The lateral cover for PL stage 3 (height ≥7 m) in our study (53.97% ± 21.59%; mean ± SD) is lower than the 70% level considered suitable for hares (Litvaitis et al. 1985), and in half of the cases is lower or close to the minimal level (40%) reported by Carreker (1985). This indicates that old plantations are suboptimal. Although we did not observe negative effects of transforming ABF into PL in the short to mid-term, hares will probably avoid PL in the long term because of the lack of lateral cover in older plantations. Plantations will also probably be used for a shorter period of time because they are tended and pruned and reach stage 3 quickly (15–25 years). In contrast, ABF stage 3 can take more than 40 years to reach this developmental stage.

The relationship between habitat use by hares and vertical cover was important only for pellet inventories. This difference might stem from analyzing pellet counts among individual plots, whereas we used the average vertical cover obtained for the whole site (n = 7 plots) for snow tracking transects. Use by hares increased with vertical cover. In contrast, Orr and Dodds (1982) observed a decrease in hare habitat when vertical cover exceeded a given threshold (>60%), but they considered only tree canopy closure, whereas we considered the closure by both trees and shrubs. Vertical cover was significantly more developed in ABF than PL in all stages of development (Fig. 1B). These differences are explained by the mechanical removal of competitive vegetation in PL stages 1 and 2, and by tree canopy closure in PL stage 3 that prevented the establishment of understory vegetation.

Contrary to our prediction, hares strongly avoided edges in our sites; however, many report the species as an edge specialist (Conroy et al. 1979; Wolff 1980; Ferron and Ouellet 1992). This difference could be explained by at least two factors. First, mammalian predators are known to stalk prey near edges (Bergman et al. 2006; Constible et al. 2006). Edges in our study sites were abrupt and probably represented a microhabitat of open space that is more favorable to predator movements and hunting behavior than stand interior, and therefore, are potentially avoided by hares. Second, the use of edges by hares is linked to the interspersion of habitats offering cover and food (Conroy et al. 1979). Lack of such interspersion in our sites probably explains why hares did not use edges. Indeed, adjacent stands were generally composed of mature aspen stands (38 out of 41 sites) with sparse understory vegetation, a habitat generally perceived as poor for hares (Wolfe et al. 1982). These stands had low lateral cover (67% ± 14% (mean ± SD); Fig. 1A). In fact, lateral cover for these stands is lower than the level considered suitable for hares, according to Litvaitis et al. (1985). Edge avoidance was more pronounced in PL than in ABF in 2005, a phenomenon probably linked to edges being

Fig. 4. (A) Model-averaged number of tracks from snowshoe hares (*Lepus americanus*) in abandoned farm fields (ABF) and plantations (PL) as a function of lateral cover and (B) model-averaged detection probabilities of tracks from snowshoe hares as a function of temperature for winter 2004–2005 in northwestern Quebec, Canada.



even more abrupt in PL. There was a similar tendency in 2006, but the effect was not as strong as in 2005. Differences between the 2 years could be explained, in part, by 2005 being the year of lowest abundance in the hare cycle in the region (Assels et al. 2007; this study). Hares were probably more selective in their habitat choices during this period than in 2006.

Fecal pellet degradation

We recovered 48.6% of the pellets after 1 year, which is consistent with the recovery rate of 57% ± 27% (mean ± SD) reported by Murray et al. (2005). However, this contradicts Prugh and Krebs (2004), who reported that only 1% of pellets in willow habitat disappeared after 1 year, whereas 14% of pellets disappeared after 1 year in sites dominated by alder and spruce. These discrepancies could be explained, in part, by the dryer climate of their study area and their experimental design, which did not allow leaves to come into contact with pellets. Although leaf cover did not influence degradation in our experiment, the plastic screen mesh we used had the undesirable effect of retaining moisture, a role similar to the one we expected leaves would play. Moisture increases fecal pellet degradation in other species (Lehmkuhl et al. 1994; Massei et al. 1998); Murray et al. (2005) also highlighted the importance of this factor in their study. Our design did not allow us to quantify the effect of the plastic screen mesh on degradation rates in ABF and PL; however, we used similar devices in a concurrent study to evaluate pellets degradation. Although the cages were in quite different habitats, their degradation rates were not as short as those that we observed in the sites of the present study (L. Imbeau, unpublished data).

Previous applications of the hare pellet–plot methods implicitly assumed that pellets persist in the field for at least 1 year (Murray et al. 2005). The high degradation rates measured in our experiment indicate that our results underestimate the real number of pellets produced in a given year, most likely those produced in summer, and that this effect is more pronounced in abandoned farm fields than in plantations. Therefore, our conclusions about habitat use by hares based on pellet inventories better represent winter rather than year-round habitat use.

The difference that we observed in degradation rate across pellet origins may be linked to diet of hares: individuals in PL consumed more Rosaceae than in ABF, probably because it is often the only browse available. Murray et al. (2005) suggested that diet was a factor in pellet degradation and showed that pellets produced by hares during summer decomposed more quickly than those produced during winter. The same authors posited that the difference observed was due to variations in protein content in the diet across seasons. Although the hare pellets used in our experiment originated from only two different sites, our results strongly support the hypothesis that pellet degradation is affected by diet. Variation in degradation between habitats, diets, and seasons could be problematic if not controlled. The high rate of degradation observed by Murray et al. (2005) and in our study also suggests that annual counts might not be enough to adequately assess habitat use and that counts should be conducted more than once a year.

Snow-tracking surveys and probability of detection

Estimating the probability of detection allowed us more flexibility than was possible in previous snow-tracking studies (Ausband and Baty 2005; Potvin et al. 2005) by widening the sampling window, as surveys at different sites could be realized over a few days and under different weather conditions. Temperature had only a weak positive effect on the probability of detecting tracks (Fig. 4B). This weak effect could be due to our use of the mean number of observations by 20 m increments in our analysis. This result could be linked to the reduced activity of hares in cold temperatures (Theau and Ferron 2000). Number of days since the last snowfall had no effect on detectability, but this might be an artifact of our design, as most inventories (77%) were conducted <48 h after a snowfall. Whereas the number of overlapping tracks (trail networks) was relatively low in our study (8%), we expect the number of networks to increase with time elapsed. Because it is impossible to discriminate between individual tracks when networks are present, we believe that investigators should strive for short sampling windows in snow-tracking studies.

Management implication

Our results show that conversion of abandoned farm fields to forest plantations does not necessarily equate to a reduction in habitat quality for hares. Plantations offer protective cover that is similar to that found in abandoned farm fields in the short term. However, plantations are mechanically pruned once they reach a certain height (≥7 m) and lose their protective quality. Because the negative effects of conversion are measurable even at a small scale, it would be important to maintain some patches of natural habitat between plantations and avoid large-scale plantations. Promoting silvicultural techniques that maintain cover above a critical threshold for hares (lateral cover >70%) could also preserve habitat quality for a longer proportion of rotation time of the plantation and would also benefit predators of this key species. This goal could be reached by adopting alternative strategies, such as pruning trees over several years, instead of applying it simultaneously to all trees of the stand or using species that do not require pruning.

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