UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

ÉVALUATION DE L'IMPACT DE LA TRANSFORMATION DES TERRES EN FRICHES EN PLANTATIONS RÉSINEUSES SUR LES ESPÈCES DE PETIT GIBIER EN ABITIBI-TÉMISCAMINGUE

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AVANT-PROPOS

Conformément aux exigences du programme de maîtrise en biologie, ce mémoire comprend deux articles rédigés en langue anglaise portant sur les effets de la transformation des terres en friches en plantations résineuses sur les espèces de petit gibier en Abitibi-Témiscamingue, ainsi qu'une introduction et une conclusion générales. Le premier article porte plus spécifiquement sur le lièvre d'Amérique et sera soumis au périodique scientifique *The Journal of Wildlife Management*. Le second article porte sur la gélinotte huppée et sera soumis au périodique scientifique *Canadian Journal of Forest Research*. J'ai procédé à toutes les étapes de collecte, de traitement et de l'analyse des données pour ces deux articles en plus d'en être le premier auteur. Louis Imbeau et Marc Mazerolle en sont les co-auteurs.

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RÉSUMÉ

Au Québec, il devient de plus en plus apparent qu'en aménagement forestier, l'atteinte de la conservation de la biodiversité ne pourra pas être réalisée sans une diminution substantielle du volume ligneux prélevé en forêt publique. Afin de maintenir des niveaux d'approvisionnement stables, certains scientifiques ont proposé d'appliquer le concept de la Triade. Dans ce système, une partie du territoire est allouée à l'utilisation de plantations ligneuses afin de combler les pertes d'apprivoisement occasionnées dans les zones de conservation et d'aménagement écosystémique. Toutefois, les plantations sont généralement mal perçues par le public et elles ont des impacts négatifs sur la biodiversité. Pour ces raisons, on recommande généralement de les installer dans des endroits qui sont déjà dégradés. En Abitibi-Témiscamingue, la conversion de friches agricoles en sites voués à la ligniculture est attrayante, car elle permettrait d'accroître la production de matière ligneuse à proximité des usines de transformation tout en remettant des sites abandonnés en production. Toutefois, les sites en début de régénération représentent généralement un habitat propice pour plusieurs espèces de petit gibier et leurs prédateurs. La transformation rapide d'un milieu hétérogène dominé par une strate arbustive en un milieu homogène pourrait donc avoir un impact négatif sur la faune. Le but de notre étude était donc d'évaluer et de comparer le potentiel faunique de plantations et de friches agricoles afin de déterminer leur contribution respective au maintien de la faune gibier régionale. Pour ce faire, nous avons réalisé des inventaires fauniques dans des plantations (n = 19) et des friches (n = 22) de différents stades de croissance. Deux espèces étaient visées : le lièvre d'Amérique et la gélinotte huppée. Pour le lièvre, des inventaires de crottin ont été réalisés en 2004, 2005 et 2006 et des transects de pistage hivernal ont été réalisés à l'hiver 2004-2005. Les résultats des deux techniques utilisées concordent et indiquent que l'abondance du lièvre est principalement influencée par le couvert végétal disponible plutôt que par le type de milieu. Toutefois, les inventaires de végétation nous indiquent que le couvert latéral, un élément important de l'habitat du lièvre, diminue de façon importante dans le temps dans les plantations ce qui indique que celles-ci auront un effet négatif sur le lièvre à long terme. Dans le cas de la gélinotte huppée, des inventaires auditifs de mâles tambourineurs ont été réalisés au printemps 2005 et 2006. L'analyse des résultats de l'année 2005 n'a pas déterminé de différences dans l'utilisation des deux milieux par les mâles tambourineurs, mais nous avons probablement sous-estimé notre rayon d'audibilité lors de cet inventaire. Les inventaires auditifs ont été répétés au printemps 2006, toutefois, le site de tambourinage de chaque mâle entendu a été répertorié afin de déterminer si celui-ci était à l'intérieur du site d'étude. Des 22 friches inventoriées, 14 étaient utilisées par la gélinotte huppée alors que seulement 2 des 19 plantations étaient occupées. L'analyse des résultats en 2006 démontre que les plantations sont évitées par les gélinottes huppées et que la transformation des friches en plantations résineuses a des effets négatifs sur cette espèce. Puisque les deux espèces seront affectées négativement par la transformation des friches agricoles en plantation, une attention particulière devra être portée à leur installation et leur configuration dans la matrice agroforestière pour diminuer ces impacts.

Mots-clés : Friches, plantations, lièvre d'Amérique, gélinotte huppée

INTRODUCTION GÉNÉRALE

La foresterie est actuellement considérée comme un facteur majeur de perturbation de l'écosystème forestier boréal (Imbeau, 2001 ; Niemela, 1999 ; Ostlund, Zackrisson et Axelsson, 1997) et est même devenue dans certaines parties de la forêt boréale la perturbation principale (Franklin et Forman, 1987 ; Spies, Riple et Bradshaw, 1994). Bien que la foresterie se rapproche en certains points des perturbations naturelles, il y a toutefois des différences notables entre les deux types de perturbations. Notamment, le système de révolution de coupe actuel est plus court que le cycle de perturbation naturel (Bergeron *et al.*, 2007 ; Bergeron *et al.*, 2001 ; Bergeron *et al.*, 2002 ; Gauthier, Leduc et Bergeron, 1996). Les coupes, bien qu'elles soient généralement de taille inférieure aux incendies forestiers, sont généralement agglomérées dans l'espace ce qui conduit à des superficies contiguës de parterres en régénération plus étendues que ce que sous-tendent les régimes naturels de perturbations (Bergeron *et al.*, 2007 ; Bergeron *et al.*, 2002 ; Leduc *et al.*, 2000). De plus, la structure des peuplements après coupes est généralement beaucoup plus simple que des peuplements régénérés naturellement (Fraver, Wagner et Day, 2002 ; Hunter, 1999 ; Imbeau, 2001). Pour ces raisons, plusieurs intervenants du milieu même de la foresterie doutent que les pratiques actuelles permettent de préserver la biodiversité dans son ensemble et que celles-ci permettent d'atteindre une exploitation durable de la forêt (Coulombe *et al.*, 2004).

La Triade

Dans le but de minimiser les impacts négatifs de l'aménagement forestier, les écologistes se rallient depuis quelques années au principe selon lequel les aménagements devraient s'inspirer des paysages hérités du régime des perturbations naturelles (Bergeron *et al.*, 2001 ; Franklin, 1993 ; Kneeshaw *et al.*, 2000). Cette approche s'inscrit dans le cadre d'un « aménagement écosystémique » (Galindoleal et Bunnell, 1995 ; Grumbine, 1994). Cette forme de gestion vise à permettre la conservation de la biodiversité et la conciliation des intérêts des différents utilisateurs de la forêt. Toutefois, certains craignent qu'elle impose des contraintes au maintien des niveaux d'approvisionnement ligneux. Afin de maintenir des niveaux d'approvisionnement stables, il a été proposé d'appliquer l'aménagement écosystémique dans un cadre de gestion du territoire plus global nommé Triade (Hunter, 1990 ; Hunter et Calhoun, 1995 ; Seymour et Hunter, 1999). Ce concept subdivise la forêt en trois grandes zones : une zone de conservation destinée à assurer le maintien de la biodiversité, une zone couvrant la majorité du territoire dans laquelle la forêt serait aménagée sous un régime écosystémique et finalement une zone d'exploitation intensive qui viserait à combler les pertes d'apprivoisement occasionnées par les deux autres zones. Il est important de noter que ce système n'implique pas une allocation du territoire égale entre les différentes zones (Messier et Kneeshaw, 1999 ; Seymour et Hunter, 1999). Ainsi, une perte d'approvisionnement ligneux causée par à la conservation de 10% du territoire en réserves écologiques devrait facilement être contrebalancée par un programme de ligniculture intensive sur une petite partie du territoire (Seymour et Hunter, 1999).

Plantations, friches et biodiversité

La perception générale du public est que l'aménagement de la forêt influence négativement la biodiversité (Wagner *et al.*, 1998) et qu'une augmentation de la production de fibres entraîne nécessairement une baisse de la biodiversité (Hartley, 2002). Comparées aux forêts régénérées naturellement, les plantations sont souvent perçues de manière défavorable par le public et les écologistes (Carnus *et al.*, 2003 ; Hartley, 2002). Pour appuyer cette idée, la faune aviaire des plantations a été fréquemment reportée comme étant moins diversifiée que celle de forêts naturelles ou semi-naturelles (Baguette, Deceuninck et Muller, 1994 ; Gjerde et Saetersdal, 1997 ; Twedt *et al.*, 1999). En fait, la plupart des recherches comparant des forêts non aménagées avec des plantations ont démontré une faune aviaire ou une flore appauvrie dans ces dernières (Moore et Allen, 1999 ; Palik et Engstrom, 1999). La présence d'espèces rares ou menacées est également rarement mentionnée dans les plantations (Carnus *et al.*, 2003). Puisque la désignation d'aires de sylviculture intensives peut soulever une controverse et afin de minimiser les impacts négatifs, l'utilisation de sites dégradés devrait être le plus souvent envisagée (Hunter, 1990 ; Seymour et Hunter, 1999).

Au Québec, beaucoup de propriétaires de lots agricoles sont encouragés par le gouvernement à planter des essences commerciales dans les champs abandonnés (Hamel, Falardeau et Savard, 1999). La conversion de friches agricoles en sites voués à la ligniculture intensive est attrayante, tout d'abord parce que ces milieux possèdent généralement les qualités requises pour l'établissement de plantations, mais aussi parce qu'elle permet d'accroître la production de matière ligneuse à proximité des usines de transformation et qu'elle remet des sites abandonnés en production. Toutefois, bien que cette option offre de nombreux avantages économiques, les friches agricoles peuvent jouer un rôle important en offrant des conditions d'habitats qui peuvent être absentes du paysage agroforestier. Les sites en début de régénération, tels que les friches, représentent également un habitat propice pour des espèces tel que le lièvre d'Amérique (*Lepus americanus*) une espèce clé de la forêt boréale (Boutin *et al.*, 2003 ; Keith, 1990 ; Krebs, 1996), la gélinotte huppée (*Bonasa umbellus*) (Dessecker et McAuley, 2001 ; Rusch *et al.*, 2000) ainsi que pour plusieurs autres animaux à fourrure importants pour la trappe (Fuller et DeStefano, 2003 ; Litvaitis, 2001 ; Litvaitis, Tash et Stevens, 2006). Au regard de nos connaissances actuelles, on peut donc s'attendre à ce que la transformation des friches, un milieu hétérogène caractérisé par une strate arbustive dense, en un milieu homogène et moins diversifié dans sa structure verticale va entraîner la disparition d'espèces spécialisées par des espèces plus généralistes. D'un point de vue de conservation et de maintien des populations animales, cet appauvrissement sera perçu de manière négative. Au Québec, une étude réalisée au Lac Saint-Jean a déjà montré que la conversion des friches agricoles en plantation de pin gris (*Pinus baksiana*) avait un effet négatif sur les communautés d'oiseaux, plus particulièrement si les sites étaient dégagés mécaniquement (Hamel, Falardeau et Savard, 1999).

Impacts sociaux économiques

En Abitibi-Témiscamingue, la chasse au petit gibier est une activité importante pour les résidents des collectivités rurales (FAPAQ, 2002). La région se classait deuxième quant aux nombre des permis de chasse au petit gibier vendus en 2000 (15 880 permis), soit tout juste derrière la Montérégie (MRNF, 2003) et la majorité des chasseurs (95%) pratiquent plus de 75% de leurs activités dans la région (MRNF, 2003). Contrairement aux autres types de chasse, la majorité des jours de chasse (62%) lors la chasse au petit gibier sont réalisés en expédition plutôt qu'en voyage (MRNF, 2003). Les retombés économiques de la chasse au petit gibier se font donc sentir localement et elles peuvent représenter un apport économique substantiel puisque les dépenses moyennes des chasseurs ont été évaluées à 430$/an (MRNF, 2003). Si la transformation massive de friches en plantations proche des zones habitées entraîne une baisse de population des espèces gibiers, cette conversion pourrait avoir des impacts sociaux et économiques négatifs pour les activités de chasse au petit gibier en région.

Objectif de l'étude

L'objectif général de la présente étude est donc d'évaluer et de comparer le potentiel faunique de plantations résineuses et de friches agricoles de différents stades de croissance afin de déterminer leurs contributions respectives au maintien de la faune gibier régionale. Bien que des plantations de peupliers hybrides soient installées dans la région et que cette option soit sérieusement envisagée dans le plan de développement régional, l'impact de celles-ci ne sera pas étudié en raison de la faible superficie (≤ 3 ha) et de la faible variété de l'âge des dispositifs expérimentaux présents dans l'aire d'étude (≤ 5 ans) au début du projet.

Ce projet de recherche s'inscrit dans le cadre du projet pilote visant à évaluer la faisabilité du concept de la Triade dans la région de l'Abitibi-Témiscamingue démarré par la Chaire industrielle CRSNG-UQAM-UQAT en aménagement forestier durable. Cette étude tente de répondre en partie à l'objectif 2 : Évaluation des effets de la conversion de sites sur la diversité biologique. La question sera posée à savoir si les plantations résineuses représentent un apport ou une perte au niveau de l'habitat de deux espèces gibier, soit le lièvre d'Amérique et la gélinotte huppée.

Le mémoire s'articule en deux articles indépendants qui concernent respectivement chacune des deux espèces. Le premier article concerne le lièvre et son principal objectif est d'évaluer l'utilisation de l'habitat par cette espèce dans des plantations et des friches de différents stades de développement. Un objectif secondaire était de comparer pour le lièvre les mesures d'utilisations obtenues à l'aide de deux techniques d'inventaires distinctes, soit le pistage hivernal le long de transects et les dénombrements de crottins dans des parcelles circulaires. Puisque l'interprétation des inventaires de crottins peuvent être biaisés par des taux de dégradation différents en fonction des milieux (Murray, Ellsworth et Zack, 2005 ; Prugh et Krebs, 2004), nous avons également mené une expérience visant à déterminer les taux de dégradation de crottins afin de contrôler ce facteur. Le deuxième article porte sur l'impact de la transformation des friches agricoles en plantations résineuses sur la gélinotte huppée. Des inventaires auditifs de mâles tambourineurs ont été réalisés au printemps 2005 et 2006 afin d'estimer l'utilisation des deux types de milieux par la gélinotte huppée, en tenant compte de facteurs pouvant affecter la détection de ceux-ci.

ARTICLE I

Snowshoe Hare Habitat use in Abandoned Farm Fields and Plantations

SNOWSHOE HARE HABITAT USE IN ABANDONED FARM FIELDS AND PLANTATIONS

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Abstract

Intensively managed plantations are increasingly needed to fulfill societal needs for wood products. Abandoned farm fields are often targeted for conversion to plantations since they are already degraded and are generally located close to the mills. While plantations offer many advantages in terms of fiber production, they are often perceived negatively because of their impact on biodiversity. Indeed, early seral stages of abandoned farm fields generally represent good habitat for snowshoe hare (*Lepus americanus*), a keystone species in the boreal forest. Transforming abandoned farm fields into homogeneous plantations could therefore represent a loss of habitat for this important game species. Our main objective was to compare habitat potential of plantations (n = 19) and old-fields (n = 22) for hare. We used pellet counts and snow tracking to assess habitat use in both habitat types. Pellet counts were analyzed using generalized estimating equations that integrated autoregressive correlations within sites, while snow tracking results were analyzed using repeated count data and models explicitly estimating detectability. Both techniques yielded similar results: hare winter habitat use is mostly affected by vegetation cover rather than habitat type. In the short term, plantations offer protective cover similar to the one found in abandoned farm fields. However, upon reaching a certain height ($\geq$ 7m), plantations are mechanically pruned and lose their protective quality. Both survey techniques seemed reliable, but each had its limitations. We suggest that snow tracking is more appropriate to differentiate habitat use, since fecal pellet inventories can be affected by differential degradation rates between habitats, likely linked to changes in diets among habitats in the current study.

Résumé

Les plantations à haut rendement seront de plus en plus nécessaires pour remplir les besoins grandissants de la société pour les produits dérivés du bois. Les friches agricoles sont souvent visées par des programmes de conversion en plantations, car ces milieux sont déjà dégradés et sont généralement à proximité des usines de transformation. Bien que les plantations offrent plusieurs avantages en ce qui concerne la production de fibres ligneuses, elles sont souvent perçues de manière négative à cause de leurs impacts sur la biodiversité. En effet, les peuplements en régénération tels que les friches sont généralement des bons habitats pour le lièvre d'Amérique (*Lepus americanus*) une espèce clé de la forêt boréale. Transformer les friches en milieux homogènes et résineux pourrait donc représenter une perte d'habitat pour le lièvre. Notre objectif principal était donc de comparer le potentiel des plantations (n = 19) et des friches (n = 21) en tant qu'habitat pour le lièvre. Nous avons effectué des inventaires de crottins et du pistage hivernal pour évaluer le potentiel des deux types d'habitat. Les inventaires de crottin ont été analysés à l'aide d'équations d'estimations généralisées qui intégraient une corrélation autorégressive dans les sites. Les résultats du pistage ont été analysés à l'aide de mesures répétées qui permettent d'estimer à la fois l'abondance et la détectabilité. Les deux techniques d'inventaires ont donné des résultats sensiblement similaires : l'utilisation d'habitat d'hiver du lièvre est influencée par le couvert végétal plutôt que par le type d'habitat. À court terme, les plantations offriront le même couvert de protection que les friches. Toutefois, après un certain âge, les plantations sont élaguées et n'offrent plus de protection au lièvre. Les deux techniques d'inventaire utilisées se sont montrées fiables, mais toutes deux ont des limitations. Nous croyons que le pistage est plus approprié pour les comparaisons d'habitat puisque les inventaires de crottins peuvent être biaisés par le rythme de dégradation des crottins. Celui-ci peut varier entre les différents milieux en fonction de différents facteurs écologiques tels que l'alimentation, comme nos résultats semblent l'indiquer dans cette étude.

Key Words: abandoned farm fields, fecal pellet counts, plantations, snowshoe hare, snow tracking.

Introduction

Sustainable forest management has replaced sustained yield as the new management strategy in most natural forests allocated to forestry (Messier and Kneeshaw 1999). As a result, forest planners must now consider both an increasing number of alternative forest objectives and an increasing pressure to use the forest resources more efficiently (Boyland et al. 2004). 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). Since 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). Plantations are much more productive than natural stands (Binkley 1997, South 1999) and require less area to produce industrial wood (Sedjo and Botkin 1997, Sedjo 1999). Gains in productivity made through the use of intensive plantations could fulfill societal needs for wood products, but could also allow managers to reduce the pressure on natural forests and create new conservation areas (Hunter and Calhoun 1995, Seymour and Hunter 1999, Boyland et al. 2004).

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 part, by the scientific literature available. For instance, the avifauna in plantations is frequently reported as less diversified than that in natural forests and semi-natural forests (Gjerde and Saetersdal 1997, Moore and Allen 1999, Palik and Engstrom 1999, Twedt et al. 1999). Negative effects have also been shown for other less-studied taxa, such as amphibians, small mammals (Moore and Allen 1999, Waldick et al. 1999), and arthropods (Fahy and Gormally 1998, 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 negative impacts (Hunter 1990, Ehrlich 1996, 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 the fields' owners to benefit financially from otherwise unproductive land. The scenario described above occurs in Quebec, where rural depopulation of northern regions has left many agricultural lands abandoned (Gachet et al. 2007). At the end of the 1970s, the provincial government created programs of subsidies to encourage owners of abandoned farm fields to transform them into plantations (Hamel et al. 1999).

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 hare (*Lepus americanus*) (Litvaitis 2001, Fuller and DeStefano 2003), which is a game species providing an important socio-economic benefit in several regions (Bittner and Rongstad 1982, MRNFQ 2003). Thus, the rapid transformation of heterogeneous abandoned farm fields with a developed shrub layer into homogenous habitats, such as mono-specific plantations, could be negative for snowshoe hare populations. Due to its significant impact on both vegetation and predators, snowshoe hare is considered a keystone species in the boreal forest of North America (Keith 1990, Krebs 1996, Boutin et al. 2003). Consequently, management decisions affecting snowshoe hare 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 snowshoe hare habitat use. Since cover is an important factor for snowshoe hare, we predicted that snowshoe hare habitat use would depend on lateral cover in both habitat types (Wolfe et al. 1982, Litvaitis et al. 1985b, Ferron et al. 1998), but that this species would use the edges of plantations more intensively than the interior since deciduous browse would be limited in that habitat. We used snow tracking and pellet counts to attain this objective.

Study area

The study was conducted in the Abitibi region, northwestern Quebec, Canada (Figure 1). While many old fields have already been converted to plantations in Quebec, approximately 100,000 ha of abandoned farm fields are present to date in Abitibi. As a result, this region offered a good opportunity to study the effects of old farm field conversion to plantations on snowshoe hare. This region is part of the northern Clay Belt of Quebec and Ontario, a large physiographic area created by lacustrine deposits left after the maximal extension of the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Consequently, the main surficial deposits are silt, clay, and varved sands originating from the proglacial lake Ojibway (Vincent and Hardy 1977), and the topography is generally flat (Vincent 1995).

The study area was located at the southern limit of the boreal forest and vegetation was characterized by a mixed-wood composition dominated by balsam fir (*Abies balsamea*), black spruce *(Picea mariana*), and paper birch (*Betula papyrifera*), with white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) as codominants (Rowe 1972). In the agricultural part of the landscape, the forest was composed 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. Annual precipitation was 823 mm, of which 639 mm falls as rain from April to November. The mean frost-free period was 64 days (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) in the agro-forested landscape of Abitibi. Plantations consisted of jack pine (*Pinus banksiana*, n = 14), or more infrequently, white spruce (n = 5). All sites selected had at least one adjacent forest stand. Since we wanted to asses edge effect in our design, distance to the other edges had to at least twice the distance to the edge we selected (e.g. ≥ 150 m.) Most sites were ≥ 9ha (300 m x 300 m) but in some cases, a site was used if the area behind it was not susceptible to being used by wildlife (e.g., farm field, grazing field, major road) and the distance from the forested edge was at least 200 m (e.g. ≥ 6ha (300m x 200m)). Each site was ≥ 1 km apart from the nearest neighboring site, in order to be considered statistically independent from one another.

We wanted to investigate habitat use during all stages of development in both ABF and PL so we tried to diversify the sites selected for our study. It was impossible to include age as a stratification variable either for ABF, because their colonization by Gramineae sp. induced a pattern of succession by woody vegetation that was inconsistent across time, or for PL, because growth varied greatly across species and soil types. Instead, we used an index based on the developmental stage of the woody vegetation to represent the evolution of ABF and PL through time (Table 1). Twenty-nine sites were chosen during spring 2004, 5 were added during autumn 2004, and 7 were added during spring 2005, for a total of 41 sites (Table 1).

Methods

There are many techniques, both direct and indirect, to measure snowshoe hare abundance and habitat use. Since we wanted to cover a large area and wide array of conditions, we opted for two techniques that were inexpensive: snow tracking and pellet counts (Litvaitis et al. 1985a, Mullen 2003). Each method has its advantages and limitations. Snow tracking is inexpensive for studying a large area, but it can only provide information about winter habitat use (Litvaitis et al. 1985a, Mullen 2003). Another important limitation is that snow tracking can be influenced by weather, since snowshoe hare activity is affected by temperature (Theau and Ferron 2000, 2001). Fecal pellet counts are inexpensive, simple to carry out, do not require much manpower (Litvaitis et al. 1985a), and are used frequently. However, the degradation rate of fecal pellets has to be estimated, especially if this technique is used to compare habitat use between structurally different habitat types (Prugh and Krebs 2004, Murray et al. 2005). For that part of our data analysis concerning snow tracking, we used an approach based on the estimation of the probability of detection to account for temperature and delay since the last snowfall. We also designed a pellet degradation experiment to estimate differential pellet degradation within each habitat type.

Fecal pellet and vegetation inventory

Seven permanent sampling stations were placed along a 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. Each station was identified with a permanent marker. We estimated snowshoe hare habitat use by counting fecal pellets in a circular 1-m radius plot at each station in the spring (April-May), shortly after snow melt and before the onset of vegetation outburst, (Krebs et al. 1987, Krebs et al. 2001, Murray et al. 2002). Snowshoe hare populations 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 than either rectangular plots or smaller round plots (0.155 m^2) (Murray et al. 2002).

All available browse stems (0.3–2.0 m from the ground) present in the 1 m plot were counted and browsed stems were identified according to Potvin (1995). Lateral cover was estimated by placing a 0.3 m × 2 m profile board (Nudds 1977) at 15 m on each side of the station. The vertical canopy closure of trees (> 4 m high) and shrubs (1.5–4 m) was evaluated with 5 interception points (3-m spacing) on each side of the station (Bertrand and Potvin 2003). Cover measures were repeated in line with the transect at 10 and 20 m in the forested edge. Forested edges stand composition was indentified and classified according to the Quebec Ministry of

Natural Resources and Wildlife (MRNFQ) classification. Vegetation measures were made in either 2004 or 2005 when we established the stations. Fecal pellet counts were repeated in 2004, 2005, and 2006. Since using uncleared plots for analysis can lead to biased estimates (Krebs et al. 2001, Prugh and Krebs 2004, Murray et al. 2005), we only used data from cleared plots for 2005 and 2006 in our analysis.

Fecal pellet degradation

Prugh and Krebs (2004) and Murray et al. (2005) reported different degradation rates for fecal pellets in different habitat types. When we conducted the first inventories in 2004, we also observed a difference in size and shape between fecal pellets found in ABF and PL (C. Roy pers. observ.). To determine if habitat type influenced pellet degradation, we quantified degradation rates of fecal pellets on our sites, according to 1) the two habitat types sampled, and 2) the origin of the pellets. All fecal pellets were collected during one day in one ABF and one PL, during winter 2004-2005. Pellets were collected away from the stations toward the center of the site. We constructed 30 pellet cages (30 cm diameter x 20 cm high) out of 6.3-mm mesh hardware cloth. Prugh and Krebs (2004) used mesh hardware cloth on the tops of their cages to prevent new pellets from entering during winter but this design excluded fallen leaves. Since leaf deposition could play an important role in our study, we opted to sew a plastic screen mesh at the bottom of our cages that would prevent the deposition of new pellets during winter while at the same time allowing leaves to come into contact with the fecal pellets.

We placed a cage in the center of 15 ABF and 15 PL during spring 2005 (April –May). 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 (April –May): 27 cages were still intact and 3 (all in ABF) that had been damaged 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). A pellet was considered "new" if it looked firm, was lightly colored on the outside, and had a greenish hue on the inside. A pellet was considered "old" if it was showing evident signs of degradation, or if the outside was dark brown and the inside was brownish. For each cage, we also categorized fallen leaf cover in four different classes (0-25%; 26-50%; 51-75%; 76-100%) and recorded whether the drainage of the ground on which the cage rested was considered good or poor.

Snow tracking

We conducted snow track counts from December 2004-March 2005 as well as from December 2005-March 2006 to evaluate the utilization of habitat by snowshoe 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. A transect was permanently flagged for repeated surveys in the center of each site (i.e., same sites were used for two sampling techniques). On a band extending 1 m on either side of every transect, we noted each track that crossed our path and its location, relative to the start of the transect, was measured with a thread distance counter (i.e., chain man ±1 m). Signs of snowshoe 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 significant snowfall for each visit and we calculated the mean temperature for the nights since the last snowfall using data obtained from the closest Environment Canada weather station. Twenty sites were visited three times and 14 sites were visited twice during winter 2004-2005. Optimal snow conditions were much more restrictive in 2005-2006: every site was visited at least once and few were visited twice. Since models estimating detection probability require at least two visits (see below), data collected during winter 2005-2006 were not considered for this analysis.

Statistical analyses

Fecal pellet inventory. — Fecal pellet counts from the inventory stations were analyzed with generalized estimating equations (GEEs), using the GENMOD procedure in SAS 9.1 (Stokes et al. 2001). This method was an efficient way of dealing with the non-independence of the seven stations within any given site and avoiding pseudoreplication (Hurlbert 1984). 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 did not follow a Poisson distribution (i.e., data were substantially overdispersed), we used a negative binomial GEE model (McCullagh and Nelder 1989). Data were analyzed separately for 2005 and 2006.

We defined a set of candidate models using habitat variables that we measured and which could influence hare habitat use, according to the literature. Explanatory variables that were considered included habitat type (ABF or PL), lateral cover (Litvaitis et al. 1985a, Ferron et al. 1998, de Bellefeuille et al. 2001), vertical cover (Wolfe et al. 1982, Potvin et al. 2005), a quadratic effect of the vertical cover (Orr and Dodds 1982), and the logarithm of the distance from the edge (Conroy et al. 1979, Wolff 1980, Ferron and Ouellet 1992). To minimize the number of explanatory variables and avoid overfitting our models, we combined indices of vertical canopy closure for trees and shrubs by collapsing their values into a single index.

Typical model selection with the Akaike information criterion (AIC) is based on maximum likelihood (Burnham and Anderson 2002), whereas GEEs rely on alternative (non-likelihood based) fitting strategies (Pan 2001). Thus, we used a modification to the AIC, where the likelihood is replaced with the quasi-likelihood that was calculated from the estimating equations (Pan 2001) to determine a quasi-likelihood information criterion (QIC) value for each model. We then calculated ΔQIC and weights (ω_i) for each model following conventional procedures (Burnham and Anderson 2002). The effect of each variable was then assessed using multimodel inference (Burnham and Anderson 2002).

Pellet degradation. — To determine the influence of the variables of interest on pellet degradation, we used as 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 the cage at the beginning of the experiment. Given that the 30 pellets in a given cage are not independent trials, we used a generalized mixed-linear model (GLMM) for binomial responses that treated cage as a random effect. Data analysis was performed with function glmmPQL of the MASS and nlme packages in R 2.5.1 (Venables and Ripley 2002). We used the origin of the pellet, the type of habitat, leaf cover (because of data aggregation data were collapsed to a binary variable: $\leq 50\%$ or $> 50\%$), drainage, and the interaction between habitat and origin as explanatory variables.

Snow tracking. — For each site, we calculated the sum of all snowshoe hare tracks observed in the first 200 m of transect. Single tracks counted for one. Most trails contained two tracks, so we gave them a value of 2. Networks were given an arbitrary value of 3, since by definition, they were impossible to count. We then reported the number of observations by 10-m distance increments. Data were analyzed with repeated count models (Royle 2004b) that allowed us to estimate the probability of detection. We constructed different models that considered the effects of days since the last snowfall and temperature on nights preceding each survey on the probability of detection (p) and the effect of habitat type, lateral cover, and vertical cover on the abundance (λ) of tracks. As the snowshoe hare is a nocturnal animal (Gilbert and Boutin 1991), we used the average temperature during the previous nights since the last snowfall if the track count was conducted after more than one day. For lateral cover and vertical cover, we used the average of the seven stations for each site (described above). The quadratic effect of vertical cover was not included to avoid overfitting our models. Each model was subsequently run in PRESENCE 2.0 and we used Akaike's information criterion corrected for small samples (AIC_c) to select the most parsimonious models (Burnham and Anderson 2002). Multimodel inference was also used to determine the effects of each parameter (Burnham and Anderson 2002). We assessed model fit of the global model with a parametric bootstrap procedure described by Royle (2004a), which we implemented in R.

Browse inventory. — Browse data were summarized 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 9.1, with habitat type and the logarithm of available browse as explanatory variables. Each stem class was analyzed separately.

Vegetation cover. — We calculated average 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 9.1. We used vegetation stage, habitat type, and their interaction as explanatory variables.

Results

Fecal pellet inventories

In 2005, 54.7% of the 203 plots contained pellets and there was an average of ten pellets per plot ($\bar{x} \pm$ SD: 10.64 ± 25.46). The general model ranked highest among our candidate models, with a QIC weight of 0.99 (Table 2). Lateral cover (Model-averaged β = 0.039, 90% CI: 0.029, 0.049) and vertical cover (Model-averaged β = 0.018, 90% CI: 0.003, 0.033) had a positive effect on hare habitat use. We found significant interactive effects of habitat type and the logarithm of the distance from the edge for hare habitat use in 2005. Hare avoided the edge more strongly in PL than in ABF (Model-averaged β = -0.868, 90% CI: -1.487, -0.249). The other parameters did not influence snowshoe hare habitat use.

In 2006, 69.3% of the 287 plots contained pellets, and on average, there were twenty pellets in each plot ($\bar{x} \pm$ SD: 19.97 ± 48.54). The model consisting of (Type + LC + VC + DE + DE*Type) ranked highest (w_i = 0.846), with the general model following in second place with a ΔQIC =

3.40 (Table 3). Here again, lateral cover (Model-averaged β = 0.015, 90% CI: 0.008, 0.022), vertical cover (Model-averaged β = 0.013, 90% CI: 0.006, 0.020), and the logarithm of distance from the edge (Model-averaged β = 0.379, 90% CI: = 0.734, 0.024) had a positive effect on hare habitat use. None of the other parameters influenced the response variable.

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 one year. Leaf cover was highly variable ($\bar{x}$ ± SD: 42.78% ± 41.89%) and 8 sites were well-drained, whereas the remainder of the sites (n = 19) had poor drainage. Because the interaction between habitat type and origin was not significant (β = -0.482, SE = 0.383, t = -1.259, P = 0.219), it was deleted from the mixed model. Pellet degradation was not affected by habitat type, leaf cover, or drainage class, but the pellets from ABF degraded faster than those originating from a PL (β = 0.427; SE= 0.193; P = 0.036, Table 4).

Snow tracking

Surveys were conducted on 18 different days in 2004-2005. Eight surveys were conducted the day following a snowfall, 6 were conducted two days after snowfall, and 4 were conducted three days after snowfall. Mean temperature on nights preceding surveys varied between -1.6°C and -35.0°C ($\bar{x}$ ± SD: -20.4°C ± 5.8°C). We encountered snow tracks in 86 (79%) of our 106 transects. Of these tracks, 80.0% occurred as single tracks, 11.7% as multiple tracks (trails), and 8.3% occurred as networks (overlapping and indistinguishable tracks). On average, we detected fourteen tracks per site ($\bar{x}$ ± SD: 14.34 ± 16.93). The general model provided a good fit to the data (parametric bootstrap P = 0.946, n = 1000 iterations). Three count models ranked highly ($\Delta AIC_c < 2$) among our candidate model set, followed by a fourth one with ΔAIC_c of 2.16 (Table 5). These models consistently included the effect of lateral and vertical cover on abundance and the effect of days since the last snowfall on detectability. Following multimodel inference, lateral cover positively increased snowshoe hare habitat use (Figure 2), whereas the other parameters on abundance had wide confidence intervals (Table 6). Days since the last snowfall did not influence the probability of detection (Table 6), but temperature increased the detection of snowshoe hare tracks (Figure 3).

Browse

Overall, the proportion of browsed deciduous stems in ABL did not differ from that in PL (β = 0.0349, SE = 0.4854, P = 0.943) and the same results held for conifer stems (β = 0.4787 SE =

0.5110, P = 0.349, Table 7). However, significantly fewer Rosaceae were browsed in ABF than in PL (β =-0.8511, SE = 0.321, P = 0.011).

Vegetation cover

We found significant interactive effects of habitat type and vegetation Stage on lateral cover ($F_{2,2}$ = 4.25, P = 0.022). Though lateral cover gradually increased between Stages for ABF, there was a sharp decrease for Stage 3 in PL (Figure 4). Vertical cover increased significantly with vegetation Stage in both ABF and PL ($F_{2,2}$ = 29.018, p<0.001) but was more developed in ABF than in PL ($F_{2,1}$ = 11.243, P = 0.002).

Discussion

Snowshoe Hare habitat use

Snowshoe hare habitat use was more closely linked with the development of vegetative cover, especially lateral cover, rather than with habitat type per se (ABF vs. PL). The strong relationship between lateral cover and snowshoe hare has already been reported in the literature (Wolfe et al. 1982, Litvaitis et al. 1985b, Ferron et al. 1998, de Bellefeuille et al. 2001, Ausband and Baty 2005) and shows that conversion of abandoned fields to plantations in our region may have limited effect on snowshoe hare populations if adequate lateral cover is maintained. However, lateral cover did not show the same progression for ABF and PL. While lateral cover increased with the development of ABF, it reached a maximum with Stage 2 in PL and diminished drastically in Stage 3 (Figure 4). Indeed, most plantations are pruned when they reach a height ≥7 m (15-25 years after establishment) and canopy closure in mature plantations prevents the establishment of understory vegetation. The average lateral cover for PL Stage 3 ($\bar{x}$ ± SD: 53.97 ± 21.59) is lower than the 70% level considered suitable for snowshoe hare (Litvaitis et al. 1985b) and close to the minimal level (40%) measured by Carreker (1985), which indicate that these habitats are suboptimal. Although we did not observe negative effects of transforming ABF into PL in the short- to mid-term, snowshoe hare 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 since they are tended and pruned and will reach Stage 3 quickly (15-25 years). In comparision ABF Stage 3 take more than 40 years to reach this stage.

The relationship between snowshoe hare habitat use 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. Snowshoe hare use increased with vertical cover. In contrast, Orr and Dodds (1982) observed a decrease in snowshoe hare habitat when vertical cover exceeded a given threshold, 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 (Figure 4). These differences are explained by the removal of competitive vegetation in PL Stages 1 and 2, and by tree canopy closure in Stage 3 that prevented the establishment of understory vegetation.

Snowshoe hare strongly avoided edges in our sites, though 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 (Vernes et al. 2001, Bergman et al. 2006, Constible et al. 2006, Holmes and Laundre 2006). The 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 the stand interior, and therefore, are potentially avoided by snowshoe hare. Second, the use of edges by snowshoe hare is linked to the interspersion of habitats offering cover and food (Conroy et al. 1979). The lack of such interspersion in our sites probably explains why hare did not use edges. Indeed, the adjacent stands were generally composed of mature aspen stands (38 sites out of 41) with sparse understory vegetation, a habitat generally perceived as poor for snowshoe hare (Wolfe et al. 1982, Guay 1994). These stands had low average lateral cover ($\bar{x} \pm$ SD: 67% ± 14%) (Figure 4). In fact, average lateral cover for these stands is lower than the level considered suitable for snowshoe hare, according to Litvaitis et al. (1985b). Only 16 adjacent stands in our study had an average lateral cover over the level (70%) considered suitable to snowshoe hare according to Litvaitis et al. (1985b), and only 5 stands had an average lateral cover over the level (85%) described as optimal by Ferron and Ouellet (1992). Edge avoidance was more pronounced in PL than in ABF in 2005, a phenomenon probably linked to the fact that edges are 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 two years could be explained, in part, by the fact that 2005 was the year of lowest abundance in the snowshoe hare cycle in the region (Assels et al. 2007; this study) and hare 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 one year, a result consistent with those published by Murray et al. (2005), who reported an average recovery rate of 57% ± 27% ($\bar{x}$ ± SD). However, this contradicts Prugh and Krebs (2004), who reported that only 1% of pellets in willow habitat disappeared after 1 yr, whereas 14% of pellets disappeared after 1 yr in alder and spruce sites. 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. While 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), and Murray et al. (2005) 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, and we encourage researchers to use another design avoiding this potential problem to measure pellet degradation. Drainage quality of the sites had no effect on pellet degradation, but both of our habitat types had an agricultural past, and consequently, better drainage than one would expect to find in natural forests.

An implicit assumption in previous applications of the hare pellet-plot methods is that pellets persist in the field for at least 1 year (Murray et al. 2005). Assuming that the plastic screen mesh we used in this experiment did not bias our results, our pellet degradation experiment shows that this assumption can be unrealistic. 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 hare habitat use based on pellet inventories likely better represent winter rather than year-round habitat use.

The difference that we observed in degradation rate across pellet origins supports our previous observations that pellets in different habitats had a distinct color and shape. We hypothesize that this difference is linked to the diet of snowshoe hare: 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 the difference in protein content in the diet that varied across season. 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 which is probably present in this study, also suggests that annual counts might not be enough, in some cases, to adequately assess habitat use and that counts should be conducted more than once a year. For studies covering a large geographic area, these additional surveys could be an important constraint. However, conducting several inventories at different times of the year enables the assessment of habitat use across seasons (Litvaitis et al. 1985a, Mullen 2003). Although we did not assess probability of detection for fecal pellet inventories in our study, all habitat types had an agricultural past and a relatively similar substrate (i.e., bare clay), and therefore, we assumed that detection was comparable across habitat types. However, this assumption probably does not hold for all kinds of substrate, namely those consisting of lichens or moss, and should be formally checked with approaches enabling the estimation of detectability (e.g., Williams et al. 2002; MacKenzie et al. 2006).

Snow tracking and probability of detection

Estimating the probability of detection allowed us much more flexibility than was possible in previous studies (Ausband and Baty 2005, Potvin et al. 2005) by widening the sampling window, as surveys at different sites could be conducted on different days and weather conditions. Temperature had weak positive effects on the probability to detect tracks (Figure 3). This result could be linked to the reduced activity of snowshoe hare in cold temperatures (Theau and Ferron 2000; 2001, Mullen 2003). The 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 less than 48 hours after a snowfall. A greater variation in delay after snowfall before conducting surveys would likely influence track counts. Whereas the number of overlapping tracks (trail networks) was relatively low in our study (8%), we also expect this number of networks to increase with time elapsed. Considering the impossibility of discriminating individual tracks when networks are present, we believe that the occurrence of trail networks should be avoided as much as possible in a given snow tracking study. In habitats with high densities of the target species, such as some sites in this study, it means that the sampling window can be short and limited to a few days after snowfall. The main drawback linked to snow tracking surveys, therefore, is that field biologists are highly dependent on suitable weather conditions (sufficient snow, delay between snowfall, etc.). Opportunities for snow tracking also occur randomly, with only a few days or hours notice, and can be a logistical problem if the field staff is not readily available.

Management implications

Our results lead us to conclude that the transformation of abandoned farm fields into plantations could have a negative impact on hare populations in Abitibi. 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 age and lose their protective quality. The impact of transforming abandoned farm fields into plantations will depend on the scale and speed of conversion (Hartley 2002). We concur with Hartley (2002) that the transformation of abandoned farm fields into plantations in several regions will have to be monitored at the landscape scale in order to minimize its negative impacts.

Both techniques that we used in this study to assess snowshoe hare habitat use yielded similar results. However, we suggest that snow tracking is probably more appropriate to measuring habitat use since fecal pellet inventories can be affected by differential degradation rates. With careful planning, snow tracking could also be used to monitor mammal communities (Thompson et al. 1989, Pellikka et al. 2005) instead of only one focal species. However, fecal pellet inventories are probably more appropriate for determining the real abundance of snowshoe hare (e.g., Krebs et al. 2001, Murray et al. 2002, Homyack et al. 2006), as long as fecal pellet degradation rates are correctly estimated. Both techniques might be affected by detection issues and care should be taken to control for this factor whenever it is possible.

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Table 1 Stratification of study sites in each vegetation Stage in 2004-2006 for abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada.

	ABF			PL		
	Spring 2004	Fall 2004	Spring 2005	Spring 2004	Fall 2004	Spring 2005
Stage 1[a]	5	5	8	0	2	4
Stage 2[b]	7	7	9	5	7	7
Stage 3[c]	5	5	5	7	8	8

[a] Stage 1 of ABF had at least 25% and below 50% of the ground covered by woody vegetation, dominant trees of stage 1 in PL were 1-3 m high.

[b] Stage 2 of ABF had >50% of their ground covered by woody vegetation, dominant trees of stage 2 in PL were 3-7 m high.

[c] Stage 3 of ABF had young shade intolerant trees established on most of their area, dominant trees of stage 3 in PL were > 7 m high.

Table 2 Model selection results for the GEE models that included variables for habitat type (TY), lateral cover (LC), vertical cover (VC), quadratic effect of lateral cover (VC2) and log of distance from the edge (DE), fitted to data from inventories conducted in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during spring 2005.

Model	Quasi-likelihood	K[a]	QIC_c	ΔQIC	ω_i
TY LC VC VC^2 DE DE×TY	-1263.19	8	2542.911	0.00	0.990
TY LC VC DE DE×TY	-1268.83	7	2552.072	9.16	0.010
LC VC VC^2	-1330.78	4	2671.779	128.87	0.000
LC VC	-1343.1	3	2694.345	151.43	0.000
TY DE DE×TY	-1468.69	3	2945.525	402.61	0.000
TY	-1482.19	2	2968.423	425.51	0.000

[a] No. of estimating parameters in candidate model.

Table 3 Model selection results for the GEE models that included variables for habitat type (TY), lateral cover (LC), vertical cover (VC), quadratic effect of lateral cover (VC2), and log of distance from the edge (DE), fitted to data from fecal pellet inventories conducted in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during spring 2006.

Model	Quasi-likelihood	K[a]	QIC_c	ΔQIC	ω_i
TY LC VC DE DE×TY	-1840.97	7	3699.44	0.00	0.846
TY LC VC VC^2 DE DE×TY	-1841.61	8	3703.87	3.40	0.154
TY DE DE×TY	-1999.63	5	4008.40	311.15	0.000
TY	-2010.4	2	4027.47	330.54	0.000
LC VC VC^2	-2015.18	4	4042.12	344.23	0.000
LC VC	-2030.23	3	4069.60	372.25	0.000

[a] No. of estimating parameters in candidate model.

Table 4 Results for the fixed effects of the generalized mixed-linear model for binomial responses on pellet degradation measured in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, in 2005-2006. Note that the probability of not degrading was modeled (i.e., number of pellets with low degradation/total number of pellets) and that names in parentheses denote the reference level for each categorical variable included.

	Estimate	SE	P
Origin (PL)	0.427	0.193	0.036
Type (PL)	0.162	1.431	0.911
Leaf cover (≤ 50%)	0.579	1.368	0.676
Drainage (dry)	0.383	1.304	0.771

Table 5 Model selection results based on AICc of Royle count models for snow tracking inventories in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during winter 2004-2005.

Model[a]	Model likelihood	K[b]	AIC_c	ΔAIC_c	ω_i
$\lambda(LC + VC)\ p(DL)$	-84.390	5	183.891	0.00	0.328
$\lambda(TY + LC + VC)\ p(DL)$	-83.100	6	184.478	0.59	0.245
$\lambda(LC + VC)\ p(DL + T)$	-83.085	6	184.508	0.62	0.241
$\lambda(TY + LC + VC)\ p(DL + T)$	-82.145	7	186.050	2.16	0.112
$\lambda(.)\ p(DL)$	-93.495	3	188.159	4.27	0.039
$\lambda(TY)\ p(DL)$	-89.390	4	189.783	5.89	0.017
$\lambda(.)\ p(DL + T)$	-88.820	4	190.683	6.79	0.011
$\lambda(TY)\ p(DL + T)$	-89.270	5	192.521	8.63	0.004
$\lambda(.)\ p(.)$	-88.705	2	193.790	9.90	0.002

[a] Models included the effects of habitat type (TY), lateral cover (LC), and vertical cover (VC) on the number of tracks per 10 m of transect (λ), and the effects of temperature (T) and days since the last snowfall (DL) on probability of detection (p).

[b] No. of estimating parameters in candidate model.

Table 6 Model-averaged parameter estimates of Royle count models used to estimate the number of tracks per 10 m from snow tracking inventories conducted in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during winter 2004-2005.

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

Table 7 Average ± SE of available stems, browsed stems, and proportion of browsed stems for three classes of snowshoe hare browse measured in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during spring 2004-2005.

	Browsed stems				Available stems				Proportion Browsed	
	ABL		PL		ABL		PL		ABL	PL
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	%	%
Deciduous	86	128	28	45	845	637	219	292	10.20	15.26
Rosaceae	21	36	52	69	141	345	128	143	15.01	40.62
Conifers	12	29	89	203	232	698	2013	3190	4.97	4.44

Figure 1 Distribution of 41 study sites surveyed to assess snowshoe hare habitat use in abandoned farm fields (ABF) and plantations (PL) in the Abitibi region of the Province of Quebec, in 2004-2006. ABF sites are represented by a black triangle, PL sites are represented by a gray square, and major cities are represented as a black dot, surrounded by a gray circle.

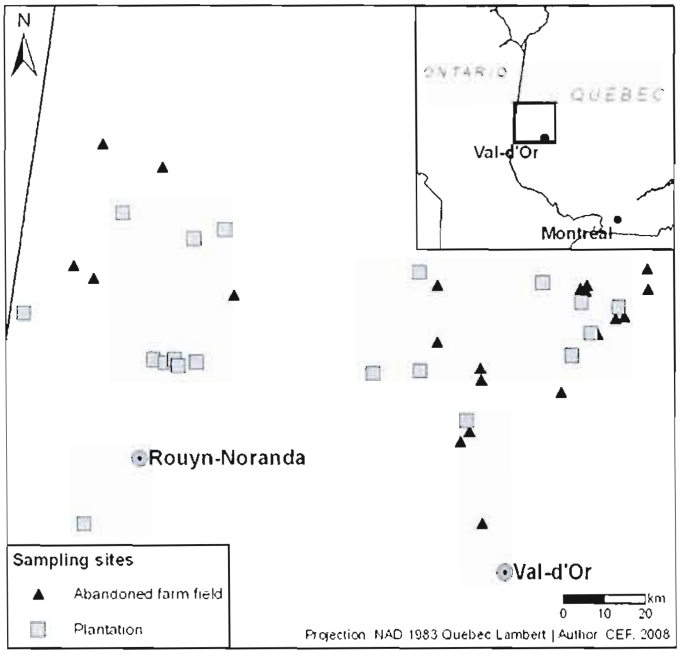


Figure 2 Predicted numbers of snowshoe hare tracks in abandoned farm fields (ABF) and plantations (PL), according to model-averaged predictions as a function of lateral cover, winter 2004-2005 in the Abitibi region, Canada.

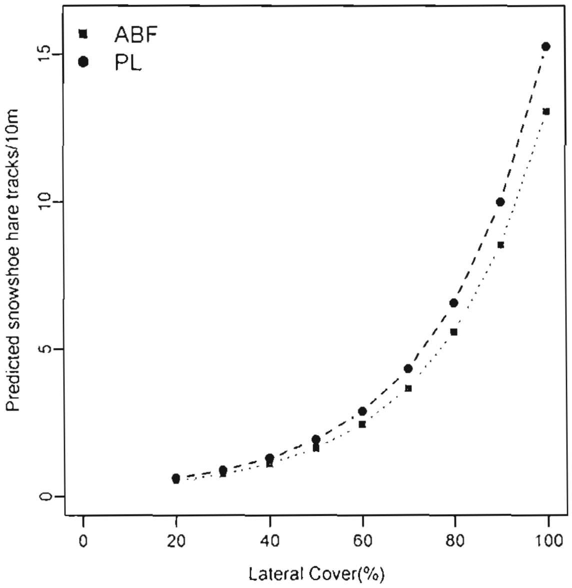


Figure 3 Predicted detection probabilities of snowshoe hare tracks in abandoned farm fields (ABF) and plantations (PL), according to model-averaged predictions as a function of temperature, winter 2004-2005 in the Abitibi region, Canada.

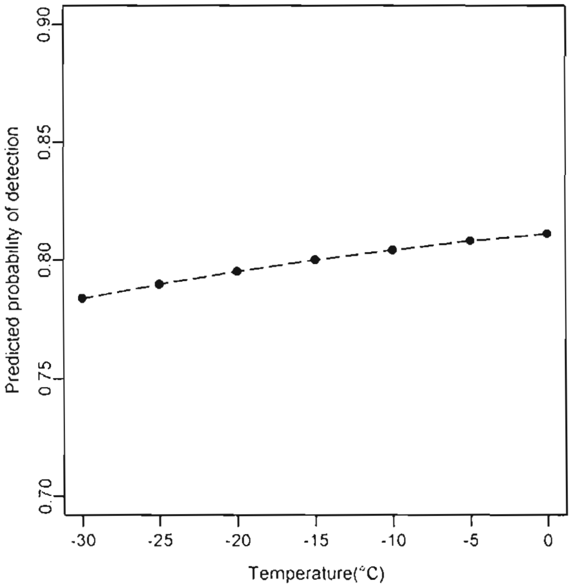
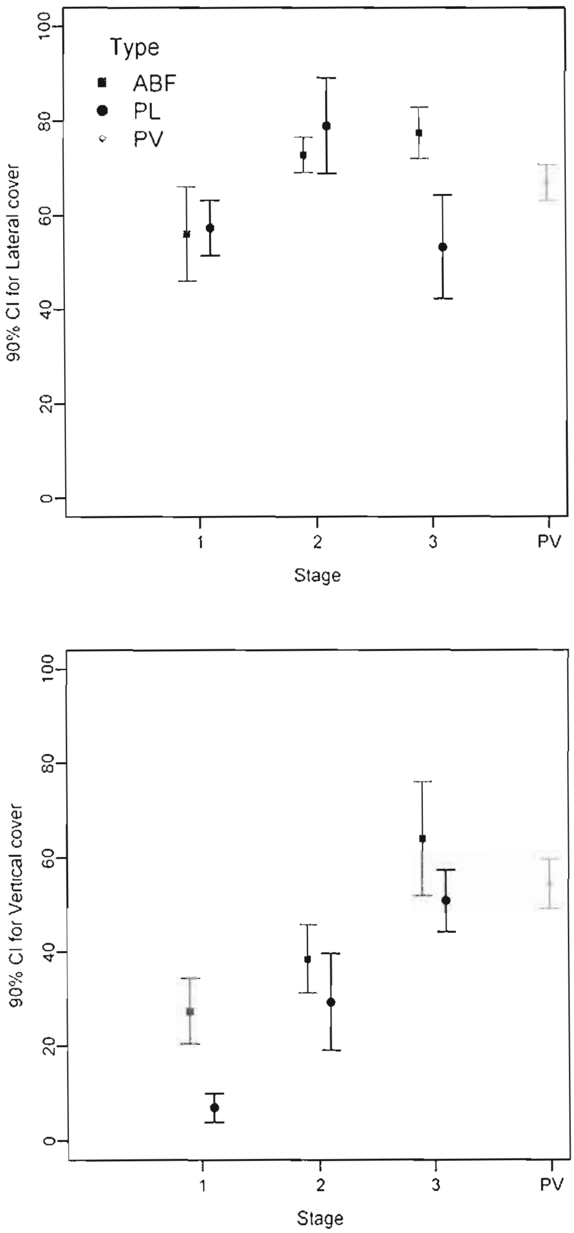


Figure 4 Average lateral cover (LC) and vertical cover (VC) ± 90% CI measured in abandoned farm fields (ABF), plantations (PL) and adjacent forested edges (FE) in Abitibi, Canada, during spring 2004-2005. Stage 1 of ABF had at least 25% and below 50% of the ground covered by woody vegetation, Stage 2 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. Stage 1 was 1-3 m high, Stage 2 was 3-7 m high and Stage 3 was > 7 m high.



ARTICLE II

Impact of transforming abandoned farm fields into plantations on the ruffed grouse in Abitibi

IMPACT OF TRANSFORMING ABANDONED FARM FIELDS INTO PLANTATIONS ON THE RUFFED GROUSE IN ABITIBI

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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. Currently, abandoned farm fields are often targeted for conversion to coniferous plantations. These sites are generally in an early deciduous successional forest stage, an important habitat type for species such as the ruffed grouse. Thus, the conversion could represent a loss of habitat for this species. We evaluated the effects of transforming old fields (n = 22) into coniferous plantations (n = 19) by conducting drumming surveys in 2005 and 2006. We analyzed the number of individuals detected with repeated count models. Results of the auditory surveys conducted in 2005 did not reveal differences in habitat use, but our results were probably influenced by differences in audibility range across habitat types. In 2006, to correct any audibility bias, we located all drumming males heard in each site. Our results show that habitat type was clearly affecting drumming male abundance in 2006, while lateral cover had a consistent positive effect in both years. Temperature and Julian day affected detection probability in 2005 and 2006, respectively. These results suggest that the conversion of old fields into plantations will have a negative effect on ruffed grouse habitat availability, and that planning stand conversion at the landscape scale will be important to minimize such effects. We also suggest that the date of ground snowmelt, rather than photoperiod, influenced the peak drumming period of males in our study area.

Résumé

Les forêts naturelles ne pourront pas subvenir à elles seules aux besoins de notre société pour l'obtention de fibres ligneuses et par conséquent des plantations à haut rendement pourraient s'avérer une source alternative de bois dans le futur. Actuellement, les terres en friches sont souvent visées pour l'établissement de plantations résineuses. Ces milieux sont toutefois généralement composés de milieux en régénération et de forêts de seconde venue, des milieux qui sont importants pour des espèces telles que la gélinotte huppée. La transformation des friches en plantations pourrait donc représenter une perte d'habitat pour cette espèce. Pour évaluer les effets de la transformation des friches (n = 22) en plantations résineuses (n = 19), nous avons réalisé des inventaires auditifs de tambourinage en 2005 et 2006. Les données ont été analysées à l`aide de modèles répétés permettant d'estimer à la fois l'abondance et la probabilité de détection des mâles tambourineurs. Les résultats en 2005 n`ont pas révélé de différences dans l'utilisation des deux milieux, mais nos résultats ont probablement été influencés par un rayon d'audibilité variable entre les deux types d'habitats. En 2006, afin de corriger tout biais lié au rayon d'audibilité, nous avons localisé les mâles qui utilisaient chaque site. En 2006, nos résultats démontrent que le type d'habitat avait un impact sur le nombre de mâles tambourineurs alors que le couvert latéral avait un effet positif constant au cours des deux années. La température et le jour julien ont affecté les probabilités de détection en 2005 et 2006, respectivement. Ces résultats suggèrent que la conversion des friches en plantations résineuses aura des impacts négatifs sur l'habitat de la gélinotte huppée et que la planification de ces conversions devra se faire à l'échelle du paysage afin de minimiser ceux-ci. De plus, nous suggérons que dans notre aire d'étude, c'est la date de la fonte de la neige au sol qui influence le pic de tambourinage plutôt que la photopériode.

Key Words: abandoned farm fields, detection, drumming, plantations, ruffed grouse.

Introduction

Despite regional variations, worldwide demand for wood products is still rising (FAO 2007). Since natural forests may not be able to sustainably answer our needs for wood fibers in the near future, the utilization of plantations might be inevitable (Fenning and Gershenzon 2002; Sedjo and Botkin 1997). Currently, most plantations are established on former agricultural lands (Sedjo 1999). These lands offer many advantages: they are generally productive, close to road networks and mills, and allow the fields' owners to benefit financially from otherwise unproductive land (Sedjo 1999). Using abandoned farm fields also has the advantage of being more ecologically and socially acceptable than transforming natural forests into plantations (Seymour and Hunter 1999). Plantations established on abandoned farm fields could also be included in a TRIAD-type of management, where gains made from intensive plantations could relieve the industrial pressure placed on natural ecosystems (Hunter and Calhoun 1995). In the Province of Quebec, conversion of abandoned farm fields to grow wood fiber began in the early 1980s, following rural depopulation in northern regions. The provincial government also promoted the transformation of abandoned farm fields to plantations by creating a program of subsidies (Hamel et al. 1999). In northwestern Quebec, specifically in the Abitibi-Temiscamingue region, many old fields have subsequently been planted back into conifer plantations.

Although the use of plantations offers many potential advantages, plantations are often viewed unfavorably both by the public and by conservation biologists (Hartley 2002). This perception is supported, in part, by the scientific literature available. For instance, the avifauna in plantations is frequently reported as less diversified than in natural forests and semi-natural forests (Gjerde and Saetersdal 1997; Moore and Allen 1999). Negative effects have also been shown for other less-studied taxa, such as amphibians (Waldick et al. 1999), small mammals (Moore and Allen 1999), and arthropods (Magura et al. 2000). In contrast to plantations, early successional forests or shrub-dominated habitats, like those found on abandoned farm fields, are important for many game species and their predators (Dessecker and McAuley 2001; Fuller and DeStefano 2003; Litvaitis 2001). Ruffed grouse (*Bonasa umbellus*), one of the most popular small game animals in the Province of Quebec (Bourret 1992), is most often found in deciduous and mixed forests of second-growth (Dessecker and

McAuley 2001; Rusch et al. 2000). The high stem densities that are characteristic of shrub-dominated and young forest habitats protect grouse from predators and enable local populations to attain levels substantially greater than in landscapes dominated by mature forests (Dessecker and McAuley 2001; Rusch et al. 2000). Dense deciduous stands are especially important to drumming males in the spring (Thompson et al. 1987), whereas young stands with high stem density or older stands with a well-developed understory of shrubs are important for brooding in the summer (Giroux et al. 2007; Haulton et al. 2003). Ruffed grouse use conifers for roosting or thermal protection during winter (Blanchette et al. 2007; Whitaker and Stauffer 2003), but otherwise avoid pure conifer stands (Endrulat et al. 2005).

Deciduous stands are generally uncommon in the Abitibi region and ruffed grouse are more closely associated with mixed stands (Dussault et al. 1998). A notable exception is the agricultural part of the region, which is composed mainly of second-growth forests that are dominated by aspen because of overexploitation and repeated uncontrolled slash fires during colonization of the region in the 1930s (Vincent 1995). These aspen forests are sometimes interspersed with abandoned old fields, which are dominated by shrub vegetation. Since ruffed grouse are closely associated with both types of vegetation (Dessecker and McAuley 2001; Rusch et al. 2000), the agricultural parts of the land present a diversity of habitats in a relatively small area. This situation is generally seen as beneficial for the ruffed grouse (Gullion 1977). Thus, the transformation of abandoned farm fields with a deciduous and heterogeneous shrub layer into a homogenous habitat dominated by conifers could decrease habitat availability for grouse. In this study, we evaluated the effects of converting abandoned farm fields to conifer plantations on the ruffed grouse. Because this species generally avoids conifer stands, we hypothesized that the transformation of old fields into plantations would reduce ruffed grouse habitat quality and lead to lower population levels in these habitat types.

Materials and methods

Study area and sampling design

The study was conducted in the Abitibi region, northwestern Quebec, Canada (Figure 1). While many old fields have already been converted to plantations in Quebec, approximately 100,000 ha of abandoned farm fields are still present to date in Abitibi. As a result, this region offered a good opportunity to study the effects of old farm field conversion to plantations on ruffed grouse. The region is part of the northern Clay Belt of Quebec and Ontario created after the maximal extension of the proglacial lakes Barlow and Ojibway and characterized by silt, clay, and varved sands deposits (Vincent and Hardy 1977), and a generally flat topography (Vincent 1995).

The study area was located at the southern limit of the boreal forest. The climate is continental with a mean annual temperature of 0.6°C. Annual precipitation is 823 mm, of which 639 mm falls as rain from April to November. The mean frost-free period is 64 days (Environment Canada 1982). The vegetation is characterized by a mixed-wood composition dominated by balsam fir (*Abies balsamea*), black spruce *(Picea mariana*), and paper birch (*Betula papyrifera*), with white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) as codominants (Rowe 1972). We conducted the study in the agro-forested landscape of Abitibi, where human disturbances (agriculture and logging) have transformed the original forest cover. Here, the landscape mainly consisted of agricultural fields, early-successional habitats, and second-growth forest tracts that had originated from overexploitation and burning in the 1940s (Vincent 1995).

The study sites (n = 41) consisted of old fields that had been abandoned (ABF) or planted with conifers (PL). Plantations consisted of jack pine (*Pinus banksiana*, n = 14), or more infrequently, white spruce (n = 5). All sites selected had at least one adjacent forest stand. Distance to the other edge had to at least equal to the distance to the edge we selected (e.g. ≥ 150 m.) In some cases, a site was used if the area behind it was not susceptible to being used by ruffed grouse (e.g., farm field, grazing field, major road) and the distance from the forested edge was at least 200 m (eg. 300m x 200m). Each site was ≥ 1 km apart from the nearest neighboring site, in order to be considered statistically independent from one another.

We wanted to investigate habitat use during all stages of development in both ABF and PL, so we tried to diversify the sites selected for our study. It was impossible to include age as a stratification variable either for ABF, because their colonization by Gramineae induced a pattern of succession by woody vegetation that was inconsistent across time, or for PL, because growth varied greatly across species and soil types. Instead, we used an index based on the development of the woody vegetation to represent the evolution of ABF in time. We defined the three stages of ABF as follows: Stage 1 of ABF (n = 8) had at least 25% and below 50% of the ground covered by woody vegetation (herbaceous-dominated abandoned farm fields), Stage 2 (n = 9) had >50% of the ground covered by woody vegetation (shrub-dominated abandoned farm fields), whereas Stage 3 (n =5) had young shade-intolerant trees established on most of the area (young forest-dominated abandoned farm fields). In 2006, one ABF Stage 2 was cleared during the spring to make way for a plantation and was consequently not used for the surveys. Similarly, we defined an index for PL, based on the height of dominant trees, because age could not be determined precisely for some plantations and growth was variable among tree species. The three stages of PL consisted of: Stage 1 (n = 4) had trees 1-3 m high, Stage 2 (n = 7) consisted of trees 3-7 m high, and Stage 3 (n = 8) was composed of trees > 7 m high.

Vegetation inventories

We used vegetation inventories from a concurrent study on the snowshoe hare (*Lepus americanus*) to characterize vegetation. Seven permanent sampling stations were established along a transect 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. Each station was identified with a permanent marker. Lateral cover was estimated by placing a 0.3 × 2 m profile board (Nudds 1977) at 15 m on each side of the station. The vertical canopy closure of trees (> 4 m high) and shrubs (1.5–4 m) was evaluated with 5 interception points (3-m spacing) on each side of the station (Bertrand and Potvin 2003). Vegetation measures were made once in each site either in 2004 or 2005, when we established the stations. We computed the average of vertical canopy cover across all stations at a site and used these in subsequent statistical analyses.

Ruffed grouse surveys

During the spring mating season, males use a breeding and territorial display called drumming, by beating their wings back and forth (Rusch et al. 2000). Males are faithful to their drumming site and the habitat surrounding these sites is important to the grouse during all seasons and for most life-history stages (Gullion 1984). Females also spend part of their lifetime in these habitats and the sex-ratio is 1:1 for the species during the breeding season (Rusch and Keith 1971). Consequently, drumming surveys have been frequently used to study grouse populations (Dussault et al. 1998; Zimmerman and Gutierrez 2007). For this study, we conducted a drumming survey in each site in spring 2005 and 2006.

A listening station was placed 150 m from the forested edge in each site. We conducted surveys once snow had melted and birds had begun drumming (Dussault et al. 1995). Each survey was conducted by two technicians between 30 minutes before dawn and 6 hours after dawn. Technicians listened for 5 minutes, noting each bird they heard (Dussault et al. 1998) and the general direction of the drumming individual (in degrees). Observations were used only if both technicians could hear the bird and if they could agree on the general direction of the drumming bird. We tallied the number of individuals detected at a station at the end of each survey. Obervers were the same for both years. Date, time of day, and temperature were also recorded. No surveys were conducted if the wind speed exceeded 3 on the Beaufort scale or during rainy days (Gullion 1989). We repeated surveys twice in each site and alternated the time of day at which we conducted the surveys.

A previous study in the region had determined that the audibility range for ruffed grouse was generally < 100 m (Dussault et al. 1998). During the first year of this study in 2005, we were confident that drumming males detected at a given station would be associated with the selected sites since our listening stations were always ≥ 150 m from the adjacent forest. We tried to verify this assumption at the end of the drumming season by searching for drumming structures but we could not always localize them, particularly in PL. We concluded that some of the ruffed grouse were probably not associated with the sites and instead used the adjacent forest stands. In 2006, we modified our approach to correct for the potential problem associated with underestimating our drumming range audibility. After each drumming survey in 2006 was completed, for each bird that was heard, a technician walked carefully until he could spot the drumming male or meet the edge of the surveyed site. We could then determine if the bird we heard was associated with the site or an adjacent stand.

Statistical analysis

Ruffed grouse surveys

Detectability is a problematic component of animal sampling and not accounting for it in wildlife studies can lead to spurious conclusions (Anderson 2001; Mazerolle et al. 2007). Thus, we analyzed the number of individuals detected with repeated count models (Royle 2004a). These models enabled the estimation of abundance (i.e., assuming a Poisson distribution), the probability of detection, as well as the effect of parameters of interest (e.g., lateral cover, temperature) on either abundance or detectability. The major assumptions of these models include: 1) population abundance at each site is closed to emigration, immigration, birth, and death between the first and last visit; and 2) detections during a visit are independent of detections during other visits.

Drumming survey analyses were conducted separately for 2005 and 2006. For the analysis of the 2005 data, we used all the grouse that we heard since we could not determine for sure whether the grouse were associated with the site or the adjacent forest. For 2006, we used the number of grouse that were actually using the site rather than the number of birds we heard because we wanted to measure more precisely ruffed grouse habitat use. We defined a set of candidate models using variables which could influence ruffed grouse habitat use or detection, according to the literature. Explanatory variables that were considered included the effects of temperature (Gullion 1966; Zimmerman and Gutierrez 2007), Julian day, and the quadratic effect of Julian Day (Zimmerman and Gutierrez 2007) on the probability of detection (p), and the effect of habitat type and vertical cover (Rusch et al. 2000) on the abundance (λ) of grouse. Each model was subsequently run in PRESENCE 2.0 and we used Akaike's information criterion, corrected for small sample size (AIC_c), to select the most parsimonious models (Burnham and Anderson 2002). Multimodel inference was also used to determine the effects of each parameter (Burnham and Anderson 2002). We assessed model fit of the global model for each year with a parametric bootstrap procedure described by Royle (2004b), which we implemented in R 2.6.2 (Ihaka and Gentleman 1996).

Ruffed grouse localization

During the 2005 field season, we assumed that the audibility range would not exceed the size of our sites, based on the literature (see above). Because we had not located all the ruffed grouse that were heard, we decided to test if the association with adjacent forest stands was more prevalent in PL than ABF. For each grouse that we heard in 2005, we determined if it was associated with an adjacent forested edge, based on a forest map and the general direction from which we heard the grouse. If the forested edge and direction of calling/drumming intersected, we assumed that this bird was associated with the edge. Otherwise, we assumed the grouse was associated with the sampled site. For this analysis, we used both surveys at the same time since we could not determine with certainty whether birds detected during the first inventory were the same as those heard in the second inventory. We used a Pearson chi-square (X^2) test to determine site/edge association for detected individuals relative to habitat type (PL vs ABF).

Vegetation cover

We calculated average 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 9.1. We used vegetation stage, habitat type, and their interaction as explanatory variables. For vertical cover, we summed the canopy closure of trees and shrubs into a single index.

Results

2005 Ruffed grouse surveys

Surveys were conducted between May 2 and May 26 2005. Temperature averaged 10.2°C (SD = 5.2). We detected grouse in about half of the surveys (54.9 %) and detected an average of 0.80 drumming males per visit (SD = 0.89). The global model fit the data well (P = 0.782). One count model ranked highly ($\Delta AIC_c < 2$) among our candidate model set, followed closely by three models with $\Delta AIC_c < 3$ (Table 1). These models consistently included the effect of vertical cover on abundance. Following multimodel inference, vertical cover (Model-averaged β = 0.496, 90% CI: 0.246, 0.746) positively increased ruffed grouse habitat use (Figure 2), whereas the effect of habitat type had wide confidence intervals (Model-averaged β = -0.263, 90% CI: -0.783, 0.256). Temperature negatively affected the detection of ruffed grouse (Model-averaged β = -0.623, 90% CI: -1.143, -0.102; Figure 3a), while Julian day (Model-averaged β = -0.171, 90% CI: -0.569, 0.226) or the quadratic effect of Julian day (Model-averaged β = -0.056, 90% CI: -0.504, 0.616) did not influence the probability of detection.

Ruffed grouse localization

In ABF, 14 of 45 grouse were associated with a forested edge, while 14 of 26 grouse were associated with a forested edge in PL. There was a strong tendency for ruffed grouse in PL to be more associated with forested edge than those in ABF ($X^2 = 3.566$, df = 1, P = 0.059).

2006 Ruffed grouse surveys

Drumming season began earlier in 2006 and surveys were conducted between April 25 and May 15. Temperatures were colder than 2005 and averaged 4.5°C (SD = 7.9). We detected grouse in more than half of the surveys (58.0%) and detected an average of 1.08 drumming males per visit (SD = 1.45). The vast majority (76.2%) of ruffed grouse detected in ABF occupied the site (n = 32) while few (14.3%) of the grouse heard in PL were actually in the site (n = 2). The global model fit adequately the data (P = 0.072). Four count models ranked highly ($\Delta AIC_c < 2$) among our candidate model set (Table 2). These models consistently included the effect of habitat type and vertical cover on abundance. Following multimodel inference, vertical cover (Model-averaged β = 0.463, 90% CI: 0.187, 0.741) positively increased ruffed grouse habitat use (Figure 2) and ruffed grouse selected ABF more than PL (Model-averaged β = -2.603, 90% CI: -3.805, -1.406). Temperature (Model-averaged β = -0.618, 90% CI: -1.676, 0.440) and Julian day (Model-averaged β = -0.515, 90% CI: -1.089, 0.058) did not influence the probability of detection, but the quadratic effect of Julian day influenced the detection of ruffed grouse (Model-averaged β = -0.568, 90% CI: -1.108, -0.027; Figure 3b).

Vegetation Cover

We found significant interactive effects of habitat type and vegetation stage on lateral cover ($F_{2,2}$ = 4.25, P = 0.022). While lateral cover gradually increased between stages for ABF, there was a sharp decrease for Stage 3 in PL (Figure 4). The relationship with vertical cover was similar in ABF and PL ($F_{2,2}$ = 29.018, p<0.001; Figure 4) but was more important in ABF than in PL ($F_{2,1}$ = 11.243, P = 0.002) Adjacent stands were generally dominated by aspen (36 sites out of 41). Most stands were deciduous (n = 23) or mixed-deciduous (n = 18) while only 2 stands were coniferous. This translated into a low tree canopy closure ($\bar{x}$ ± SD = 63% ± 28%). Understory vegetation was sparse, which translated into low average lateral cover ($\bar{x}$ ± SD = 67 % ± 14%) and low average shrub canopy closure ($\bar{x}$ ±SD = 46% ± 25%).

Discussion

Audibility range

Our results for 2005 did not indicate a difference in use of habitat types by drumming males. These findings probably stem from a difference in audibility range in PL and ABF, specifically, an underestimated audibility range in PL. The range in audibility reported in the literature is variable; Dorney et al. (1958) reported a radius of ¼ of a mile (402 m), Petraborg et al. (1953) reported a radius of 1/8 of a mile (201 m) in the southern part of the ruffed grouse range, whereas Dussault et al. (1998) reported a maximum audibility range of 150 m in a study conducted in Abitibi. Differences between these publications are probably related to differences in local forest composition. At a local scale, Zimmerman and Gutierrez (2007) did not find an effect of forest type, forest structure, and the interaction of these variables with distance on detection probabilities within 175 m. The only factors that have been recognized as influencing audibility of drumming grouse are the emergence of vegetation and topography (Dorney et al. 1958; Petraborg et al. 1953; Rodgers 1981). Whereas the finding of Zimmerman and Gutierrez (2007) may be applicable to a forested environment where forest types have similar structure, the two habitat types in our study were markedly different. ABF was generally closed with dense undergrowth vegetation, while PL was open, with trees regularly spaced and undercover vegetation removed. Sound attenuation has been shown to differ among habitats for other species of birds (Marten and Marler 1977; Richards and Wiley 1980; Schieck 1997) and plantations have been singled out as having low sound attenuation (Aylor 1972; Wiley and Richards 1978). Therefore, we hypothesize that audibility range was probably greater in PL. In support of this hypothesis, most of the birds that we heard in PL were associated with a forested edge in 2005, while more accurate localizations of drumming males in 2006 showed a limited use of plantations.

Ruffed grouse habitat use

There is a scarcity of data on the use of coniferous plantations by ruffed grouse. Gysel (1966) and Gullion (1984) reported negative effects of coniferous plantations on ruffed grouse. However, Gullion (1990) later hypothesized that ruffed grouse could use plantations and attain relatively high densities if aspen were dispersed in small stands on about 10% of the plantations. Zimmerman et al. (2007) used data from the same area to develop a tree stocking guide for plantations and ruffed grouse. Unfortunately, the term ‘‘plantation’’ is broad and without universal definition (Hartley 2002), and can mean anything from replanting commercially harvested natural forests (reforestation) to establishing regularly spaced monocultures on land that had not been occupied by forest (afforestation). While our study was more concerned with the results of afforestation on ruffed grouse, previous results have been more concerned with reforestation.

Results obtained for 2006 surveys indicate that ABF can be a good habitat for drumming males. ABF at Stage 1 had low grouse counts, most likely because of low lateral cover and the absence of overstory vegetation (Figure 4), whereas ABF Stages 2 and 3 had high grouse counts ($\bar{x}$ = 2.8 SD = 2.2) because of their well-developed vegetative cover (Dussault et al. 1998; Rusch et al. 2000; Rusch and Keith 1971). We can estimate a density of 0.18 drumming grouse/ha by using the average size of these sites (15.35 ha) or a density of 0.40 drumming grouse/ha by using a 150m audibility range. In a review Rusch et al. (2000) report an average recorded densities of 0.08 drumming males/ha in the spring but indicate that good habitats are overrepresented in these studies. ABF Stage 3 are particularly attractive because of the development of vertical cover (Figure 4), which is an important factor in protecting grouse from their most important predators, predatory birds (Rusch et al. 2000). In contrast, only 2 PL were used for drumming and in both cases, the drumming structure was on the edge of the plantation (< 12 m). Such a low level of use suggests that ruffed grouse avoid PL during the drumming season. This is consistent with previous studies where pure conifer stands are also avoided during the drumming season (Frank and Fritzell 1989; Gullion and Alm 1983; Rusch and Lloyd 1971). Moreover, plantations lack the overstory component necessary to protect the grouse from avian predators while they are young (Figure 4). At later stages, they are mechanically tended to control the growth of understory vegetation and this consequently reduces lateral cover that protects grouse from predators (Figure 4). Thus, the transformation of ABF into PL will have a negative effect on ruffed grouse drumming habitat.

Ruffed grouse also use early successional forests for brooding in the summer (Giroux et al. 2007; Haulton et al. 2003). In a study conducted in the boreal mixed forest of Quebec, females with broods selected sites that had high stem density and lateral cover that averaged ca. 76% (Giroux et al. 2007). Although we do not have stem density data for ABF, average lateral cover of Stage 2 (73%) and Stage 3 (78%) of ABF was near the range reported for hen brooding. Thus, our ABF Stages 2 and 3 could potentially be used during this critical period. In contrast, PL will probably be avoided by hens, since they generally avoid pure coniferous stands for brooding in natural forests (Giroux et al. 2007) and mechanical thinning of plantations has been proven to drive away ruffed grouse (Bélanger 2000). Finally, forests in the landscape are generally mature aspen stands with low lateral cover. In fact, the average lateral cover for our adjacent stands was closer to the value measured at random points (ca. 67-68%) in the study by Giroux et al. (2007); these random points had a markedly lower lateral cover than the brooding habitat. Therefore, mature forests in the agro-forested landscape are probably not suitable for brooding. The transformation of ABF could thus affect brooding habitat in the agro-forested landscape.

Weather variables and probability of detection

Field conditions affected detection during our grouse surveys. In our study, temperature had a negative effect on detectability in 2005 (Figure 3A). Temperature did not affect detectability in 2006, but surveys were conducted during a colder spell of weather ($\bar{x}$ ± SD: 4.5 ± 7.9°C) and detection probably was higher for the majority of the surveys (β_0 + SD: 2005, 0.583 ± 0.610; 2006, 0.727 ± 0.635). This result is consistent with reports in the literature. Zimmerman and Gutierrez (2007) observed a similar effect, although morning temperature correlated only weakly with detection probabilities in their study. Gullion (1966) also reported that, except for heavy rainfall, low or high temperature is apparently the most important environmental factor that discourages daily drumming. In 2006, detectability was affected by the date on which we conducted the survey (Figure 3B). Snow melt began earlier than usual in 2006 and heavy rainfall prevented us from conducting surveys at earlier dates. According to our results, we probably began the surveys just before the drumming peak, and therefore, detected fewer birds at the end of our surveys (Figure 3B). Similar variation in detection of drumming grouse had been noted both qualitatively (Rusch et al. 2000) and quantitatively (Zimmerman and Gutierrez 2007). There was no such relation between date and the probability of detection in 2005, but this could indicate that our surveys occurred during the drumming peak.

In our study, the drumming period did not occur at the same moment in 2005 and 2006. Gullion (1966) proposed that the beginning of drumming was governed by the photoperiod and suggested that the peak in drumming activity occurred within a 3 day window each year. Although this hypothesis seems to be supported by a recent study in Minnesota (Zimmerman and Gutierrez 2007), it is not the case for our study area where drumming peak dates varied between years. The phenology of local vegetation may also affect the peak of drumming (Dorney et al. 1958), but we ended both surveys before the emergence of leaves on trees. The difference in drumming peaks in our study could be potentially due to ground snowmelt date. This factor has been reported to influence the beginning of ruffed grouse drumming in some instances (Gullion 1966; Petraborg et al. 1953) and has been shown to be important for timing of the display period in closely related species, such as the spruce grouse (Keppie and Towers 1990) and rock ptarmigan (Cotter 1999). While other factors might be more important in southern latitudes (e.g., photoperiod and phenology of the vegetation), snowmelt is probably the most important in our region because of the important snow cover during winter.

Conclusions

Because the impact of transforming abandoned farm fields into plantations is negative for the ruffed grouse, it will be important to monitor the scale and the speed at which these conversions are undertaken (Hartley 2002). Planning at the landscape scale will be important to minimize the negative impacts of abandoned farm field conversions (Hartley 2002). This is particularly true in Quebec where decision-makers have recently decided to bolster investments in intensive plantations (Coulombe et al. 2004). Our results also highlight the importance of accounting for detection probability. Detection rates were variable among years ($\beta_0 \pm$ SD: 2005, 0.583 ± 0.610; 2006, 0.727 ± 0.635) and were affected by weather variables. The effect of not controlling for other species has been underlined by others (Mazerolle et al., 2005; MacKenzie et al 2006) and we agree with Zimmerman and Gutierrez (2007) that year-to-year trends and relative habitat use cannot be inferred from grouse drumming surveys unless they are corrected for detection probabilities.

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Table 1 Model selection results based on AIC_c of Royle count models for ruffed grouse drumming surveys in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during spring 2005.

Model[a]	Model likelihood	K[b]	AIC_c	ΔAIC_c	ω_i
λ(VC) p(TE)	-79.90	4	171.51	0.00	0.374
λ (VC) p(.)	-82.23	3	173.56	2.05	0.134
λ (TY+VC) p(TE)	-79.56	5	173.59	2.08	0.132
λ (VC) p(JD+TE)	-79.69	5	173.85	2.34	0.116
λ (VC) p(JD)	-81.87	4	175.44	3.93	0.052
λ (TY+VC) p(.)	-81.89	4	175.49	3.98	0.051
λ (TY+VC) p(JD+TE)	-79.34	6	176.06	4.55	0.038
λ (VC) p(JD+JDsqr+TE)	-79.65	7	176.69	5.18	0.028
λ (VC) p(JD+JDsqr)	-81.44	5	177.35	5.84	0.020
λ (TY+VC) p(JD)	-81.50	5	177.47	5.96	0.019
λ (TY+VC) p(JD+JDsqr+TE)	-79.31	7	179.11	7.60	0.008
λ (TY+VC) p(JD+JDsqr)	-81.02	6	179.43	7.92	0.007
λ (.) p(TE)	-85.41	3	179.92	8.41	0.006
λ (TY) p(TE)	-84.60	4	180.91	9.40	0.003
λ (.) p(JD+TE)	-84.86	4	181.42	9.91	0.003
λ (TY) p(JD+TE)	-84.04	5	182.55	11.04	0.002
λ (.) p(.)	-88.04	2	182.72	11.20	0.001
λ (.) p(JD)	-87.21	3	183.53	12.02	0.001
λ (TY) p(.)	-87.26	3	183.62	12.11	0.001

λ (.) p(JD+JDsqr+TE)	-84.68	5	183.82	12.31	0.001
λ (TY) p(JD)	-86.43	4	184.56	13.05	0.001
λ (TY) p(JD+JDsqr+TE)	-83.90	6	185.18	13.67	0.000
λ (.) p(JD+JDsqr)	-87.00	4	185.70	14.19	0.000
λ(TY) p(JD+JDsqr)	-86.12	5	186.71	15.20	0.000

[a] Models included the effects of habitat type (TY) and vertical cover (VC) on the number of drumming males (λ), and the effects of temperature (TE), Julian day (JD) and the quadratic effect of Julian Day (JDsqr) on probability of detection (*p*).

[b] No. of estimating parameters in candidate model.

Table 2 Model selection results based on AIC_c of Royle count models for ruffed grouse drumming surveys in abandoned farm fields (ABF) and plantations (PL) in Abitibi, Canada, during spring 2006.

Model[a]	Model likelihood	K[b]	AIC_c	ΔAIC_c	ω_i
λ(TY+VC) p(JJ+JJsqr)	-58.55	6	134.59	0.00	0.254
λ(TY+VC) p(JJ)	-60.20	5	134.94	0.35	0.214
λ(TY+VC) p(TE)	-60.23	5	135.01	0.42	0.207
λ(TY+VC) p(.)	-62.30	4	136.35	1.76	0.105
λ(TY+VC) p(JJ+TE)	-59.87	6	137.24	2.65	0.068
λ(TY+VC) p(JJ+JJsqr+TE)	-58.47	7	137.58	2.99	0.057
λ(VC) p(JJ+JJsqr)	-71.46	5	157.47	22.88	0.000
λ(VC) p(JJ)	-73.24	4	158.23	23.64	0.000
λ(VC) p(TE)	-73.84	4	159.43	24.84	0.000
λ(VC) p(JJ+JJsqr+TE)	-71.36	6	160.22	25.63	0.000
λ(VC) p(.)	-75.60	3	160.33	25.74	0.000
λ(VC) p(JJ+TE)	-73.14	5	160.83	26.24	0.000
λ(.) p(JJ+JJsqr)	-77.09	4	165.94	31.35	0.000
λ(.) p(JJ)	-78.74	3	166.62	32.03	0.000
λ(.) p(TE)	-79.18	3	167.50	32.91	0.000
λ(.) p(JJ+JJsqr+TE)	-77.07	5	168.68	34.09	0.000
λ(.) p(JJ+TE)	-78.56	4	168.87	34.28	0.000
λ(.) p(.)	-81.27	2	169.20	34.61	0.000
λ(TY) p(TE)	-63.59	4	138.93	4.34	0.029

λ(TY) p(JJ+JJsqr)	-62.42	5	139.39	4.80	0.023
λ(TY) p(JJ)	-63.93	4	139.62	5.03	0.021
λ(TY) p(JJ+TE)	-63.32	5	141.18	6.59	0.009
λ(TY) p(.)	-66.21	3	141.55	6.96	0.008
λ(TY) p(JJ+JJsqr+TE)	-62.41	6	142.31	7.72	0.005

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[a] Models included the effects of habitat type (TY) and vertical cover (VC) on the number of drumming males (λ), and the effects of temperature (TE), Julian day (JD) and the quadratic effect of Julain Day (JDsqr) on probability of detection (p).

[b] No. of estimating parameters in candidate model.

Figure 1 Distribution of 41 study sites surveyed to assess ruffed grouse habitat use in abandoned farm fields (ABF) and plantations (PL) in the Abitibi region of the Province of Quebec, in 2004-2006. ABF sites are represented by a black triangle, PL sites are represented by a gray square, and major cities are represented as a black dot, surrounded by a gray circle.

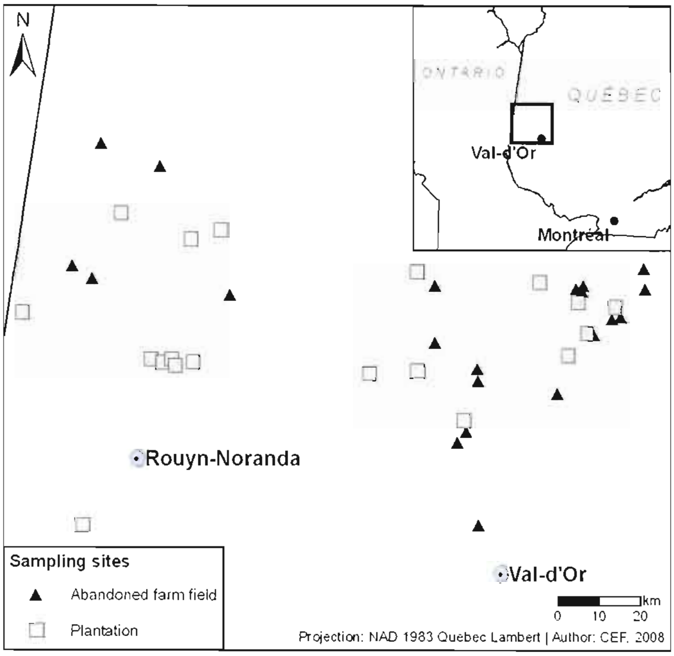


Figure 2 Predicted numbers of ruffed grouse in abandoned farm fields (ABF), according to model-averaged predictions as a function of vertical cover during the spring breeding seasons of 2005 and 2006 in the Abitibi region, Canada.

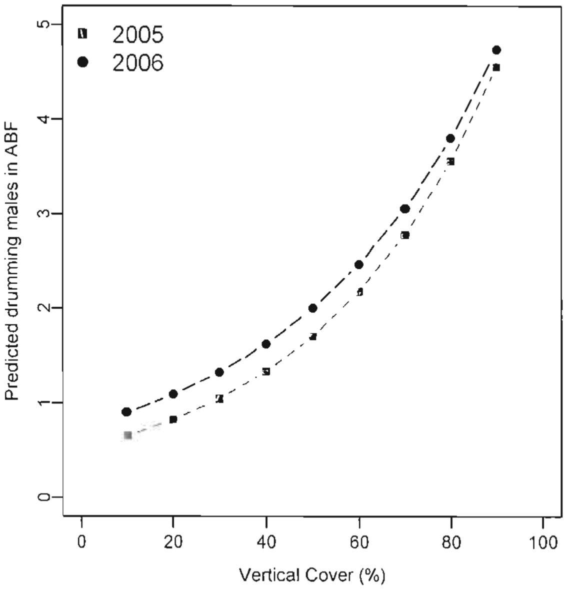


Figure 3 Predicted detection probabilities of drumming ruffed grouse in abandoned farm fields (ABF) and plantations (PL), according to model-averaged predictions as a function of temperature (A) during the spring breeding season of 2005 and date (B) during the spring breeding season of 2006 in the Abitibi region, Canada.

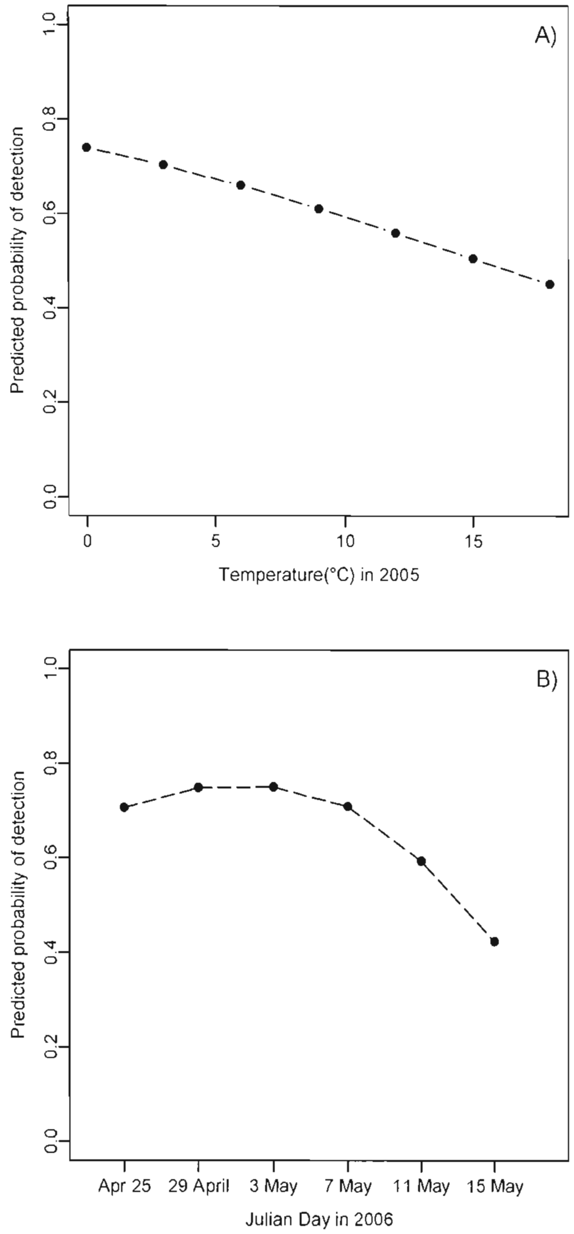
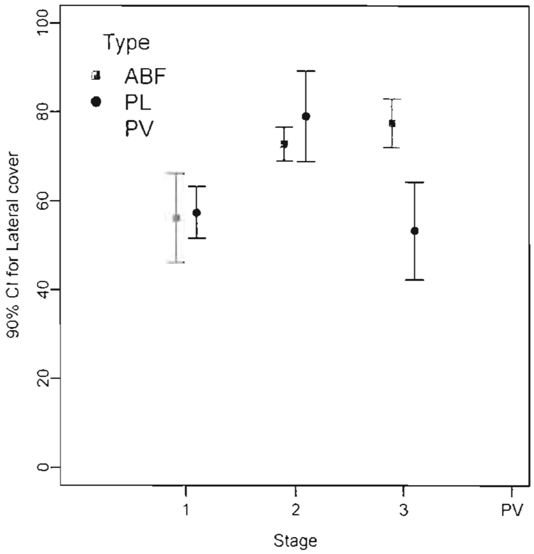
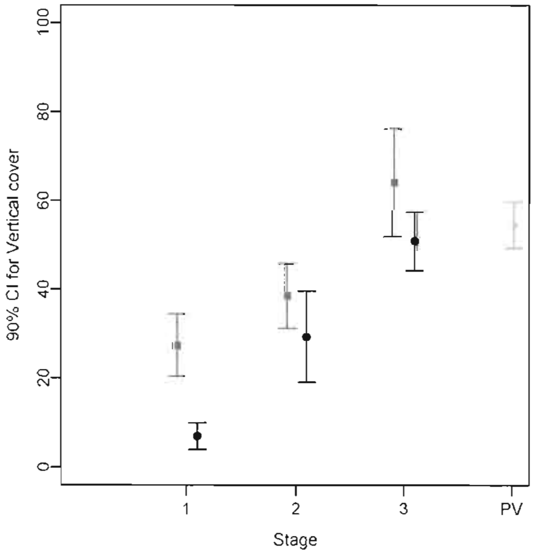


Figure 4 Average lateral cover (LC) and vertical cover (VC) ± 90% CI measured in abandoned farm fields (ABF), plantations (PL) and adjacent forested edges (FE) in Abitibi, Canada, during spring 2004-2005. Stage 1 of ABF had at least 25% and below 50% of the ground covered by woody vegetation, Stage 2 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. Stages 1 were 1-3 m high, Stage 2 were 3-7 m high and Stage 3 were > 7 m high.





CONCLUSION GÉNÉRALE

La conversion des friches en plantations résineuses va affecter négativement les populations locales de lièvre d'Amérique et de gélinotte huppée dans la matrice agroforestière de l'Abitibi-Témiscamingue. Dans le cas du lièvre les impacts négatifs ne seront pas ressentis immédiatement puisqu'il est capable d'utiliser les jeunes plantations de 3 à 7 m de haut et que ces milieux présentent même des caractéristiques d'habitat qui peuvent être intéressantes. Toutefois, les plantations plus vieilles (≥7m) qui sont élaguées offrent un couvert latéral insuffisant et seront désertées. Dans le cas de la gélinotte, une espèce associée aux forêts feuillues ou mixtes à dominance feuillue et qui évite les peuplements résineux, les effets seront immédiats. Cette espèce pourrait être plus particulièrement affectée, car les friches représentent un habitat de tambourinage de premier choix et qu'elles sont probablement les meilleurs milieux d'élevage pour les couvées dans la matrice agroforestière.

Les friches peuvent être vues comme des milieux « anthropiques » et leur maintien dans le paysage pourrait être critiqué. Il est toutefois important de souligner que les friches sont situées dans un milieu qui a été fortement perturbé par les activitées anthropiques. Une grande partie de la forêt dans le paysage agroforestier Abitibien est constituée de peupleraies matures qui offrent peu de diversité en termes d'habitats fauniques. En conséquence, les friches agricoles risquent de représenter un élément de variabilité important dans le paysage et vont offrir des habitats fauniques aux espèces qui sont associées aux milieux en régénération.

Les nouvelles orientations du MRNF semblent accorder beaucoup d'importance aux zones de sylviculture intensives (MRNF 2008) sans toutefois définir les activités qui auront lieu dans ces zones ni où seront situées ces zones. Il est toutefois clair que la conversion de friches agricoles en plantations pourrait et devrait être utilisée pour atteindre les objectifs que le gouvernement s'est fixé. Toutefois, à la lumière de nos résultats, il sera important d'adopter une stratégie qui permettra de minimiser les impacts négatifs qu'entraîne cette conversion. Les facteurs les plus importants à considérer pour déterminer l'impact de ces plantations seront leur taille, leur localisation et à quel degré la région ou le paysage sera affecté. Des plantations de taille modeste telles que celles utilisées actuellement (>15 ha) établies sur des friches herbacées et bien réparties dans le paysage auront un impact moins important que la transformation massive de grande superficie. La gestion des lots boisés environnants jouera également un rôle important dans la mitigation des effets négatifs des plantations. L'utilisation de plantations mixtes ou des plantations de type agroforestières qui permettraient de garder une composante feuillue ou une végétation de sous couvert développée pourraient également être envisagée.

Notre étude a également mis en évidence l'importance de prendre en compte les facteurs qui influencent la probabilité de détection des espèces ou des indices de présence inventoriés. Dans le cas du lièvre, il s'agit probablement d'une des premières études à utiliser cette approche statistique en relation avec le pistage hivernal. Cette approche offre de nombreux avantages. Auparavant, sans incorporer de facteurs pouvant affecter la détection, les inventaires de pistages hivernaux devaient tous être réalisés en même temps pour ne pas être biaisés. Une approche incorporant la probabilité de détection, qui permet notamment de contrôler les effets du délai depuis la chute de neige, offre plus de flexibilité pour espacer les visites sur le terrain et ainsi réaliser les inventaires de tous les sites sur plus d'une journée. Cette approche permet également de contrôler les effets de la température sur la probabilité d'observer des indices, un avantage qui peut être important puisque la température est reconnue comme un facteur qui influence l'activité des mammifères durant l'hiver (Banfield 1987).

Dans le cas de la gélinotte huppée, la période d'inventaire pour les mâles tambourineurs est difficile à déterminer et commencer trop tôt ou trop tard peu biaiser les résultats d'inventaires. L'utilisation d'une approche avec probabilité de détection peut permettre de tenir compte de ce phénomène. Nos résultats ont également souligné les problèmes relatifs à la réalisation d'inventaires de tambourinage dans des milieux qui ont des propriétés acoustiques différentes. Cette problématique pourrait être une source de biais importante puisque les inventaires de tambourinage sont généralement conduits avec un rayon d'audibilité fixe indépendamment de l'habitat.

Nos résultats soulignent également l'importance de prendre en compte la dégradation du crottin de lièvre lorsque l'on utilise les inventaires de crottins. Bien que d'autres auteurs aient également démontré des différences dans la dégradation en fonction des habitats (Murray, Ellsworth et Zack, 2005 ; Prugh et Krebs, 2004), nous sommes les premiers à souligner un lien avec la diète des lièvres.

Perspective de recherche

Bien que notre étude ait répondu à certaines interrogations, celle-ci nous a permis d'identifier un certain nombre de questions encore inexplorées. Au niveau des espèces étudiées, certaines avenues de recherche sont encore à approfondir :

- Plusieurs facteurs semblent influencer la dégradation du crottin de lièvre. Toutefois, l'hypothèse selon laquelle la diète serait responsable des différences observées dans notre étude reste à être étudiée plus en profondeur;
- Les facteurs qui influencent la probabilité de détection des mâles tambourineurs en fonction des différents habitats. Nos résultats ont démontré que la température et la date influencent les probabilités de détection, mais d'autres facteurs pourraient jouer un rôle important, notamment le rayon d'audibilité. Les inventaires auditifs sont utilisés dans plusieurs états américains afin d'estimer les populations locales et ce facteur, s'il n'est pas contrôlé, pourrait entraîner des biais substantiels;
- Dans la littérature scientifique, le choix des habitats de tambourinage est dicté en partie par la présence d'un promontoire. Toutefois, en raison de leur passé agricole, les friches n'offrent généralement pas les promontoires recherchés par les mâles et lors de nos inventaires, nous avons observé plusieurs gélinottes tambourinant sur le sol ou sur des débris ligneux de petite taille. Ce phénomène n'a pas été documenté encore et mériterait qu'on s'y intéresse de plus près.

En ce qui concerne les effets de l'établissement de plantations dans le paysage agroforestier :

- La répartition spatiale des plantations sera un facteur important pour déterminer leurs effets sur la biodiversité. Des analyses spatiales pourraient être utilisées pour déterminer les effets des plantations à l'échelle du paysage afin d'élaborer des recommandations plus précises à cette échelle;
- La bécasse d'Amérique, un oiseau migrateur en déclin dans certaines parties de son aire de répartition, est un autre utilisateur obligatoire des milieux en régénération. Cette espèce va probablement être également affectée négativement par l'établissement de plantations et il serait intéressant de quantifier le rôle que jouent les friches agricoles dans son habitat en Abitibi-Témiscamingue.

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