UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE NATURELLE DES PETITS MAMMIFÈRES ET EFFETS DES COUPES PARTIELLES SUR LA STRUCTURE DE LEURS POPULATIONS EN FORÊT BORÉALE DE L'EST DE L'AMÉRIQUE DU NORD

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
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DÉCEMBRE 2003

REMERCIEMENTS

Je voudrais remercier en tout premier lieu mon directeur Pierre Drapeau pour m'avoir offert la chance de travailler sur ce projet, pour les longues heures qu'il m'a consacrées alors qu'il n'avait pas le temps, pour les merveilleuses lettres de recommandations qu'il m'a faites et surtout pour son enthousiasme et sa passion communicative. Je voudrais aussi remercier mon co-directeur Yves Bergeron pour la rapidité de ses réponses, pour sa confiance et pour ses commentaires judicieux. Merci aussi à Louis Imbeau pour sa disponibilité, pour son aide précieuse lors de la rédaction de mon premier chapitre et pour sa générosité. Je ne pourrais passer sous silence l'aide de mes collègues de labo qui m'ont souvent guidé ou conseillé durant ce projet.

Je ne pourrais oublier l'aide précieuse de mes aides de terrain, Dominique Lafleur, pour ne pas s'être découragé devant l'absence de captures de l'été 2001, et Annie-Ève Gagnon, pour sa bonne humeur et son amitié aussi bien sur le terrain (été 2002) que lors de l'identification des espèces en laboratoire. Je voudrais aussi remercier les nombreux stagiaires ou amis qui ont passé quelques jours avec moi dans les forêts abitibiennes : Simon-Pierre Babski, Maxime Ducoulombier, Marjorie Gobeil, Nicolas Luigi, Johanne Pelletier, et surtout, Geneviève Farley et Dominic Sénécal. Je tiens à souligner l'accueil chaleureux des gens de l'Abitibi et tout particulièrement du camp Jérémie et de la compagnie Norbord qui ont permis que nos longs séjours dans le bois soient moins ennuyeux et même agréables.

Je voudrais aussi remercier Robert Morin (FAPAQ) pour m'avoir donné accès à la base de données de l'*Atlas des Micromammifères du Québec*, Jacques Larivée pour avoir fait de même avec *EPOQ* (*Études de populations d'oiseaux du Québec*) et Gilles Lupien pour m'avoir initié à l'identification des espèces de petits mammifères. Merci aussi aux gens du GREFi et de la Chaire en aménagement forestier durable pour leur soutien technique et financier.

Enfin, je remercie infiniment mes parents qui m'ont permis de poursuivre mes études à l'étranger et qui m'ont toujours encouragé dans mes choix. Mes derniers remerciements iront à Robin, simplement pour tout.

AVANT-PROPOS

Le projet tel qu'il avait été structuré au départ diffère sensiblement de la version finale. En effet, il était prévu que nous traiterions de l'effet des coupes forestières sur les populations de petits mammifères, ce qui représente le 2^{e} chapitre de ce mémoire. Cependant, lors de l'échantillonnage des données de terrain de l'été 2001, nous avons été confrontés à un très faible taux de capture qui ne permettait pas de satisfaire aux exigences du programme de maîtrise. Il a été décidé qu'une seconde campagne d'échantillonnage était indispensable durant l'été 2002. De plus, nous avons ajouté un 2^{e} secteur d'étude au cas où l'absence de petits mammifères serait récurrente. Par ailleurs, ce très faible succès de capture nous a amené à nous interroger sur ses causes possibles. Ce questionnement nous a mené à la rédaction du 1er chapitre qui traite de la cyclicité des populations de petits mammifères en forêt boréale de l'est de l'Amérique du Nord.

Ce mémoire a été rédigé sous la forme de deux articles scientifiques en anglais et comporte une introduction et une conclusion générales rédigées en français. Conformément aux exigences de la Maîtrise en Biologie, j'ai procédé à la supervision et à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de premier auteur. Le premier chapitre intitulé **« Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America** » a été soumis à la revue suédoise *Oikos*. Mes directeurs Pierre Drapeau et Yves Bergeron ainsi que le collaborateur Louis Imbeau en sont les coauteurs. Le deuxième article, intitulé « **Short-term effects of partial cutting on small mammal populations in the eastern boreal forest of Canada** » sera lui aussi soumis à une revue scientifique. Dans ce cas, seuls mes directeurs Pierre Drapeau et Yves Bergeron en seront les coauteurs.

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RÉSUMÉ

Les petits mammifères sont souvent utilisés comme outil de suivi dans des études sur les effets des perturbations anthropiques. Ce groupe d’espèces joue un rôle important dans le fonctionnement des écosystèmes forestiers, il est donc souvent présenté comme un indicateur de l’état des populations de tout un cortège de prédateurs, qui se nourrissent des petits mammifères. Cependant, la dynamique naturelle de ce groupe d’espèces est mal connu en Amérique du Nord.

Le premier chapitre de ce mémoire traite du potentiel de cyclicité des différentes espèces de petits mammifères présents dans la forêt boréale de l’est de l’Amérique du Nord. En effet, des cycles d’abondance chez plusieurs espèces de campagnols sont observés en Scandinavie, alors qu’il semble que la communauté scientifique ait accepté leur absence en Amérique du Nord. Des cycles d’invasions hivernales de quatre ans ont été détectés chez la nyctale de Tengmalm (*Aegolius funereus*), une chouette qui se nourrit essentiellement de campagnols à dos roux (*Clethrionomys gapperi*). De plus, les fluctuations d’abondance de ce petit mammifère sont très fortement corrélées aux années de déplacements de la nyctale de Tengmalm, de la chouette épervière (*Surnia ulula*) et de la chouette lapone (*Strix nebulosa*). Il semble donc qu’une dynamique cyclique, basée sur les petits mammifères et engageant plusieurs espèces de prédateurs, existe en Amérique du Nord de façon très semblable à celle qui a cours en Scandinavie.

Le second chapitre de ce mémoire traite des effets des coupes partielles sur les populations de petits mammifères en forêt boréale de l’est du Canada. Ces coupes encore expérimentales ont mieux protégé l’habitat des petits mammifères que les coupes totales actuellement utilisées, et ce, à la fois en forêt boréale mixte et dans la pessière à mousses. Elles ont aussi conservé une communauté d’espèces de petits mammifères plus proche de celle retrouvée en forêt naturelle. Les abondances du campagnol à dos roux et de la souris sylvestre (*Peromyscus maniculatus*), les deux espèces les plus importantes de la forêt boréale, étaient similaires dans les coupes partielles et les forêts matures. Le campagnol à dos roux était presque absent des coupes totales, et ce, durant tout l’été. Au contraire, la souris sylvestre était plus abondante dans ce milieu. La structure des populations de campagnol à dos roux était similaire dans les coupes partielles et les vieilles forêts, présentant des niveaux comparables d’activité reproductrice. Par contre, les coupes totales pourraient servir de puits de dispersion pour le campagnol à dos roux en forêt boréale mixte. Les populations de souris sylvestres, bien que ne présentant pas de différence d’abondance entre les traitements, étaient majoritairement composées de mâles adultes après coupes en forêt boréale mixte. Ceci suggère que cette espèce pourrait avoir des difficultés à se maintenir à long terme dans les coupes partielles et les coupes totales sans apport extérieur d’individus.

INTRODUCTION

1.1. Dynamique naturelle et exploitation forestière

La dynamique naturelle de la forêt boréale est principalement contrôlée par les feux (Bergeron *et al.* 2001). Si la fréquence des feux est constante, la distribution des classes d'âge des peuplements forestiers suit une exponentielle négative (Bergeron *et al.* 2002) (figure 1a). Si l'on considère la durée d'un cycle de feux d'environ 100 ans et le fait que la probabilité de brûler est indépendante de l'âge de la forêt, alors la forêt devrait théoriquement être constituée de peuplements entre 0 (environ 10%) et 250 ans (environ 1%). Toujours selon ce modèle, l'âge moyen des peuplements serait 100 ans et 37% des peuplements seraient plus vieux que cet âge. Or, l'estimation historique du cycle de feu est d'environ 139 ans en Abitibi (Bergeron *et al.* 2001) et 48% des peuplements ont plus de 100 ans (Harper *et al.* 2002).

L'exploitation forestière, au contraire, suit actuellement un aménagement équien basé sur une rotation de 100 ans qui tend à normaliser la forêt. La distribution des classes d'âge des peuplements est alors régulière entre 0 et l'âge d'exploitation commerciale (environ 100 ans) (figure 1b). L'âge moyen des peuplements est alors de 50 ans, et les forêts plus vieilles que l'âge d'exploitation disparaissent avec le temps (Seymour & Hunter 1999).

Dans un cadre de gestion durable des forêts, de nouvelles façons d'exploiter la forêt ont été suggérées. Ces approches s'inspirent de sa dynamique naturelle (Bergeron *et al.* 1999). Un des enjeux pour l'avenir sera de protéger l'ensemble des stades de développement (approche « filtre brut »), y compris les forêts plus anciennes que l'âge d'exploitation commerciale.

1.2. Approche d'« aménagement multicohorte »

Bergeron *et al.* (1999) suggèrent une approche d'aménagement écosystémique (« aménagement multicohorte ») qui vise le maintien des caractéristiques écologiques des écosystèmes grâce à l'emploi de pratiques sylvicoles s'inspirant des perturbations naturelles dans leurs impacts, et ce, afin de favoriser la conservation d'une structure écosystémique similaire à celle de la forêt non aménagée (Bergeron et *al.* 1999). À l'échelle des peuplements, les méthodes de coupes devraient être apparentées aux perturbations rencontrées dans le type de peuplement forestier à aménager. À l'échelle des paysages, la conservation d'une variabilité spatiale et temporelle représentative de celle qui émane de la dynamique naturelle est visée, et ce, de façon à maintenir une composition et une structure de la mosaïque forestière diversifiée.

En pratique, cette approche dite d'« aménagement multicohorte » propose de varier les traitements sylvicoles en fonction de la structure de la forêt (figure 2). La cohorte initiale (entre 0 et 100 ans) étant constituée de peuplements réguliers issus des grandes perturbations telles que le feu, pourrait être récoltée par coupe totale, ce qui représente l'homologue du passage d'un feu. La seconde cohorte (entre 100 et 200 ans), est constituée de peuplements plus ouverts composés d'arbres établis immédiatement après feu mais aussi d'une jeune régénération établie plus tard. Cette cohorte pourrait être traitée par coupe partielle, qui permet la récolte des plus gros arbres uniquement, en laissant la régénération immature sur place. La troisième cohorte (plus de 200 ans) représente les forêts anciennes et irrégulières, qui pourraient être exploitées par coupe sélective, ce qui mime leur dynamique naturelle par trouées (mort d'un arbre ou d'un groupe d'arbres) (Bergeron *et al.* 2002). Ainsi une portion des vieilles forêts pourraient être conservée au delà de l'âge habituel d'exploitation, tout en permettant une certaine récolte de bois.

Bien qu'utilisées dans les provinces de l'Ouest canadien, les coupes partielles sont encore expérimentales en forêt boréale québécoise. L'objectif essentiel de l'utilisation de telles coupes est le prélèvement d'une partie des arbres avant leur mort naturelle, ce qui a aussi l'avantage de favoriser la croissance des plants demeurés en place par réduction de la compétition pour les ressources. Un gain rapide de productivité du peuplement pourrait ainsi être obtenu (Doucet *et al*. 1996). Dans un cadre d'aménagement écosystémique, cette pratique a pour but d'accélérer les processus naturels de la succession végétale et d'amener le peuplement à une structure complexe de vieille forêt plus rapidement (Bergeron *et al.* 1999).

Le présent mémoire s'insère dans une étude plus globale qui vise à évaluer la faisabilité écologique et économique de l'utilisation des coupes partielles au sein d'une approche alternative à l'aménagement actuel des forêts québécoises pour le maintien de la biodiversité.

1.3. Les petits mammifères comme outil de suivi

Avant d'appliquer de façon plus extensive cette approche, il faut, entre autres, tester les effets des coupes partielles sur la diversité biologique afin de s'assurer que le peuplement résultant possèdera non seulement les attributs des forêts anciennes et surannées mais permettra également d'y maintenir les populations biologiques associées à ces environnements. Pour étudier l'aptitude des coupes partielles à rencontrer cet objectif, il est nécessaire de se doter d'un outil de suivi rendant compte de l'état de l'écosystème. Comme il est impossible de suivre l'ensemble des espèces animales et végétales, certaines espèces ou groupes taxonomiques sont choisis comme indicateurs. Il existe différents types d'indicateurs : de la diversité génétique (variabilité génétique au sein des populations), de la diversité spécifique (nombre d'espèces animales et végétales présentes), de la diversité écosystémique (nombre d'écosystèmes dans le paysage) (CCMF 2000), et de la diversité fonctionnelle (processus écologiques). Dans la présente étude, ce sont les petits mammifères qui seront utilisés comme outil de suivi de la diversité fonctionnelle, et donc, de l'état des forêts après coupe.

Dans la présente étude, les petits mammifères considérés seront restreints aux familles des Cricétidés (souris et campagnols) et des Soricidés (musaraignes). Les espèces les plus fréquemment rencontrées en forêt boréale sont le Campagnol à dos roux (*Clethrionomys gapperi*), la Souris sylvestre (*Peromyscus maniculatus*), le Phénacomys d'Ungava (*Phenacomys intermedius*) (Banfield 1977; Crête *et al.* 1995; Sims & Buckner 1973), ainsi que la Musaraigne cendrée (*Sorex cinereus*) (Innes *et al.* 1990).

Les petits mammifères ont un rôle fonctionnel prépondérant dans les écosystèmes forestiers : ils peuvent être qualifiés de groupe d'espèces clé. En effet, ils sont souvent à la base du réseau trophique pour bon nombre de prédateurs terrestres (petits et moyens carnivores) et aviaires (oiseaux de proie) (Hanski *et al.* 1991; Potter 1978). Ils peuvent aussi servir d'alimentation de substitution lors du déclin d'autres populations-proies, lors des creux de cycles d'abondance d'autres espèces (Poole & Graf 1996) ou selon la période de l'année

(Dibello *et al.* 1990). D’autre part, les petits mammifères sont, eux mêmes, prédateurs de graines, de champignons, de lichens, de plantes et d’invertébrés (Martell 1981; Martell & Macaulay 1981; McCay & Storm 1997; Ure & Maser 1982). Par exemple, la souris sylvestre peut retarder la régénération d’une forêt de début de succession par l’importance de sa consommation de graines (Potter 1978; Sullivan 1979) et même en affecter la composition par prédation différentielle des graines des diverses espèces (Chew 1978). Le campagnol à dos roux affecte, pour sa part, la dispersion des spores de champignons symbiotiques nécessaires à l’établissement et à la survie des conifères (Maser *et al.* 1978; Terwilliger & Pastor 1999). De plus, les musaraignes, mais aussi les autres petits mammifères, consomment une quantité non négligeable d’invertébrés, pouvant ainsi aller jusqu’à contrôler les populations d’invertébrés décomposeurs du sol (Potter 1978). Ils participent donc, par tous ces moyens, à l’accélération du cycle de renouvellement des éléments nutritifs à l’intérieur de l’écosystème (Potter 1978). Ainsi, les petits mammifères représentent un maillon clé du fonctionnement des écosystèmes forestiers.

1.4. Dynamique naturelle des petits mammifères

La dynamique naturelle à long terme et à grande échelle des petits mammifères est, par ailleurs, relativement mal connue. En Scandinavie, les petits mammifères de la forêt boréale présentent des cycles d’abondance périodique de 3 à 5 ans selon les régions (Hanski *et al.* 1991). Cette dynamique cyclique régit les fluctuations de nombreuses espèces de prédateurs et de proies de façon directe ou indirecte, aussi bien chez les mammifères que chez les oiseaux. Une certaine synchronie existe entre les pics d’abondance des différentes espèces sur de grandes distances (Ims & Andreassen 2000; Steen *et al.* 1996). Par contre, en Amérique du Nord, malgré une structure forestière et une communauté animale similaire à la Scandinavie, il semble qu’il ait été accepté qu’une telle dynamique n’existait pas (Boutin *et al.* 1995; Hansson & Henttonen 1985). Si une dynamique cyclique existait en Amérique du Nord, il pourrait y avoir de fortes conséquences, notamment quant à l’utilisation de ce groupe d’espèces comme indicateur de suivi des effets des perturbations anthropiques sur la faune.

1.5. Objectifs du projet de recherche

La présente étude se propose donc dans un premier chapitre de statuer sur la dynamique naturelle à long terme de plusieurs espèces de petits mammifères dans l’est de l’Amérique du Nord. Une cyclicité similaire à celle observée en Scandinavie est-elle possible en forêt boréale nord-américaine? Nous abordons cette question en analysant les tendances des populations pouvant être dégagées à partir de bases de données d’inventaires de petits mammifères et de chouettes existant pour le Québec ainsi que pour l’est de l’Amérique du Nord. Dans un second chapitre, nous mesurons dans un dispositif expérimental la réponse des populations de petits mammifères aux coupes partielles en forêt boréale mixte ainsi qu’en pessière à mousses, dans le nord-ouest du Québec.

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Figure 2 : Distribution des classes d’âge des peuplements (par tranches de 10 ans) pour une forêt exploitée selon un aménagement multicohorte, où les pratiques forestières (coupe totale, coupe partielle et coupe sélective) varient en fonction de la structure de la forêt, et ce, dans le but de se rapprocher de la courbe en exponentielle négative de la distribution des classes d’âge des forêts naturelles. Adapté de Bergeron *et al.* (2002).

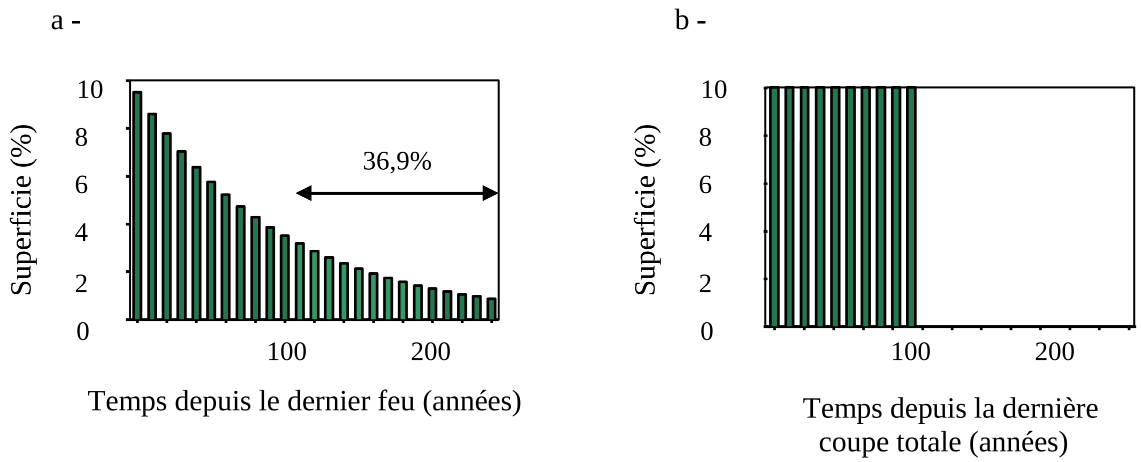
a -
Superficie (%)
10
8
6
4
2
0
36,9%
100
200
Temps depuis le dernier feu (années)
b -
Superficie (%)
10
8
6
4
2
0
100
200
Temps depuis la dernière coupe totale (années)

Figure 1

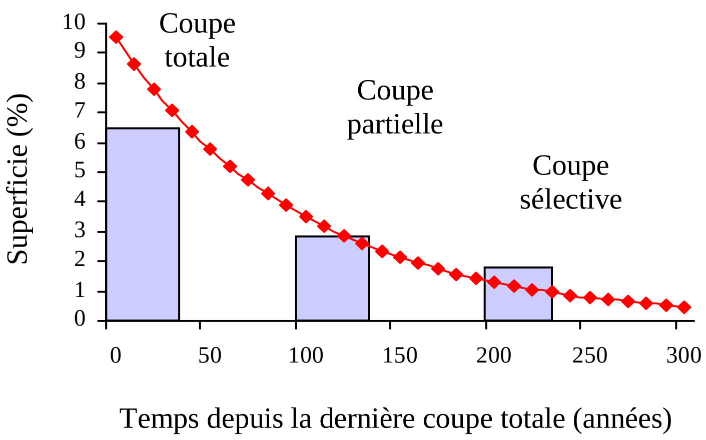
Superficie (%)
10
9
8
7
6
5
4
3
2
1
0
Coupe totale
Coupe partielle
Coupe sélective
0
50
100
150
200
250
300
Temps depuis la dernière coupe totale (années)

Figure 2

OWL WINTER IRRUPTIONS AS AN INDICATOR OF SMALL MAMMAL POPULATION CYCLES IN THE BOREAL FOREST OF EASTERN NORTH AMERICA

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Abstract

Contrary to what is observed in Fennoscandia, it seems to be widely accepted that small mammals do not exhibit regular population cycles in the boreal forest of North America. However, some elements suggested the existence of such a dynamic. With information collected from existing databases, we examined the presence of cycles in small mammals and their main avian predators. Temporal autocorrelation analyses have been conducted : 1) on owl field observations recorded by Quebec and eastern North American birding associations and 2) on small mammal population surveys from the *Atlas des Micromammifères du Québec.*

Our results indicated that Tengmalm's owl (*Aegolius funereus*) winter invasions are periodic, with a 4-yr cycle in Quebec. Moreover, populations of one species of small mammal, the Red-backed vole (*Clethrionomys gapperi*), fluctuated in a periodic way in Quebec boreal forests (north to 48°N). Furthermore, Tengmalm's owl, which has a preference for red-backed voles as a prey species, show invasion cycles which correspond to years of low density of this small mammal. Otherwise, winter observations of two other boreal owls south of their usual distribution increased in years of low density of red-backed voles.

Contrary to what is generally accepted in the scientific literature, our results suggest that a cyclic dynamic exists in the boreal forest of eastern North America between voles and owls, which is very similar to the one observed in Fennoscandia.

Keywords: Red-backed vole, *Clethrionomys gapperi*, Tengmalm's owl, *Aegolius funereus*, Great gray owl, *Strix nebulosa*, Northern hawk owl, *Surnia ulula*, population cycles, small mammals, predator-prey relationships

Introduction

Small mammals, and voles in particular, are known for their regular multi-annual population fluctuations, with a periodicity between 3 to 7 years documented in several countries (e.g. Russia, Japan, Finland and Scotland (Stenseth 1999), France (Salamolard *et al.* 2000) and Switzerland (Weber *et al.* 2002)). However, most of the studies showing the presence of such cycles were done in Fennocandia (Norrdahl & Korpimäki 2002; Hanski *et al*. 1993; Hansson & Henttonen 1985; Hörnfeldt 1978). In this area, north of 60° N, abundance cycles of microtine voles generally increase in duration (3 to 5-yr) and amplitude as a function of latitude. Conversely, these cycles are not observed further south (Hanski *et al.* 1991). A likely explanation of this general latitudinal gradient lies in the geographic distribution of microtine vole specialist predators, which are responsible for the regular multi-annual cyclic dynamic of their prey. Indeed, Turchin & Hanski (1997) have shown that specialist predators occur in greater proportion in the northern part of Fennoscandia, whereas generalist predators generally dominate further south. The greater proportion of generalist predators in more southern localities is assumed to stabilize rodent populations in these regions, because of their possibility of having several alternative prey species (Hanski *et al.* 1991).

Among vole specialist predators found in Fennoscandia, two distinct functional categories can be recognized: *resident specialists* (small mustelids) have weak dispersion capacities, and thereby drive the predator-prey cycle, while *nomadic specialists* (raptors and owls) can move over great distances in response to varying prey availability. In the case of some owl species restricted to the boreal zone (e.g. Tengmalm's owl), their winter irruptions south of the boreal forest are well documented in Fennoscandia (Sonerud *et al*. 1988; Korpimäki 1986; Mysterud 1970), where they happen during periods of low abundance of small mammals within their usual distribution range (Mikkola 1983). In this case, owls react to a lack of prey in the North by massively moving to the South, where small mammal cycles are non-existent. Such large scale movement patterns can thus be good indicators of the population fluctuations of small mammals in the North.

As opposed to Fennoscandia, far less is known in North America about the abundance cycles of small mammal populations. Lemming cycles in the tundra are well documented (Béty *et al.* 2002; Turchin *et al*. 2000; Framstad *et al.* 1993; Pitelka *et al*. 1955), as are those of snowshoe hares and lynx in the boreal forest (Krebs *et al.* 2001; Elton & Nicholson 1942). However, it has become largely accepted that most species of voles in North America do not present regular cycles, in boreal forest species (*Clethrionomys gapperi*) as well as in tundra species (*Clethrionomys rutilus*, which is though cyclic in Fennoscandia) (Boutin *et al.* 1995; Hansson & Henttonen 1985). Accordingly, Turchin & Hanski (1997) comment that fluctuations in the abundance of small mammals exist in North America but periodicity does not. Mostly because snowshoe hares (*Lepus americanus*) replace voles as the predominant herbivore in the system, it has been suggested that specialist predators in North America are larger bodied and prey mostly upon hares instead of voles. Consequently, it has been proposed that the vole cycles of Fennoscandia are replaced by hare cycles in North America (Boutin *et al*. 1995; Hansson & Henttonen 1985).

Although one third of the world's boreal forest is found in Canada (World Resources Institute 2000), it has been relatively little studied in terms of small mammal population dynamics. The studies done to date are fragmentary and were most often conducted south of the boreal forest zone, in mixed to deciduous forest. As is the case in the southern part of Fennoscandia, these studies reveal an absence of regular cycles (Brooks *et al*. 1998; Fryxell *et al.* 1998; Grant 1976). To our best knowledge, no long term study has been done to date in the north-eastern part of the boreal forest, which has a primarily coniferous forest cover (north of 48° N)**.** This begs the question whether or not it is simply a lack of knowledge which leads us to think that no regular small mammal population cycles occur in eastern North America's boreal forests, especially when the resident specialist predators present (small mustelids) are similar to those responsible for the abundance cycles of voles in Fennoscandia. Indeed, Johnson *et al* (2000) have suggested that ermine (*Mustela erminea*) populations present fluctuations in abundance which amplitude increases with latitude in eastern North America. Using a limited number of published long-term data sets on different species of small mammals from boreal North America, these authors were the first to suggest that a latitudinal gradient in cyclic dynamics was occurring in this region, similar to that of microtine rodent populations in northern Europe. In agreement with this hypothesis, winter owl irruptions south of the boreal forest have already been observed by ornithologists in North America (Bondrup-Nielsen 1978; Catling 1972). Although these irruptions of nomadic specialists could possibly be the result of a phenomenon similar to that observed in northern Europe, the possible cyclicity of these irruptions in North America has however yet to be demonstrated.

In this paper, we formulate the hypothesis that small mammal abundance cycles exist in the coniferous boreal forest of eastern North America, similar to those observed in Fennoscandia. To test this hypothesis, we used a comparative approach based on the analysis of available ornithological and small mammal data bases in order to 1) evaluate the cyclic nature of boreal owl irruptions and small mammal population fluctuations, and 2) measure the quantitative association between these two data sets.

Materials and methods

Databases

Large data bases of bird sightings are compiled each year using the observations of amateur ornithologists in Canada as well as in the United States. Such sources of information have already been used to monitor long term fluctuations in bird populations (Koenig 2001; Droege *et al.* 1998; Cyr *et al*. 1997; Dunn *et al.* 1996).

In this study, two such data bases were used. The first was compiled from the journal "*American Birds*" (1971-1994), renamed "*National Audubon Society Field Notes*" (1994-1997), then "*American Birding Association Field Notes*" (1998), and finally "*North American Birds*" (1999-2001). This journal publishes the observations of amateur ornithologists for all of North America each season. We chose to monitor three owl species that prey mostly on small mammals and whose nesting range is almost entirely within the boreal forest: Tengmalm's owl (*Aegolius funereus*) (TO) (Hayward & Hayward 1993), Northern hawk owl (*Surnia ulula*) (NHO) (Duncan & Duncan 1998) and Great gray owl (*Strix nebulosa*) (GGO)

(Bull & Duncan 1993). As a result of snow accumulation throughout the winter, it is in this season that available food becomes limiting. We therefore collected only winter observations (October to March), for all regions of eastern North America located south of the boreal forest (Maritimes Provinces, Quebec, Ontario, New England, Hudson-Delaware, Western Great Lakes) (figure 1).

The second data base, the "*Étude des populations d'Oiseaux du Québec*" (*EPOQ*) (Larivée 2001*), records the observations of amateur ornithologists made on checklists in Quebec. This data base was analyzed for the same three owl species, in winters (October to March) from 1971 to 2001 for the whole of Quebec. In this data base, only one bird per location per winter was retained in order to avoid recording the same individual several times, notwithstanding elapsed time between two observations made the same winter. Furthermore, the addition of all registered checklists for all species included allowed us to evaluate the observation effort made each winter, and thus to calibrate the number of owls recorded over the years. The *EPOQ* data base is therefore more reliable than the one taken from *American Birds*, because it can account for the observation effort. On the other hand, it covers a smaller geographical area. These ornithological data bases provide at least an abundance index of owls, but are not exhaustive, and inhabited areas are over-represent. However, they should allow general trends to be identified in the annual variations of the monitored species.

Small mammal population trends were analyzed with the data base of the "*Atlas des Micromammifères du Québec*" (*AMQ*) (Société de la faune et des parcs du Québec 2000*). This data base compiles small mammal surveys, done by various organizations, for various purposes, within the province of Quebec. The data base combines studies which were not intended to quantify cycles of abundance, and which used different sampling methods and which had varying capture periods (from May to November). Despite these limitations, to our knowledge, this database contains the best available long-term information on the abundance of small mammals in boreal north-eastern North America. Only four species provided sufficient data to be analyzed: Red-backed vole (*Clethrionomys gapperi*), Meadow vole (*Microtus pennsylvanicus*), Deer mouse (*Peromyscus maniculatus*) and Masked shrew (*Sorex cinereus*). We selected only surveys which were done in forests, north of 48° N, and for which sampling effort (number of trap-nights) was known. We were thus able to determine a summer abundance (capture rate), for all of boreal Quebec, for each species for each year. We were able to assemble a continuous data base for 1990 to 2000 only.

Statistical analyses

The normality of the data originating from the three data bases was verified using the Kolmogorov-Smirnov test. We were able to calculate the correlation (Pearson's or Spearman's r) between the ornithological data bases for each owl species, first for the Quebec region only (*EPOQ* and Quebec region in *American Birds*), and then between Quebec (*EPOQ*) and the whole of the eastern North America (*American Birds*, all regions together). Secondly, temporal autocorrelation analyses were done for each species, in order to detect a potential periodicity in the observations (Turchin & Taylor 1992). Because of the short length of the time series, temporal autocorrelation analyses could not be done for small mammals data. However, the correlation between the summer abundance of the different species of small mammals and the number of observations of the three owl species was calculated performing a one-year time lag for the small mammal data. Small mammals were captured during summer (ex : summer 1998), whereas the owls were observed the following winter (ex : winter 1998-1999 is named winter 1999). This allowed us to evaluate the numerical response of the owls to the current abundance of small mammals, through the indicative knowledge of their abundance the preceding summer.

A cross correlation was calculated between the abundance of owl species (*EPOQ*) and the abundance of small mammals. This analysis compares two time series and determines with which time lag the correlation between the two is strongest. This allowed us to hypothesize which variable controls the other (Legendre & Legendre 1998). Thus, it will be possible to determine if a low phase in a cycle of small mammals drives southern irruptions of owls, and if this is the case, with what time lag is the response observed. All statistical analyses were done using SPSS 10.0 (SPSS Institute Inc. 1999).

Results

Owls

During the period surveyed (1971-2001), a total of 6691 owls (1609 NHO, 3953 GGO and 1129 TO) were recorded in the winter reports of *American Birds*. In the *EPOQ* data base, the minimum number of owls observed was 1499 (645 NHO, 647 GGO and 207 TO), for 134,413 checklists compiled during winter from 1971 to 2001 (for more details see appendix A).

The observations for the Quebec region which are compiled in *American Birds* are highly correlated to those recorded in *EPOQ*, after weighting the data with the number of checklists filled (TO : $r = 0.465$, $P = 0.004$; NHO : $r_s = 0.819$, $P < 0.001$; GGO : $r_s = 0.892$, $P < 0.001$). In addition, observations from *EPOQ* are correlated to those for all of eastern North America (*American Birds*, all regions together) (TO : $r_s = 0.537$, $P = 0.001$; NHO : $r_s = 0.715$, $P < 0.001$; GGO : $r_s = 0.813$, $P < 0.001$). This correspondence between *EPOQ* (Quebec region only) and *American Birds* (all eastern North America) is a good indication that the information contained in *American Birds* is reliable, in spite of the absence of effort data.

Fluctuations in abundance were observed for the three owl species, in all regions of eastern sub-boreal North America (*American Birds*). However, it is in Ontario, Quebec and Western Great Lakes regions that these fluctuations were the greatest. At least four strong winter irruptions, which are relatively synchronous for the three owl species (1988-89, 1992-93, 1996-97 and 2001), have occurred south of the boreal forest in recent years (figure 2). Before 1985, irruptions of the three species were less synchronous. During the first 15 years, the northern hawk owl was mostly irregular and the great gray owl showed quite low numbers. However, irruptions of these three species of owls are positively correlated among species for the whole of eastern North America (*American Birds*) (TO-NHO : $r_s = 0.751$, $P < 0.001$; TO-GGO : $r_s = 0.705$, $P < 0.001$; NHO-GGO : $r_s = 0.737$, $P < 0.001$), as well as in Quebec (*EPOQ*) (TO-NHO : $r_s = 0.510$, $P = 0.002$; TO-GGO : $r_s = 0.497$, $P = 0.002$; NHO-GGO : $r_s = 0.523$, $P = 0.001$). Furthermore, for each owl species, the same fluctuation pattern is observed ($P < 0.05$) in the three regions (Ontario, Quebec, Western Great Lakes), except for the northern hawk owl which has a slightly different fluctuation pattern in Ontario than in Western Great Lakes ($P = 0.055$).

Temporal autocorrelations show that Tengmalm's owl has a significant irruption periodicity of 4 years, in Quebec only (*EPOQ*) (lag = 2 : $r = -0.573$, $P = 0.001$; lag = 4 : $r = 0.444$, $P = 0.02$) (figure 3). The two other owl species do not show significant regular period, either from the *EPOQ* data base or from the *American Birds* data base (all $P > 0.05$).

Small mammals

The data base consulted (*AMQ*) had 6729 recorded captures of small mammals for a total of 113,930 trap-nights (for more details see appendix B). The summer abundance of small mammals (capture rate for 100 trap-nights) has varied a lot throughout the years, but the two peaks observed in red-backed vole abundance are consistent with the hypothesis that cyclicity exist in boreal forest of Quebec (figure 4). We saw three summers with low populations : 1992, 1996 and 2000, which were all followed by winters of owl irruptions. The other small mammal species do not seem to have a periodicity.

For Quebec as a whole, the abundance of red-backed vole is inversely and significantly correlated to Tengmalm's owl observations (*EPOQ*) ($r = -0.725$, $P = 0.009$), as well as to the great gray owl (GGO : $r_s = -0.782$, $P = 0.004$) and to the northern hawk owl (NHO : $r_s = -0.804$, $P = 0.003$). The abundance of red-backed vole, in Quebec, is also significantly correlated to Tengmalm's owl observations in the whole of eastern North America (*American Birds*) ($r_s = -0.774$, $P = 0.003$), as well as to the great gray owl ($r_s = -0.629$, $P = 0.019$) and to the northern hawk owl ($r_s = -0.688$, $P = 0.01$). The other small mammal species had no significant correlations with any of these owls.

The cross correlation between Tengmalm's owls (*EPOQ*) and red-backed voles was significantly strongest at lag = 0 ($r = -0.698$), indicating that both species fluctuated simultaneously, or at least with a time lag of less than a year. For the other two species of owls (*EPOQ*), the cross correlation analysis shows that no correlation was significantly strongest with any particular lag, between these species and the red-backed vole.

Discussion

Cyclicity of owls and small mammals in eastern North America

Our results show that boreal owls make periodic irruptions in southern Quebec, as well as in the entire sub-boreal zone of eastern North-America. These irruptions are synchronous among owl species. The phenomenon of owl irruptions has been well studied in northern Europe and is indicative of fluctuations in the abundance of their prey. Indeed, the three species of owls studied are considered as nomadic specialist predators of small mammals in Fennoscandia, where their numerical fluctuations are known to follow those of voles (Mikkola 1983). Andersson (1980) has shown that it is more advantageous for a bird to adopt a nomadic strategy (movements of 100 km or more) when the abundance of its prey is cyclic. Boreal species of owls can therefore be considered as good indicators of fluctuations of small mammal abundance.

Moreover, our results reveal that during the last ten years, the abundance of red-backed voles has fluctuated in Quebec, and that there is a synchrony between their lowest abundance and the irruptions of the three species of owls, and particularly for Tengmalm's owl. This owl species shows regular 4-yr cycles in Quebec and is strongly correlated to the abundance of red-backed voles for the 1990-2000 period. These results, although limited to a relatively short time series, also argue very strongly for the occurrence of population cycles in this small mammal species. Therefore, as opposed to other authors (Boutin *et al*. 1995; Hansson & Henttonen 1985) arguing that periodicity in small mammal abundance does not exist in North America, our results on winter owl irruptions in eastern North America suggest a small mammal population fluctuation pattern which is similar to that occurring in Fennoscandia, strongly supporting the hypothesis first set forth by Johnson *et al*. (2000).

Different responses of owls

The three species of owls seem to match the fluctuations of the red-backed vole, but only Tengmalm's owl has shown significant regular cycles in its irruptions. We suggest that the stronger cyclic pattern of this latter species may be largely explained by its size and its habitat preferences. Indeed, Tengmalm's owl is one of the smallest boreal owl predator, restricted to mature and old-growth forests (Gosse & Montevecchi 2001). These two characteristics limit its choice of potential prey. Its size limits it to very small animals such as voles, whereas its preferred habitat is dominated by one prey species in North America : the red-backed vole (Boos & Watt 1997). Hayward *et al*. (1993) showed that 80% of the diet of Tengmalm’s owl consists of small mammals in North America, the majority of which are red-backed voles (*Clethrionomys*) and a further 10% of the diet derived from other species of voles (*Microtus* sp.).

In contrast to Tengmalm’s owl, the northern hawk owl and the great gray owl, because of their larger size, have access to greater numbers of prey species of various sizes. The northern hawk owl is opportunistic and therefore adapts its diet according to the abundance of various prey (Rohner *et al*. 1995). In Fennoscandia, the most available prey during the nesting season are small mammals, and consequently the diet of northern hawk owls consists of more than 90% in voles. In winter, this percentage decreases and that of birds increases (Mikkola 1983). In Yukon, this owl species responds to combined density fluctuations of *Microtus* sp. and of juvenile snowshoe hare, which have 10-yr abundance cycles (Rohner *et al*. 1995). The great gray owl, which is though a large owl species, however eats only occasionally larger prey than voles (Bull & Duncan 1993; Mikkola 1983). In western North America, this owl eats species such as the pocket gopher (*Thomomys talpoides*), in proportion of their availability (Bull *et al.* 1989), but this prey species is absent from eastern North America.

In addition to their larger size, the larger two species of owls also hunt in open environments (Gosse & Montevecchi 2001; Bull *et al.* 1988a), where *Microtus* sp. are almost exclusively found, whereas red-backed voles (*Clethrionomys*) occur in the understory of mature forests (Boos & Watt 1997). Their habitat use therefore leads both owl species to consume more *Microtus* than *Clethrionomys*, compared to Tengmalm’s owl (Rohner *et al*. 1995; Bull *et al*. 1989). Indeed, great gray owl seems to select preferentially *Microtus* sp. in any season, in Fennoscandia as well as in North America (Bull & Duncan 1993; Mikkola 1983).

Tengmalm's owls respond to low prey density within their usual distribution range by moving towards the South (Korpimäki 1986). In Norway, Sonerud *et al*. (1988) have observed that their movements are longer during small mammal population lows than during peaks. Tengmalm's owl seems to adopt a partial migration strategy, differing according to sex, age, and level of small mammal populations (Korpimäki 1986; Lundberg 1979). Females are more often nomadic (Hipkiss & Ellegren 2002), whereas males have greater advantage (rarity of nesting sites) and facility (better hunting efficiency) by protecting a territory surrounding a nesting site (Korpimäki *et al*. 1987; Löfgren *et al*. 1986). When prey populations are high, females and juveniles remain resident, or only travel short distances. When prey populations plummet, a proportion of females undertakes long migrations in search of areas where preys are more abundant, similarly to dispersing juveniles (Sonerud *et al*. 1988). The northern hawk owl seems to adopt a movement strategy similar to that of Tengmalm's owl, however it is less restricted in its choice of nesting sites (Byrkjedal & Langhelle 1986). The great gray owl seems to move, in Fennoscandia as well as in North America, over shorter distances than the northern hawk owl and the Tengmalm's owl (Bull *et al.* 1988b; Hildén & Helo 1981).

However, we should bear in mind that in spite of the absence of clear periodicity of the northern hawk owl and the great gray owl, these two species still match the cyclic fluctuations of Tengmalm's owl, as it has already been suggested (Hayward & Hayward 1993). They are thus affected by fluctuations in the red-backed vole populations, but less so than Tengmalm's owl which has a more restricted diet. Perhaps, the lack of a clear pattern for the great gray owl may also be explained by the fact that this species still seems rare in eastern North America and Quebec, with in this latter case very few confirmed nesting sites recorded to date (Gauthier & Aubry 1995).

Cause of small mammal cycles

The behavioural response of Tengmalm's owls to lack of food is immediate, and does not result in a time lag between the drop in prey populations and the migration movements (our data, Strann *et al*. 2002; Korpimäki 1985; Hörnfeldt 1978). This suggests that the owls are not the cause of small mammal cycles (Norrdahl & Korpimäki 1995; Korpimäki &

Norrdahl 1989). Their nomadic behavior would instead have a stabilizing effect on prey populations (Korpimäki 1985), as would a generalist predator (Turchin & Hanski 1997). It is more likely that it is the predation pressure of holarctic resident specialist predators, such as the ermine, and especially the least weasel (*Mustela nivalis*) which create the cycles like in Fennoscandia (Hanski *et al*. 1993; Korpimäki *et al*. 1991). In North America, ermine seems to prefer early successional habitats and hunts largely on meadow voles (Simms 1979). Contrary to ermine, least weasel seems to be able to enter in red-backed voles subnivean and subterranean tunnels, and then, preys mostly on them (Simms 1979). So, this can explain why Johnson *et al*. (2001) found no large scale continuous cycles with regular period in ermines, if this species does not predate mainly on a cyclic vole.

Swanson & Johnson (1999) have shown that ermine fluctuations were synchronous for all the Quebec province. Otherwise, Johnson *et al*. (2000) have found a latitudinal gradient of amplitude in ermines. Finally, contrary to ermines data, our study show continuous regular cycles during 30 years in Tengmalm’s owls. All this information suggest that small mustelid species, vole specialized, may act in North America in a similar way than in Fennoscandia.

Implications

To date, no study has detected the presence of regular cycles in the red-backed vole, which is though widely distributed and well studied in North America (Banfield 1977). The majority of studies do not even consider the possibility of cycles in this species. Yet, in addition to results presented on ermines by Johnson *et al*. (2000), our results on boreal species of owls, and Tengmalm’s owl in particular, appear to support that such cycles do occur in the boreal region of eastern North America. It is surprising that such an important phenomenon has gone undetected. It is now urgent to document predator-prey relationships in the boreal forest of eastern North America, and more particularly the role that resident specialist predators (ermine, weasel) may play in creating cycles in the red-backed vole.

Knowledge of abundance cycles in small mammals can also have important practical consequences, particularly for the red-backed vole which, in a sustainable management perspective, has been proposed as an indicator of the effects of human disturbances in eastern

North America. This species has been used several times before for such purposes, but without considering its potential abundance cycles (e.g. Potvin *et al*. 1999; McLaren *et al*. 1998; Génier & Bergeron 1996). Our results dictate prudence in the design of monitoring programs that use the red-backed vole as an indicator. The importance of independent controls is exacerbated with populations that undergo cyclic fluctuations, especially when using Before and After Control Impact surveys (BACI design). For example, a design where the pre-treatment period would serve as the experimental control is no longer acceptable for a species with cyclic fluctuations. In addition, we must be aware of the fact that during years of low population density, numbers can be so low that it is difficult to capture red-backed voles even in optimal sites. It is necessary to better document the periodicity and amplitude of the abundance cycles of the red-backed vole (*Clethrionomys gapperi*). We therefore strongly suggest developing monitoring programs of the abundance of small mammals in eastern North American boreal forest. Knowledge of the cycles and of the range of variation of populations could then be used as benchmarks with which to calibrate the results of population studies.

Acknowledgements

This study could not have been conducted without thousand of birders, who collected more than 130,000 records of daily observations, in winter period during the last 30 years. We thank more particularly Jacques Larivée for extracting winter owl observations from the *EPOQ* data base, used in our analyses. We thank Robert Morin from Société de la Faune et des Parcs du Québec for giving access to the "*Atlas des Micromammifères du Québec*" data base. We also thank students from P. Drapeau laboratory for all their gratefully comments on earlier draft of this manuscript. Finally, we thank Patricia Wood for the English translation of an earlier version of the manuscript. This project was funded by the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, the Quebec fund FCAR - Fonds Forestier programme d’Action Concertée, an industrial NSERC grant to Y. Bergeron, Norbord Industries Inc. and the Research Group in Forest Ecology (GREFi).

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Figure list

Figure 1 : Map of eastern North America, viewing the different study regions (in white and various grey) and localization of boreal forest (in hatched bars) (small mammals are in the boreal forest and owls invasions are south of the boreal zone). Limit of boreal forest is limit of black spruce forest based on Ansseau *et al.* (1996).

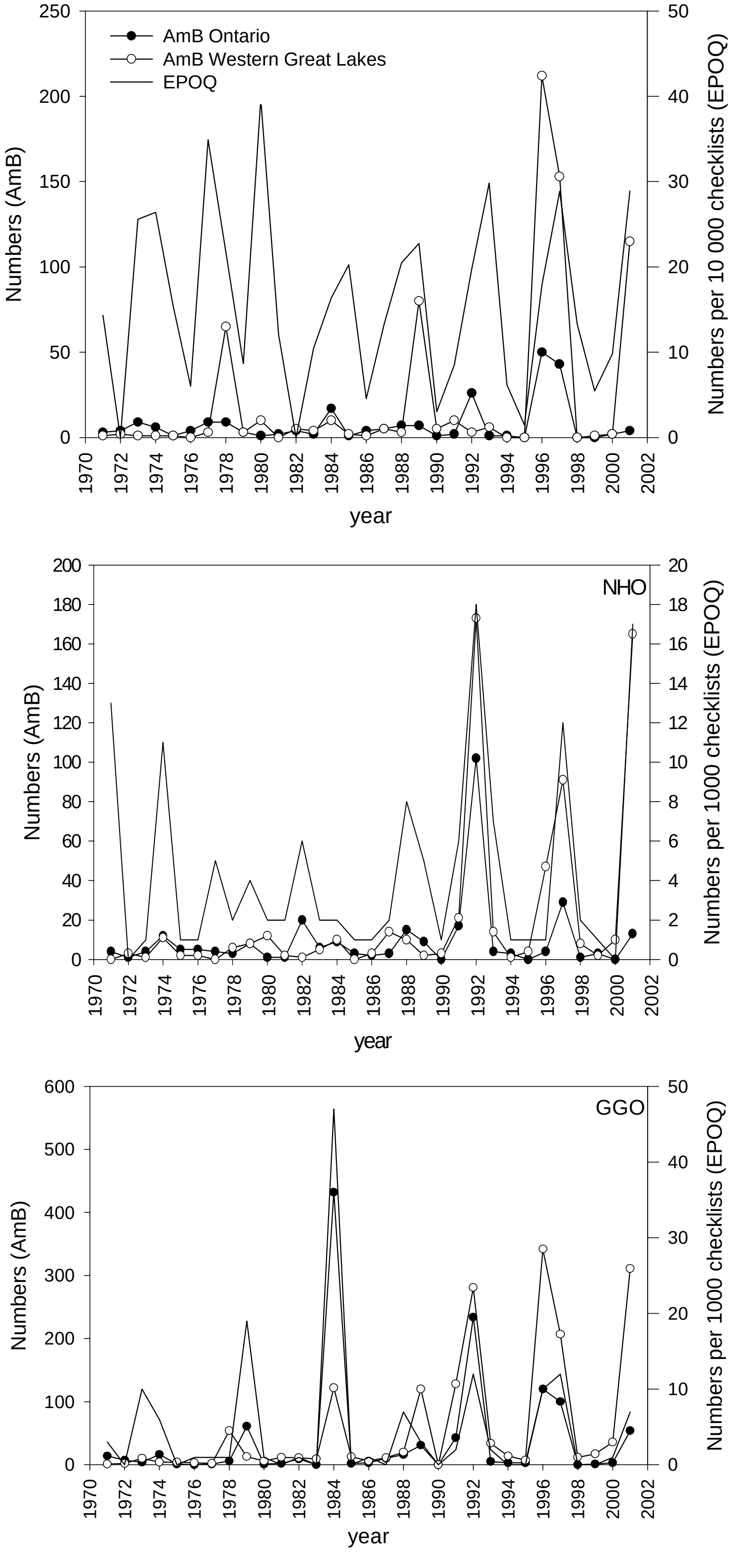
Figure 2 : Fluctuations in numbers of owl observations (TO: Tengmalm's owl, NHO: Northern hawk owl, GGO: Great gray owl) by amateur ornithologists in Ontario, Quebec and Western Great Lakes regions of eastern North America. For Quebec, we use the *EPOQ* data base because observations are weighted by the sampling effort (number of checklists produced in each winter) which is not the case for the *American Birds* data base. AmB : *American Birds* data base, EPOQ : *Étude des Populations d'Oiseaux du Québec* data base.

Figure 3 : Temporal autocorrelation coefficients (Pearson's r) at different time lag for weighted numbers of Tengmalm's owls (*EPOQ*) in Quebec. ** P < 0,05.

Figure 4 : Summer abundance (capture rate for 100 trap-nights) for 4 small mammal species (*AMQ*) north of 48°N in Quebec.


Owl winter invasions when voles are at low densities
Ontario
Maritimes Provinces
Quebec
New England
New York
Western Great Lakes
Hudson-Delaware

Figure 1


AmB Ontario
AmB Western Great Lakes
EPOQ
Numbers (AmB)
Numbers per 10 000 checklists (EPOQ)
year
NHO
Numbers (AmB)
Numbers per 1000 checklists (EPOQ)
year
GGO
Numbers (AmB)
Numbers per 1000 checklists (EPOQ)
year
0
50
100
150
200
250
0
10
20
30
40
50
0
20
40
60
80
100
120
140
160
180
200
0
2
4
6
8
10
12
14
16
18
20
0
100
200
300
400
500
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1970
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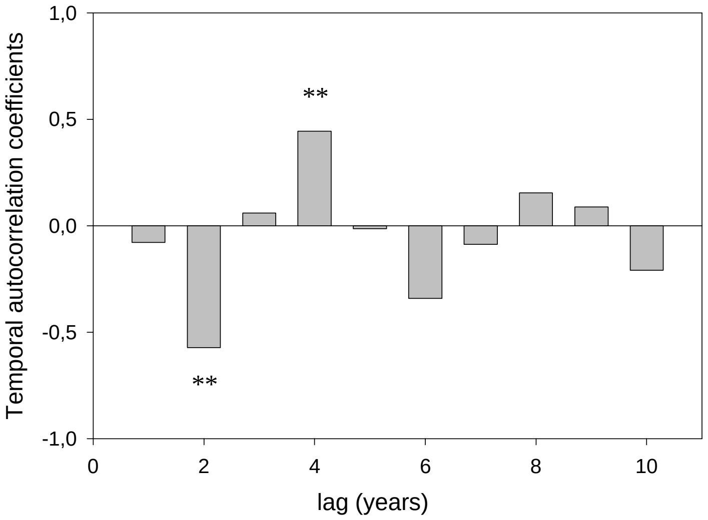
Figure 2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-0,5
-1,0
Temporal autocorrelation coefficients
**
**
0
2
4
6
8
10
lag (years)

Figure 3

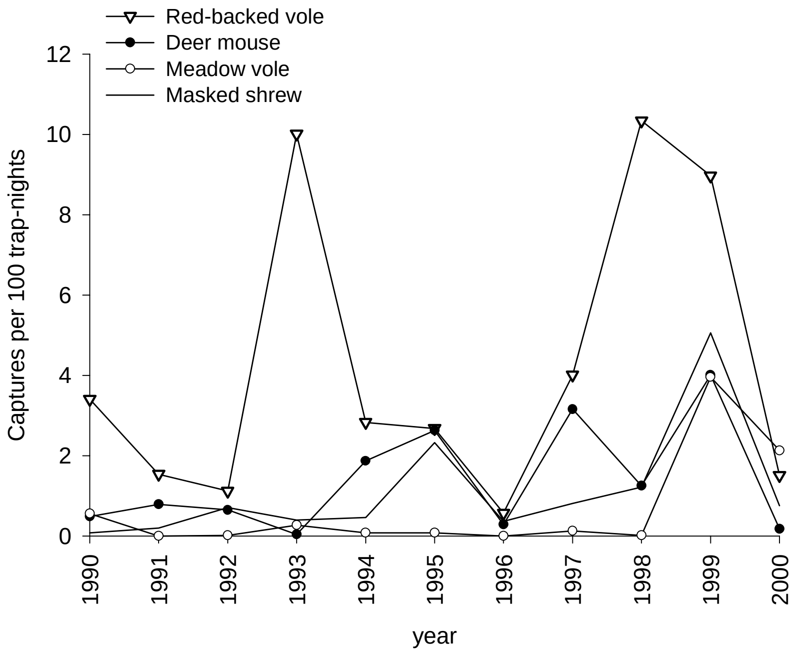
Red-backed vole
Deer mouse
Meadow vole
Masked shrew
Captures per 100 trap-nights
0
2
4
6
8
10
12
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
year

Figure 4

Appendix A : Number of records per winter (October to March) in *EPOQ* data base. October to December records for one year are regrouped with next winter year (January to March) (ex : October 1998 to March 1999 are named winter 1999). Owl number (NHO: Northern hawk owl, GGO: Great gray owl and TO: Tengmalm's owl) is a minimum number of individuals observed each winter, because only one bird per location per winter has been counted, notwithstanding time between observations in the same winter.

Winters	Number of checklists	Owl number		
		NHO	GGO	TO
1971	697	9	2	1
1972	735	0	0	0
1973	782	1	8	2
1974	1137	12	7	3
1975	1294	1	0	2
1976	1666	1	2	1
1977	1720	8	2	6
1978	1841	4	2	4
1979	2309	10	45	2
1980	2016	5	2	8
1981	2483	5	1	3
1982	2575	16	2	0
1983	3824	7	0	4
1984	3660	9	172	6
1985	5432	7	2	11
1986	4395	3	5	2
1987	4535	8	1	6
1988	5371	42	37	11
1989	5718	28	15	13
1990	6563	4	1	2
1991	7064	42	11	6
1992	7602	139	91	15
1993	7372	51	15	22
1994	6493	6	1	4
1995	6837	6	1	1
1996	8401	11	80	15
1997	7968	98	98	23
1998	6768	13	2	9
1999	5510	4	1	3
2000	6107	1	5	6
2001	5538	94	36	16

Appendix B: Number of studies compiled each year and total capture effort associated (number of trap-nights) in *Atlas des Micromammifères du Québec* data base. Total capture numbers of the four species of small mammals per year is shown.

Years	Number of studies	Number of trap-nights	Red-backed voles	Deer mice	Meadow voles	Masked shrews
1990	2	8320	284	41	47	7
1991	5	11253	173	89	0	22
1992	4	24928	278	161	4	178
1993	4	11128	1114	5	30	45
1994	7	11806	334	221	9	54
1995	6	7715	207	203	6	180
1996	4	16777	96	49	0	62
1997	6	7746	311	245	10	63
1998	7	5918	612	74	1	72
1999	7	6088	546	244	241	308
2000	3	2251	34	4	48	17

SHORT-TERM EFFECTS OF PARTIAL CUTTING ON SMALL MAMMAL POPULATIONS IN THE EASTERN BOREAL FOREST OF CANADA

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Abstract

We assessed small mammal response to partial cutting treatments used as an alternative to clear-cutting to retain structural features found in old forests of the eastern boreal forest of north-western Quebec, Canada. Effects of partial cutting treatments on small mammals were documented in both the black spruce and the mixed-wood zones that characterize the eastern boreal forest. Small mammals were trapped with *Sherman* live-traps several times during the summer in clear-cuts, partial cuts and uncut control stands in the two study areas.

At least three times more basal area of young poles (2-14 or 16 cm dbh) and larger trees (> 14 or 16 cm DBH) was maintained in partial cuts than in clear-cuts. In both study areas, vegetation composition and structure of the understory were more similar to uncut control stands in partial cuts than they were to clear-cuts. Hence, the effects of logging on small mammal microhabitat were mitigated in partial cuts.

Although species richness was less in the black spruce study area, diversity (measured by the Shannon-Weiner index) was higher than in the mixed-wood study area. Proportions of each species in the small mammal community were different among treatments in the two study areas. Moreover, in the mixed-wood study area, two species were restricted to clear-cuts, while two others were restricted to partial cuts and control stands. Red-backed vole (*Clethrionomys gapperi*) was the most abundant species in both study areas, while deer mouse (*Peromyscus maniculatus*) was co-dominant in the mixed-wood study area only.

In the mixed-wood study area, red-backed vole abundance in partial cuts was similar to that in control stands, whereas in the black spruce study area, its value was intermediate between clear-cuts and control stands. Deer mice were almost absent in the black spruce study area, except in clear-cuts, but in mixed-wood boreal forest, they were less abundant in partial cuts than in the other treatments.

Population structure and levels of reproductive activity of red-backed voles was similar in uncut control stands and partial cuts, whereas clear-cuts did not sustain a population for the entire summer. Although deer mouse abundance was not different between treatments, populations were largely composed of adult males in mixed-wood boreal forest, suggesting difficulties in persisting without external contributions of individuals.

Partial cuts maintain small mammal communities that are similar in composition, abundance and population structure to those of mature and old forests. Consequently, partial cutting represents a promising alternative to clear-cutting for maintaining sustainable small mammal populations and, hence, the web of predators associated with small mammals, in this part of the boreal forest.

Keywords: partial cutting, clear-cutting, boreal forest, mixed-wood forest, black spruce forest, small mammals, community structure, population dynamics, population structure, red-backed vole, *Clethrionomys gapperi*, deer mouse, *Peromyscus maniculatus*

Introduction

A conceptual model for maintaining biodiversity is to protect ecosystems and landscapes with a coarse-filter approach and species of special concern (e.g. endangered species) requirements with a fine-filter approach (Seymour & Hunter 1999). A coarse-filter approach might protect habitats for a wide range of species and seek to maintain interactions between species and ecosystem processes. In this context, knowledge of ecosystem dynamics is essential. The natural dynamics in the eastern boreal forest of Canada is mainly driven by wildfires, creating an age-class distribution of stands that varies regionally with the fire cycle (Bergeron *et al.* 2002). Harper *et al.* (2002) have shown that the proportion of old stands at the landscape level in the north-western boreal forest of Quebec is almost 48%, leading to a mean stand age of 139 years (Bergeron *et al.* 2001). Consequently, with a 100 year rotation and an even-aged management system, timber harvesting is currently truncating the age-class distribution of forests, and stands older than the rotation age are likely to disappear with time (Bergeron *et al.* 2002; Seymour & Hunter 1999). The retention of old forests and their structural attributes in managed forests has become a key challenge for the implementation of sustainable forest management practices throughout commercial forests of North America (Franklin *et al.* 1997). In the eastern boreal forest of Canada, a new approach derived from the concept of ecosystem management was recently suggested (see Bergeron *et al.* 1999). This approach proposes a diversification of silvicultural practices to reproduce the range of variability in stand structure that characterizes forest stands under natural disturbances including stands of irregular and uneven-aged structure such as overmature and old-growth forests. Bergeron *et al.* (1999) proposed that a proportion of the land base should be harvested with partial cutting to reproduce stand structure conditions similar to those of natural stands between 100 and 200 years. These second cohort stands are more open, composed of both trees that established immediately after fire from seed, and those that established later by layering. This study is part of an evaluation of the operational feasibility of partial cutting and its effects on biodiversity. Partial cutting is still at an experimental stage in the eastern boreal forest of Canada. More specifically, we investigated the impacts of partial cutting on small mammals.

Small mammals have often been used to evaluate the effects of timber harvesting on wildlife, in consideration of their functional role in the ecosystem (Potter 1978). They are at the base of the food-web, where they represent an important prey for many of mammalian (weasels, martens) and avian (owls) predators (Hanski *et al.* 1991). In addition, they are themselves consumers of seeds (Gagné *et al.* 1999; Martell & Macaulay 1981; Sullivan 1979), fungi (Maser *et al.* 1978), lichens, plants and seedlings (Hansson 1985; Martell 1981), and invertebrates (McCay & Storm 1997).

The commercial boreal forest of north-western Quebec is composed of coniferous forests (dominated by black spruce with jack pine) in the North and by mixed-wood forests (balsam fir forest with white spruce, black spruce, trembling aspen and paper birch) in the South (Gauthier *et al.* 2000). Small mammal assemblages in these ecoregions differ mainly in that the red-backed vole (*Clethrionomys gapperi*) is dominant in the black spruce forest, whereas the mixed-wood forest is co-dominated by the red-backed vole and the deer mouse (*Peromyscus maniculatus*). These species will potentially respond differently to silvicultural treatments in these two ecoregions. Studies in coniferous forests have documented declines of red-backed vole populations immediately after harvesting (Gashwiler 1970; Martell & Radvanyi 1977; Ramirez & Hornocker 1981; Sullivan *et al.* 1999), whereas deer mouse populations typically increase after clear-cutting (Gashwiler 1970; Kirkland 1990; Martell & Radvanyi 1977; Verme & Ozoga 1981). Fewer studies have been conducted in mixed-wood forest stands and results are not consistent from one study to another, but Génier & Bergeron (1996) found the same patterns for the two species in north-western Quebec mixed-woods as those detected in coniferous stands. Shrews (*Sorex* sp.) and meadow voles (*Microtus pennsylvanicus*) responded positively to harvesting, regardless of the forest cover type (Kirkland 1990). However, species abundance patterns can vary with time since clear-cutting (Kirkland 1977). For example, red-backed voles can stay at very low levels in clear-cuts for up to 15 years after harvest (Kirkland 1977), but they may also recover high abundance very quickly, depending on how soon herb and shrub layers regenerate and provide sufficient shelter and food (Parker 1989). Deer mice increase immediately after harvesting then decline because of a lack of seeds in young pole stages, and increase again when seed production begins in mixed-wood forest (Kirkland 1977).

In this paper, we test the hypothesis that partial cuts create small mammal habitats that are within the range of natural variation of the habitats found in old seral stages in the eastern boreal forest of Canada. Hence, partial cuts should be composed of small mammal assemblages and populations more similar to old forest sites than are those found after clear-cutting. We document patterns of distribution of small mammals in a paired experimental design of partial cut, clear-cut and old forest control treatments, replicated in both the boreal mixed-wood and the black spruce ecoregions of north-western Quebec. We make the following predictions: 1) the species composition of small mammal assemblages will show significant changes in clear-cuts only, with an increase of habitat generalists and early successional species; 2) the abundance of red-backed voles (a forest specialist) will be similar in partial cuts and old forests, but will decline strongly in clear-cuts; 3) deer mouse abundance (a generalist) will be similar in partial cuts and old forests, but will increase in clear-cuts; 4) population structure parameters of the red-backed vole in partial cuts will be more similar to those in old forests than to those in clear-cuts; and, (5) population structure parameters of the deer mouse in partial cuts will also be more similar to those in old forests than to those in clear-cuts.

Materials and methods

Study areas and experimental design

The study was conducted in the forest management units of Norbord-Nexfor Industries, for both the black spruce and the boreal mixed-wood ecoregions. The boundary between the two ecoregions is located at approximately 49°00’N (Gauthier *et al.* 2000). The black spruce study area was located in the Muskuchii Hills (50°12’N; 78°42’W), 200 km north of La Sarre, Quebec. The mixed-wood study area was located west of Opasatica Lake (Dufay township) (48°02’N; 79°23’W), south-west of Rouyn-Noranda, Quebec (figure 1). Partial cut trials were established in these two locations (Morasse 2000; Bescond *et al.* 2002).

Black spruce forest

Prior to harvesting, the black spruce study area stands were composed of old mature jack pine (*Pinus banksiana*) and black spruce (*Picea mariana)* with an understory of non commercial black and white spruce (*Picea glauca*). The canopy of these stands is in transition from jack pine to black spruce forests. Cutting concentrated mainly on old jack pines, while young spruce poles were retained. Stands were located on well drained sandy soil slopes, embedded in a lowland forest matrix of black spruce with bogs and wetlands.

Twelve sites were chosen in the black spruce study area to represent four treatments: 1) three partial cuts (PC) with a diameter-limit cutting system where above trees 14 or 16 cm dbh were harvested; 2) three clear-cuts (CC); 3) three uncut control old jack pine stands (COjp); and 4) three uncut control old black spruce stands (CObs). Partial cuts were harvested in 1998, 1999 and 2000, while clear-cuts were done in 1993, 1996 and 2001. Because ground and shrub covers are critical to small mammal occurrence, clear-cuts were chosen on the basis of the density of understory cover. In this region, understory cover reconstruction following clear-cuts may take some time depending on site quality. This is why clear-cut treatments were of different ages in our experimental design. In this study area, the goal of partial cutting was to transform jack pine forests into black spruce forests. The uncut control jack pine stands (> 120 years) represented the initial stage of the partial cut treatments prior to harvesting, whereas the uncut control black spruce stands (> 120 years) were old, open forests, that represented the reference structural stage which partial cutting treatments were intended to mimic. For some analyses, the two uncut forest types (jack pine and black spruce stands) were pooled (CO).

Boreal mixed-wood

In the mixed-wood study area, treatments were carried out in two types of local stand: almost pure black spruce stands, and black spruce stands with an important proportion of paper birch (*Betula papyrifera*), white spruce and balsam fir (*Abies balsamea*). Paper birch, red maple (*Acer rubrum*) and eastern white cedar (*Thuya occidentalis*) present in the partial cutting treatments were not harvested. Old black and white spruce trees were harvested and young spruce and fir poles were protected. In this study area, partial cuts aimed to preserve the structure of the harvested forests.

In the mixed-wood boreal forest, the heterogeneity of the forest cover induced a large variability within treatments. Hence, partial cutting created a range of intensity in disturbance and sites were chosen along a gradient of forest canopy cover generated by this silvicultural treatment. Our experimental design included five treatments: 1) two clear-cuts with no green retention trees (CC); 2) two partial cuts where residual canopy cover was 20% (PC20) (harvesting trees of more than 10 cm dbh); 3) two partial cuts where residual canopy cover was 40% and where a diameter-limit cutting system of trees above 14 cm dbh was used (PC40); 4) two partial cuts where residual canopy cover was 60% (PC60) (harvesting trees of more than 14 cm dbh); and 5) two uncut control mature forests (> 80 years) (CO). All cutting treatments were harvested in 2000 or 2001. For some analyses, the three levels of partial cutting were pooled (PC).

Small mammal populations

Small mammals were live-trapped from June to September 2002. One trapping grid (1.44 ha) was laid out on each site with 49 (7 x 7) trap stations at 20-m intervals, and one *Sherman* live-trap was located at each station. Traps were supplied with pieces of apple and peanut butter, and cotton as bedding. Pucek (1969) have shown that pit-falls are more efficient than live traps for estimating shrew populations. Hence, pit-falls were located in one station out of four in each trapping grid (13 per grid). Traps and pit-falls were set for three trap-nights and checked each day. In the black spruce study area, two trapping sessions (eight days) were conducted: one at the beginning (17-24 June) and one at the end of summer (18-25 August). In the mixed-wood study area, there were three trapping sessions (twelve days): early June (3-14 June), early July (6-17 July) and early September (26 August - 6 September). Another trapping session was initiated in early August but not completed. This additional session was considered only for analyses conducted at the community level. Shrews were sampled with pit-falls only during the final session at each study area.

All captured animals except shrews were ear-tagged with individually numbered tags, weighted, aged (adult or juvenile), sexed, reproductive condition noted, and released at the point of capture. Age classes of small mammals were estimated by body weight. Red-backed voles weighing 18g or less, and deer mice weighing 16g or less were considered as juveniles (Martell 1983a). All individuals who died accidentally during the sampling were collected and identified using Lupien (2000; 2002) identification keys.

Small mammal diversity was calculated using the Shannon-Wiener index (Krebs 1989) for each treatment, pooling the data from trapping sessions of the entire summer. Rarefaction curves (expected number of species versus numbers of individuals in a sample) were used to compare richness between treatments with different sample size. Rarefaction estimates can be interpreted as diversity measures as these estimates account for both species richness and relative abundance (Buddle 2001). Abundance of each species was calculated as the number of captures per 100 trap-nights, based on active traps only (e.g., excluding accidentally closed and displaced traps). This measure considers each individual only one time, even if it was captured several times. Recapture rates were also calculated as the proportion of recaptures on the total number of capture events. The status of captured individuals was also investigated to characterize the population structure of the two most abundant species: red-backed vole and deer mouse. Proportions of males/females, adults/juveniles and pregnant/non-pregnant adult females were calculated for each species in each treatment, for the entire summer and for each trapping session.

Habitat variables

Within each site, diameter structure of live and standing dead trees was also measured in two diagonally situated 20 x 20-m tree plots per grid. The basal area of live and dead trees was calculated for trees under and over the threshold diameter for which partial cutting was conducted. The number and decay class (I-III: Bull *et al.* 1997; Parks *et al.* 1997) of logs used by small mammals (diameter ≥ 8 cm; Bowman *et al.* 2000) were collected along a 56.5 m transect centred on the diagonal of each grid.

The understory vegetation was sampled within each trapping grid (eight plots per grid in the mixed-wood and twelve plots per grid in the black spruce study area). Each plot was subdivided into one 3 x 3-m plot for sampling percent cover of herbs and shrubs species (< 1-m height) and one 1 x 1-m nested plot for sampling percent cover of ground vegetation (mosses, sphagnum, lichens, grasses, exposed bare ground, litter and small woody debris). The percent cover at 1-m height was estimated for total vegetation cover and for each plant species. We pooled vegetation species into taxonomic groups: ferns-and-allies, sedges, forbs, shrubs and deciduous trees. Percent cover of residual mosses, sphagnum and lichens in the black spruce study area and percent cover of residual litter, mosses and lichens in the mixed-wood study area were pooled into a single value: percent cover of natural ground vegetation (NGV) in order to quantify the proportion of undisturbed understory. In both study areas, small woody debris and exposed bare ground were pooled as a new variable (DBG) to characterize the amount of disturbed understory created by harvesting.

Statistical analyses

First, we assessed the effect of harvesting on small mammal habitat. For each study area, a one-way ANOVA with Tukey post-hoc test was conducted to compare the effect of treatments on mean basal area of live and dead trees, understory vegetation characteristics (at ground level and below 1-m height) and logs. A cluster analysis was also conducted to determine the similarity of vegetation composition below 1-m height in partial cuts, clear-cuts and uncut control stands.

We analysed the small mammals at three levels: community, species abundance and population structure. At the community level, we tested our first prediction that species composition of small mammal communities would change only in clear-cut treatments. One-way ANOVA - where the sampling unit was the site - were used to determine the effect of treatments on diversity indices and species richness of small mammal assemblages. Analyses of variance for repeated-measures were also used to evaluate differences among treatments and among trapping sessions on total abundance of small mammals. Moreover, cluster analyses were used to determine if small mammal assemblages in partial cuts were closer to clear-cuts or to uncut control stands. Morisita-Horn's index of similarity, based on proportions of each species in the different treatments, was used to calculate distance matrices (Krebs 1999). Wolda (1981) recommended this index as the best overall measure of similarity for ecological use. Clusters were then formed using the unweighted arithmetic averaging clustering method (UPGMA). We used internet-based software by Brzustowski

(2003) for rarefaction and cluster analyses, both of which were conducted only on live-trap data.

At the species level, we tested the predictions that red-backed vole abundance would decline in clear-cut treatments (prediction 2) and that deer mice will increase in clear-cuts only (prediction 3). Analyses of variance for repeated-measures were used to evaluate differences among treatments and among trapping sessions on the abundance and recapture rate for each species. Recapture rates were considered as an index of residency of individuals within each trapping grid. Multiple regressions were also conducted to determine the combinations of habitat features that best explained small mammal distribution patterns within treatments. Hence, this would allow us to identify more precisely which habitat characteristics were more closely associated to the abundance of each species. Live and dead trees basal area, log density (overall values and by decay class), ground vegetation cover (NGV and DBG), total vegetation cover below 1-m height and taxonomic groups in the two study areas were used as explanatory variables.

Finally, we tested our predictions that the population structure of red-backed voles (prediction 4) and deer mice (prediction 5) would change in clear-cuts only. Analyses of variance for repeated-measures were used to evaluate differences among treatments and among trapping sessions on female, pregnant female and juvenile proportions. Chi-square statistics were also used to test for an equal distribution of males and females within treatments, for the entire summer and at each trapping sessions.

Results

Forest structure habitat

Black spruce forest

In the black spruce study area, the mean basal area of live trees (LBA) varied significantly among treatments (ANOVA; LBA2-16cm: $P < 0.001$; LBA>16cm: $P = 0.019$) (figure 2). Partial cuts protected, at least, twelve times more saplings and young poles and three times more larger trees than clear-cuts. Mean basal area of dead trees (DBA) was significantly different across the treatments ($P < 0.001$), with higher densities per hectare in uncut control stands than in clear-cut and partial cut treatments. Saplings and young poles were mostly responsible for treatment differences (DBA2-16cm: $P = 0.001$), whereas larger trees did not differ significantly (DBA>16cm: $P = 0.305$) (figure 3). There was no difference between the two types of uncut control stands (COjp and CObs), for either live or dead trees (figures 2 and 3).

Natural ground vegetation (NGV) was significantly different among treatments with higher percent cover in uncut control stands (92%) than in partial cuts (54%), followed by clear-cuts (28%) ($P < 0.001$). The opposite pattern was recorded for small woody debris and bare ground (DBG) ($P < 0.001$).

Total vegetation cover below 1-m height was significantly different among treatments ($P < 0.001$) with higher values in clear-cuts than in partial cuts and control stands (table I). Ferns-and-allies was the only taxonomic group to show similar values in partial cuts and uncut control stands. Shrub cover was significantly different among treatments, with less cover in partial cuts than in clear-cuts and uncut control stands (table I). Cluster analyses revealed that vegetation composition below 1-m height in partial cuts was more similar to that in uncut control stands than to clear-cut treatments, clustering at 82% similarity. Moreover, partial cuts in the black spruce study area were more similar to uncut control old jack pine stands which represented the “before harvest” forest cover types, than they were to old black spruce stands (the target “after treatment”).

Log density was similar among treatments for each decay class and for all decay classes combined.

Boreal mixed-wood

Mean basal area of live trees (LBA) varied significantly among treatments in the mixed-wood study area (LBA2-14cm: $P < 0.001$; LBA>14cm: $P = 0.018$) (figure 2). Partial cuts protected four times more saplings and young poles and three times more larger trees than clear-cuts, but differences are non significant. Mean basal area of dead trees (DBA) was similar across the treatments (overall: $P = 0.944$; DBA2-14cm: $P = 0.813$; DBA>14cm:

P = 0.921) (figure 3). There were no differences among the three partial cut treatments, for either live or dead trees (figures 2 and 3).

Natural ground vegetation cover (NGV) was higher in uncut control stands (86%) than in partial cuts (56%), and higher in partial cuts than in clear-cuts (10%) ($P < 0.001$). The opposite pattern was recorded for small woody debris and bare ground (DBG) ($P < 0.001$).

Total vegetation cover below 1-m height was similar across the treatments (P = 0.119) (table I). Forb cover was significantly different among treatments, with higher values in partial cuts and uncut control stands than in clear-cuts. However, deciduous trees had higher percent cover in uncut control stands than in either type of harvest (table I). Cluster analyses revealed that vegetation composition below 1-m height in partial cuts was more similar to that of uncut control stands than it was to that of clear-cut treatments (clustering at 85% similarity). The low-intensity partial cuts (PC60) were closer to uncut control stands than they were to PC20, PC40 and clear-cut treatments.

In the mixed-wood study area, log density (all decay classes pooled) was similar across the treatments, but logs in the most deteriorated decay condition (class III) were significantly more abundant in uncut control stands than in clear-cuts (P = 0.035), and were marginally more abundant than in partial cuts (P = 0.058).

Small mammals

Trapping effort represented 3 528 trap-nights and 465 pit-fall-nights in the black spruce study area, and 4 997 trap-nights and 546 pit-fall-nights in the mixed-wood study area. Small mammal species sampled included Gapper's red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), meadow vole (*Microtus pennsylvanicus*), heather vole (*Phenacomys intermedius*), rock vole (*Microtus chrotorrhinus*), southern bog lemming (*Synaptomys cooperi*), masked shrew (*Sorex cinereus*), pygmy shrew (*Sorex hoyi*), arctic shrew (*Sorex arcticus*) and short-tailed shrew (*Blarina brevicauda*).

Communities

Black spruce forest

Eight species were trapped in the black spruce study area. Richness and diversity indices were similar among treatments ($P = 0.211$ and $P = 0.059$ respectively) (table II). Estimates of the expected number of species based on rarefaction curves showed that small mammal richness was significantly higher in clear-cuts than in either partial cuts or uncut control stands (for a sub-sample of 60 individuals, figure 4).

Total abundance of small mammals was 8.2 captures per 100 trap-nights in live-traps and 12.3 captures per 100 trap-nights in pit-falls (table II). Live-trap abundance increased significantly between trapping sessions ($P = 0.005$).

Species composition was similar across the treatments. However, the relative abundance of rodent species (proportion of each species in the community) was different (figure 5). The proportion of Gapper's red-backed voles was highest in uncut control stands and decreased with the intensity of timber harvesting. Deer mice and meadow voles followed the opposite trend (figure 5). The masked shrew was the most abundant *Sorex* species, accounting for 81.6%. Overall, cluster analyses revealed that small mammal assemblages from partial cuts were more similar to those from uncut control stands than they were to clear-cut treatments (87% similarity). The two control stands (COjp and CObs) were more similar to one another than they were to the other treatments.

Boreal mixed-wood

Ten species were trapped in the mixed-wood study area. Total richness and diversity indices were similar among treatments ($P = 1.0$ and $P = 0.427$ respectively) (table II). Even though species richness was higher in the mixed-wood study area than in the black spruce study area, the equitability was lower (table II). Consequently, the diversity index was also lower (3.7 vs. 4.9), indicating a more even distribution of species abundances in the black spruce than in the mixed-wood study area, where most individuals captured were deer mice or red-backed voles (figure 5).

Rarefaction estimates revealed that small mammal richness was similar among treatments for a sub-sample of 85 individuals (figure 4). Furthermore, the accumulation of species in uncut control stands had not levelled off at this sample size, suggesting that more sampling would result in higher species richness.

Total abundance of small mammals was 13.2 captures per 100 trap-nights in live-traps and 24.4 captures per 100 trap-nights in pit-falls (table II). Live-trap abundance increased significantly between trapping sessions ($P < 0.001$).

Species composition was different among treatments in the mixed-wood study area. Indeed, two species were restricted to clear-cut treatments (meadow and heather voles) and two others were restricted to partial cuts or uncut control stands (rock vole and short-tailed shrew) (figure 5). Relative abundance of deer mouse was similar to that of the red-backed vole in this study area. Masked shrew was the most abundant *Sorex* species accounting for 84.6%. Cluster analyses revealed that small mammal assemblages from partial cuts were more similar to those from uncut control stands than they were to those from clear-cut treatments (97% similarity). Partial cuts with 20% and 40% residual canopy cover were most similar, but they resembled uncut control stands more closely than partial cuts with 60% residual canopy cover.

Species abundance

Black spruce forest

Gapper's red-backed vole was the most abundant species in the black spruce study area; its abundance was similar across the treatments ($P = 0.360$) (figure 6). Differences were not statistically significant because there was more variability within treatments than between treatments. Deer mouse abundance was low, being mostly sampled in clear-cut treatments ($P = 0.001$) (figure 6). Meadow vole abundance did not show any significant difference among treatments ($P = 0.171$). Shrew abundance was measured only by pit-falls, so their abundance was tested only among treatments for the last trapping session of each study area. Masked shrew abundance was similar across the treatments ($P = 0.883$). Recapture rates of red-backed vole and meadow vole were similar among treatments ($P = 0.236$ and $P = 0.482$ respectively). The recapture rate of deer mouse was too low to conduct statistical analyses.

Red-backed vole, deer mouse and meadow vole abundance were similar among trapping sessions (P = 0.080; P = 0.696 and P = 0.118 respectively). The recapture rate of red-backed vole was significantly different among trapping sessions, with higher values at the end of summer (P = 0.041). Recapture rate for meadow voles did not shown any significant difference between early and late summer trapping sessions (P = 0.513).

Mean abundance of red-backed vole (log transformed) was positively related to the basal area of large live trees (> 16 cm dbh). Mean abundance of meadow vole was positively related to percent cover of deciduous trees and sedges. Mean abundance of masked shrew (in pit-falls) was associated to total vegetation cover below 1-m height (table III). No significant relationships were obtained for recapture rates of any species. The other captured species were not sufficiently abundant to conduct statistical analyses.

Boreal mixed-wood

Gapper's red-backed vole was the most abundant species in the mixed-wood study area. Red-backed vole abundance was very low in clear-cuts throughout the summer and there was an interaction effect between trapping session and treatment type. There was significantly more red-backed voles captured in partial cuts than in clear-cuts and intermediate values in uncut control stands, but in early July only (P = 0.041) (figure 6). Deer mouse abundance was similar across the treatments (P = 0.378). Masked shrew abundance was similar across the treatment (P = 0.951), as was the abundance of pygmy shrews (P = 0.111). The recapture rate of red-backed voles was significantly higher in partial cuts than in clear-cuts (P = 0.043), while that of deer mice was similar (P = 0.724).

Red-backed voles abundance was significantly different among trapping sessions in partial cuts only (P = 0.001), with higher abundance in early July than in early June and early September (figure 6). Deer mouse abundance was similar throughout the summer season (P = 0.315) (figure 6). Recapture rates of red-backed voles and deer mice were similar among trapping sessions (P = 0.485 and P = 0.940 respectively).

Mean abundance of red-backed voles was positively related to percent cover of forbs and inversely to that of shrubs. Deer mouse mean abundance was positively related to deciduous tree cover. The recapture rate of deer mice was associated with the basal area of young poles (2-14 cm dbh) (table III). The number of captured individuals of other species was not high enough to conduct statistical analyses.

Red-backed vole and deer mouse population structure and dynamics

Black spruce forest

We investigated the status of individuals for red-backed vole populations in each treatment. Within uncut control stands, red-backed vole populations had equal numbers of males and females (chi-square: P = 0.821), more than two out of three of adult females were pregnant, and one third of the individuals were juveniles. We observed equal numbers of male and female adults (chi-square: P = 0.225), but more male than female juveniles (P = 0.022) (table IV). Moreover, there were similar numbers of adult and juvenile males, but five times more adult than juvenile females. Similar patterns were observed within partial cut and clear-cut treatments. Overall, there was no significant difference in red-backed vole population structure among treatments.

Changes in population structure between trapping sessions indicate that the proportion of females in the red-backed vole population of uncut control stands remained constant at around 50% (figure 7). The proportion of females seemed to be similar in partial cuts and in clear-cuts throughout the season. All the females were pregnant in partial cuts in early summer (N = 4), but this proportion declined slightly at the end of the summer (N = 8). Less than 40% of the populations were composed of juveniles during the entire summer (figure 7). The proportion of juveniles seemed to be constant in control stands from one session to another, but this proportion increased in partial cuts. Differences between trapping sessions for any of the three variables were not, however, statistically significant.

In this study area, the deer mouse was not abundant enough (15 captures for 3 528 trap-nights) for statistical analysis of population structure (table IV). Figure 8 illustrates the general trends observed in clear-cuts (12 captures for this treatment) across trapping sessions. An equal number of males and females were captured. All adult females were pregnant and a decrease of juveniles occurred in late summer.

Boreal mixed-wood

Within uncut control stands of the boreal mixed-wood, the red-backed vole population had equal numbers of males and females (chi-square: P = 0.577), 60% of adult females were pregnant, and less than 20% of the individuals were juveniles. As in the black spruce study area, we observed equal numbers of male and female adults, but more male than female juveniles. However, numbers were too low to detect significant differences in the later (table IV). There were two times more adult than juvenile males, and 15 times more adult than juvenile females. Partial cuts had a population structure quite similar to that of uncut control stands. There were no difference between treatments for any of the three response variables, but only one red-backed vole was captured in clear-cuts in the first two sessions (early June and July) and three in the third (early September). We conclude that red-backed voles did not use clear-cuts until the end of summer.

Changes in red-backed vole population structure between trapping sessions were also investigated. The proportion of females in uncut control stands remained relatively constant throughout the summer at close to 50% (figure 7). The proportion of females in partial cuts seemed to be similar to that of control stands. Partial cuts and uncut control stands showed a very similar pattern for the proportion of pregnant females (figure 7). Less than 40% of the population was composed of juveniles for all treatments, except for the mid-summer trapping session in the clear-cuts where only one individual, a juvenile, was captured. There were no statistically significant differences between trapping sessions for any of the three response variables.

Deer mouse population structure in uncut control stands was similar to that of red-backed vole: equal numbers of males and females (chi-square: P = 0.796), 75% of adult females pregnant, and 20% of the individuals as juveniles (table IV). However, deer mouse populations had an excess of adult males, particularly in partial cut treatments (chi-square between male and female adults: P = 0.001) (table IV). There were, however, no statistically significant differences between treatments for any of the three response variables.

The proportion of females in deer mouse populations was very low in partial cuts throughout the summer (figure 8). Thus, the number of pregnant females in each trapping session was too low for statistical analysis. The proportion of juveniles in partial cuts and uncut control stands showed a similar pattern of increase from early to late summer, whereas an important decrease occurred in mid-summer in the clear-cut treatments.

Discussion

Small mammal habitat

Our study is one of the first to investigate the effect of partial cutting on small mammal populations in eastern boreal forests of Canada. Our general objective was to assess whether partial cutting systems could generate the structural attributes of late-successional forest and how these attributes affect small mammal populations and communities. Our results indicate that several important structural elements are maintained in partial cut treatments in both the boreal mixed-wood and the black spruce forest. Franklin *et al.* (1997) defined criteria for variable retention of old-growth attributes in silvicultural systems: large diameter live trees, some snags, logs and fallen wood in various stages of decay, undisturbed layers of forest floor and understory vegetation. In our partially cut treatments, all of these criteria were met. The proportion of live saplings and trees below the cutting diameter threshold was quite similar to that in uncut old-growth control stands. A proportion of trees above this cutting threshold was retained in partial cut units, in some cases with no significant differences from uncut control stands (black spruce forest). The mean basal area of large snags was also similar to that of old-growth forests. Log density was similar in partial cuts than in old-growth forests in the two study areas. From the perspective of small mammal habitat requirements, less small debris and less exposed organic soils were created, and more natural ground vegetation was retained in partial cuts than in clear-cuts. Vegetation composition under 1-m height was more similar to that of uncut control stands. Martell (1983b) and Sullivan *et al.* (2001) found that understory vegetation recovery in variable retention harvest systems was more rapid than that in clear-cuts, in mixed-wood stands of Ontario and in coniferous stands of British Columbia, respectively.

Small mammal communities

Small mammal diversity in partial cut treatments was more similar to diversity in uncut control stands than to clear-cut diversity, in both study areas. Small mammal diversity was highest in clear-cuts. However, differences among treatments were significant only for black spruce clear-cuts. Vegetation cover below 1-m height was significantly higher in the older clear-cut replicates (between 1 to 9 years after harvesting) which generated suitable conditions for both forest species such as red-backed voles, habitat generalists like the deer mouse and early-successional species such as meadow voles and heather voles. Kirkland (1977) observed a diversification in vegetation as well as in small mammals during the five years after harvest. In mixed-wood boreal forest, our clear-cuts were only 1-year old and perhaps this may explain why species diversity was closer to both partial cuts and uncut control stands.

Our first prediction that species composition of small mammal communities changed after clear-cuts was supported only in the mixed-wood boreal forest. The pattern observed in this habitat was similar to the results obtained in several previous studies: early-successional and generalist species (deer mouse, meadow vole, heather vole) colonize clear-cuts, while uncut control stands were dominated by late-successional species such as the red-backed vole (Martell 1983b; Martell & Radvanyi 1977; Sullivan *et al.* 1999). However, in the black spruce forest, while species composition did not change between treatments, the relative abundance of species did. Moreover, the naturally open canopy cover of the old uncut control stands allowed early-successional species to be present, just as they were in partial cut and clear-cut treatments. Indeed, the meadow vole, an open habitat species (*sensu* Boos & Watt 1997), was present in all treatments including uncut control stands in the black spruce forest. Then, species composition and proportion of each species in partial cuts were more similar to uncut forests than to clear-cuts in both study areas.

Small mammal abundance

Red-backed voles and deer mice dominated the small mammal communities in naturally disturbed boreal forests. In the mixed-wood boreal forest, harvesting significantly influenced red-backed vole abundance, while in the black spruce forest, it affected mainly deer mouse abundance. Our second prediction that red-backed vole abundance would be similar in partial cuts and uncut control stands and lower in clear-cuts was supported in both forest cover types. Red-backed voles were not able to persist in clear-cuts in the two study areas. No more than 14 individuals in the black spruce clear-cuts and five individuals in the mixed-wood clear-cuts were captured over an entire summer. However, differences were statistically significant only in the mixed-wood boreal forest, because there was more variability within treatments than between treatments in the black spruce forest. Nevertheless, in the black spruce forest, red-backed vole abundance increased gradually from clear-cuts to partial cuts to uncut control stands. Partial cuts mitigated the impact of logging on red-backed vole abundance in this area. In the mixed-wood boreal forest, the increase of red-backed voles in partial cuts was similar to the results reported in other silvicultural experiments on partial cutting (Monthey & Soutière 1985; Steventon *et al.* 1998). This species was largely dominant in uncut control stands of the two study areas. Red-backed voles prefer mesic late-successional mixed-wood and coniferous forests (Boos & Watt 1997). In black spruce forests, this species was positively correlated with the basal area of large live trees, a result also reported by Sullivan & Sullivan (2001). Persistence of red-backed vole in black spruce partial cuts three years after the removal of trees suggests that the levels of green retention in our treatments may provide suitable habitat for the maintenance of this species in such managed forest stands. In addition, partial cutting maintained coarse woody debris and understory species for protection cover and overwintering sites (Carey & Johnson 1995; Monthey & Soutière 1985; Von Trebra *et al.* 1998). Insufficient tree cover results in local extinction of red-backed voles from recent clear-cuts for many years (Gashwiler 1970; Martell 1983b; Ramirez & Hornocker 1981), but increase in the vegetation cover with time allow recolonisation by this vole species (Monthey & Soutière 1985). Contrary to results from clear-cuts, our partial cutting results, particularly those from the mixed-wood boreal forest (sampled one year after harvesting), show that red-backed voles remain in this habitat immediately after harvest. Then, red-backed voles were maintained in partial cuts in abundance similar to mature forests, whereas they were almost absent in clear-cuts.

Our third prediction that deer mouse abundance would be similar in partial cuts and in uncut control stands but increase in clear-cuts was supported to some degree. Deer mice were almost absent in the black spruce forest, except in clear-cuts. The preference of the deer mouse for forest with a hardwood component (our results; Boos & Watt 1997) may explain its low abundance in the black spruce forest. Hence, this species occurred only in clear-cuts, the sole treatment where deciduous trees were present. Several authors have reported similar patterns of cut block use by deer mice (Martell & Radvanyi 1977; Kirkland 1977; 1990; Sullivan & Sullivan 2001). In the mixed-wood boreal forest, however, deer mice were common in all sites. Martell (1983b) found that this species was also quite abundant following selective cuts of the mixed-wood forests in Ontario. This habitat generalist apparently finds suitable conditions throughout a gradient of seral stages that ranged from open clear-cut habitats to mature mixed-wood stands, but its abundance was not significantly higher in clear-cuts than in other treatments. Perhaps the high deciduous component in all treatments overrode the differences among treatments. Then, the deer mouse abundance was similar in partial cuts and natural forests, whereas their abundance was higher in clear-cuts, but with significant differences only in the black spruce forest. The abundance of red-backed voles and deer mice varied inversely, suggesting a potential for competitive displacement (*sensu* Morris 1996), similar to that found by Martell (1983b) in a strip cutting silvicultural system.

Population structure

Van Horne (1983) showed that abundance could be a misleading indicator of habitat quality. She suggested using demographic parameters such as survival or productivity of individuals. Because small mammals may have source-sink dynamics, where the surplus of individuals produced in source habitats may disperse in secondary habitats, abundance alone is not sufficient to assess habitat quality (Van Horne 1981). Hence, knowledge on the status of individuals in the population (population structure parameters), not only their abundance, is critical for evaluating the quality of used habitats.

Our fourth prediction that red-backed vole population structure would be similar in partial cuts and in old-growth forests was supported in both study areas. Although population structure of red-backed vole varied little among treatments, session-by-session analyses revealed that, in the mixed-wood boreal forests, red-backed voles were almost totally absent within clear-cuts until the end of the summer, whereas they maintained low abundance in black spruce clear-cuts. Sex ratios were balanced, suggesting similar survival rates for males and females in partial cuts to those in undisturbed forests. The high proportion of pregnant females suggests that there are similar levels of reproductive activity of red-backed vole populations in partial cuts as in uncut control stands, for both study areas. Although clear-cut treatments were occupied at the end of summer in the boreal mixed-wood, they were not used for reproduction throughout the summer season. Spacing behaviour has mainly been studied in deer mice, but red-backed voles can also use cutting units as dispersion sinks (Sullivan *et al.* 1999). Red-backed voles are weakly sensitive to density effects (Bondrup-Nielsen 1987), and juveniles, particularly males, often disperse when populations reach the carrying capacity of environments (Lidicker 1975). Consequently, it is possible, that when all the good sites become protected territories at the end of the summer, non-territorial individuals disperse into secondary habitats, such as cut units (Van Horne 1982). This pattern is likely in our study areas given the proximity of clear-cut treatments to adjacent mature forest stands. The proportion of juvenile red-backed voles in mixed-wood boreal forest seems to follow a decreasing trend from clear-cuts to partial cuts to uncut control stands. If we assume that the proportion of juveniles reveals habitat conditions that function as sinks for dispersing animals (Van Horne 1981; 1983), clear-cuts may act as sinks in the boreal mixed-wood. However, because only five individuals were captured in clear-cuts, we must be cautious in concluding that such a pattern indeed occurs in this study area. Moreover, population structure of red-backed vole was similar in partial cuts and in mature forests in the two study areas, whereas clear-cuts may be used as sinks by red-backed voles at the end of the summer in the mixed-wood boreal forest.

Our fifth prediction that deer mouse population structure would also be similar in partial cuts and uncut control forests was not supported. Although deer mouse population abundance seemed to be unaffected by harvest in boreal mixed-wood, and even favoured by clear-cutting in black spruce forest, population structure results showed an excess of adult males in partial cut treatments in the boreal mixed-wood. This unbalanced sex ratio may reveal a difference in survival rates between males and females. If adult female survivorship is governed by food availability during the early breeding season (Sadleir 1974), we might expect that the excess of males is indicative of lower habitat quality in this treatment, particularly with regards to reproductive activity. A similar bias towards males was observed in mixed-wood clear-cuts in Ontario (Martell 1983a). However, low reproductive activity in mixed-wood partial and clear-cuts (low proportion of pregnant females) was not apparent when looking at the proportion of juveniles, which was similar across treatments. These juveniles however, may come from more productive sites such as adjacent mature forests. Then, in the mixed-wood boreal forest, deer mouse populations showed an excess of males in partial cuts, suggesting difficulties in persisting without external contributions of individuals. However, in the black spruce forest, the deer mouse was almost absent, except in clear-cuts.

Many small mammal studies have been conducted at the end of the summer (August to October) when populations reach high densities (Génier & Bergeron 1996; Parker 1989; Potvin & Breton 1997; Verme & Ozoga 1981) concluding that small mammals may not be good indicators for evaluating the effects of silvicultural treatments given their weak response to clear-cut treatments. Such conclusions may, however, be misleading. Clear-cut treatments may act as secondary habitats that become occupied mainly when juveniles or young adults disperse from adjacent forests. Sullivan *et al.* (1999) and the present study show that red-backed voles do not use clear-cut treatments before the end of the summer. Several population parameters are thus required for assessing habitat quality of small mammal populations.

Conclusions

Partial cutting retains saplings and young poles, a sufficient number of large live trees and forest understory vegetation with more of the structural attributes of natural forests than clear-cuts. Hence, this silvicultural practice seems to offer better habitat conditions for small mammals. Following partial cutting, small mammal assemblages are more similar to mature forests assemblages, both in terms of their species composition and in the abundance patterns of individual species. Red-backed vole and deer mouse, the two most abundant species in the boreal forest, were maintained at levels similar to those of natural forests. But more importantly, our results on population structure provide insight into survivorship and reproductive activity of small mammals in partial cutting system. They indicate that the population structure of old-forest habitat specialists such as the red-backed vole is likely to be maintained at a level similar to that of uncut control stands, which is not the case for clear-cut treatments. Moreover, black spruce partial cuts could act as dispersion sink in late summer for this species. These results suggest that stands treated with partial cutting are more likely to preserve the long-term dynamics of forest-dwelling small mammal populations and thus represent an interesting silvicultural alternative to clear-cutting in the eastern boreal forest of North America. In contrast, the deer mouse, a generalist species, may encounter difficulties in persisting in mixed-wood partial and clear-cuts without immigration, whereas its abundance was similar across the treatment. Partial cutting, by preserving small mammals communities, abundances, population structures and habitats, are likely to also sustain the web of predators that feeds upon them.

Finally, this study documents short-term effects of partial cutting on small mammals (1-5 years after harvesting). Our analyses were confined to the stand-level and did not consider landscape-level effects of such silvicultural treatments on small mammals. To determine whether short-term and stand-level effects reflect persistent trends in the population response and community structure of small mammals, populations should be monitored over longer periods and on larger treated areas.

Acknowledgements

We are grateful to Annie-Ève Gagnon and Dominique Lafleur for fieldwork assistance and to all other occasional helpers in the field. We thank students of the P. Drapeau laboratory for advice and support throughout the study. We thank Sybille Haeussler for reviewing the English. Finally, we thank the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management and the Research Group in Forest Ecology (GREFi) for scholarships to M. Cheveau. This project was funded by the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, the Quebec fund FCAR - Fonds Forestier programme d'Action Concertée, the Quebec Ministry of Natural Resources, Norbord

Industries Inc., a NSERC industrial partnership grant to Y. Bergeron, and a SFMN grant to P. Drapeau.

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Figure list

Figure 1 : Localization of the two study areas, in the Abitibi region, Quebec, Canada. Limits of ecoregions are based on Ansseau *et al.* (1996).

Figure 2 : Mean basal area of live trees above (grey bar) and below (black bar) the diameter-limit cutting threshold in (a-) the black spruce study area and (b-) the mixed-wood study area. Numbers above each bar are the total number of live trees for each treatment and diameter class. Significant treatment differences ($P < 0.05$) are indicated by different letters. Comparisons were made by diameter class for the three treatments and the two uncut control types in the black spruce study area and for the boreal mixed-wood, the three treatments and the three partial cut intensities respectively. Silvicultural treatments are: CC clear-cuts, PC partial cuts, CO control stands, CObs black spruce control stands, COjp jack pine control stands, PC20, PC40 and PC60 partial cuts with 20, 40 and 60% residual canopy cover, respectively.

Figure 3 : Mean basal area of dead trees above (grey bar) and below (black bar) the diameter-limit cutting threshold in (a-) the black spruce study area and (b-) the mixed-wood study area. Numbers above each bar are the total number of dead trees for each treatment and diameter class. Significant treatment differences ($P < 0.05$) are indicated by different letters. Comparisons were made by diameter class for the three treatments and the two uncut control types in the black spruce study area and for the boreal mixed-wood, the three treatments and the three partial cut intensities respectively. Silvicultural treatments are: CC clear-cuts, PC partial cuts, CO control stands, CObs black spruce control stands, COjp jack pine control stands, PC20, PC 40 and PC 60 partial cuts with 20, 40 and 60% residual canopy cover, respectively.

Figure 4 : Rarefaction estimates of small mammal diversity in (a-) the black spruce and (b-) the mixed-wood study areas. Bars are standard deviations. CC is for clear-cuts, PC partial cuts and CO control stands.

Figure 5 : Community proportions of each species captured in traps (except small shrews) in (a-) the black spruce and (b-) the mixed-wood study areas. CC is for clear-cuts, PC partial cuts and CO control stands.

Figure 6 : Red-backed vole and deer mouse abundance (captures per 100 trap-nights) by treatment and trapping session in (a-) the black spruce and (b-) the mixed-wood study areas. Significant treatment differences ($P < 0.05$) are indicated by different letters. Significant within-treatment differences among trapping sessions are indicated by *. CC is for clear-cuts, PC partial cuts and CO control stands.

Figure 7 : Proportions of females, pregnant females and juveniles in the red-backed vole populations in (a-) the black spruce and (b-) the mixed-wood study areas. CC is for clear-cuts, PC partial cuts and CO control stands. * indicates percentage calculated from less than 4 individuals.

Figure 8 : Proportions of females, pregnant females and juveniles in the deer mouse populations in (a-) the black spruce and (b-) the mixed-wood study areas. CC is for clear-cuts, PC partial cuts and CO control stands. * indicates percentage calculated from less than 4 individuals.

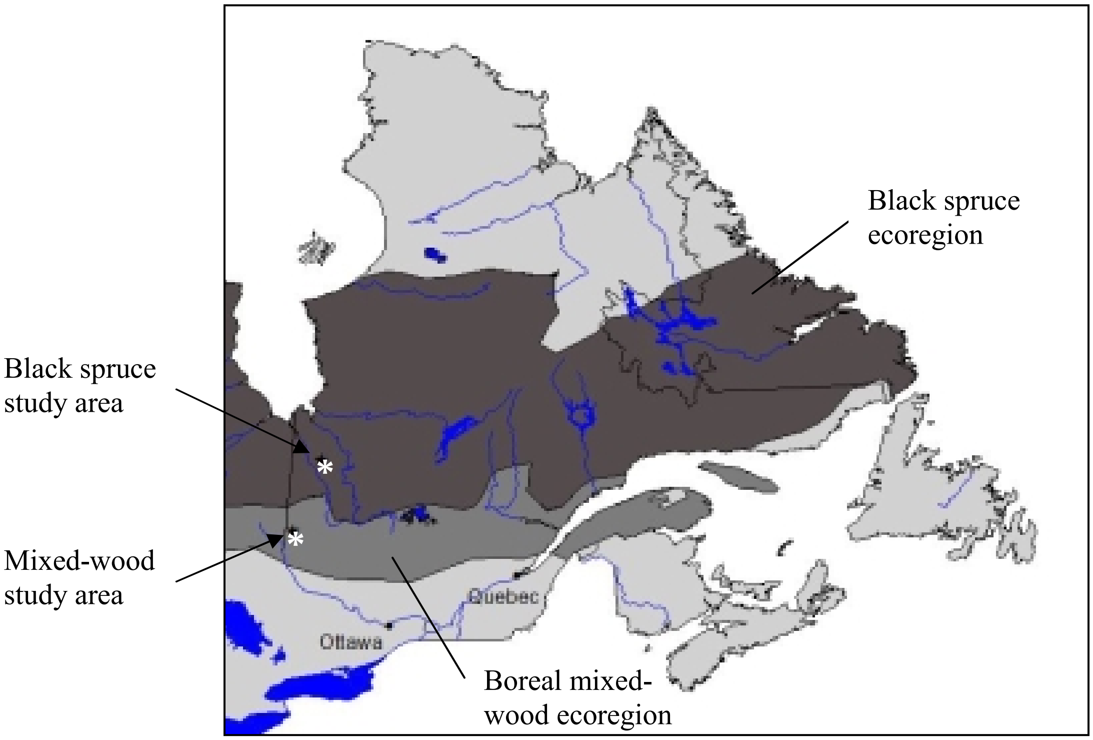
Black spruce ecoregion
Black spruce study area
Mixed-wood study area
Quebec
Ottawa
Boreal mixed-wood ecoregion

Figure 1

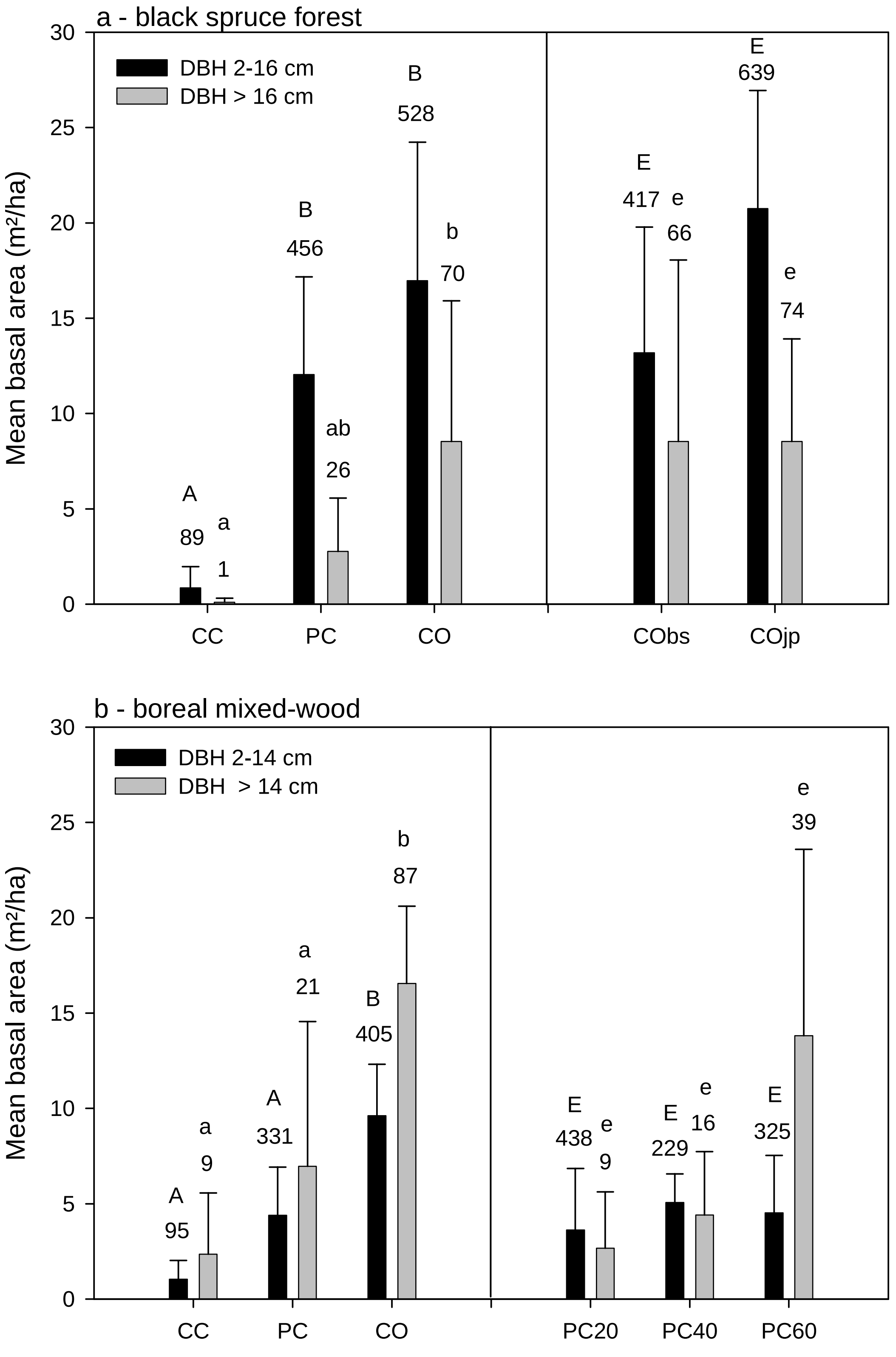
a - black spruce forest
Mean basal area (m²/ha)
DBH 2-16 cm
DBH > 16 cm
A 89
a 1
B 456
ab 26
B 528
b 70
E 417
e 66
E 639
e 74
CC
PC
CO
CObs
COjp
b - boreal mixed-wood
DBH 2-14 cm
DBH > 14 cm
A 95
a 9
A 331
a 21
B 405
b 87
E 438
e 9
E 229
e 16
E 325
e 39
CC
PC
CO
PC20
PC40
PC60
0
5
10
15
20
25
30

Figure 2

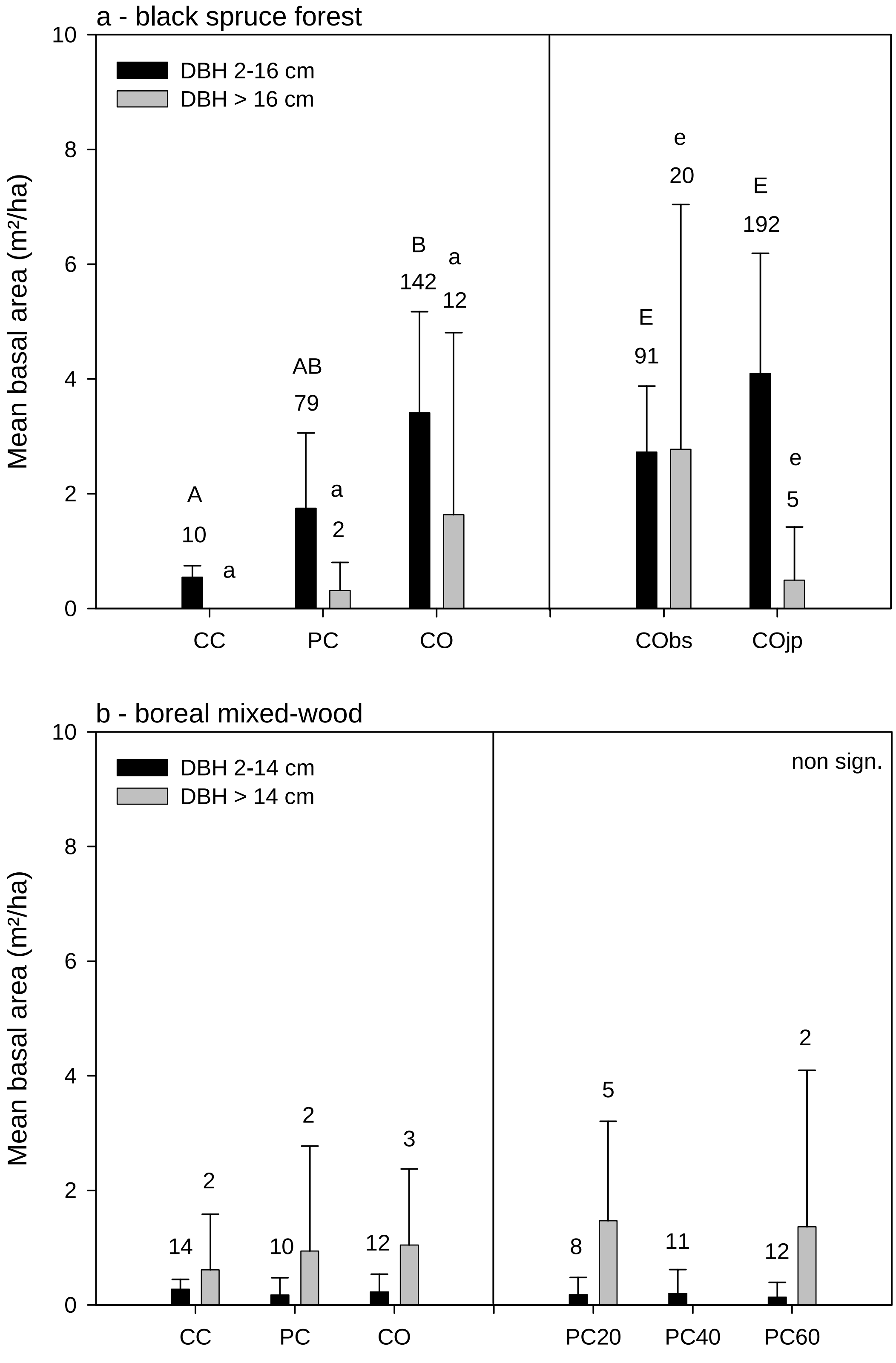
a - black spruce forest
Mean basal area (m²/ha)
0
2
4
6
8
10
DBH 2-16 cm
DBH > 16 cm
A
10
a
AB
79
a
2
B
142
a
12
E
91
e
20
E
192
e
5
CC
PC
CO
CObs
COjp
b - boreal mixed-wood
Mean basal area (m²/ha)
0
2
4
6
8
10
DBH 2-14 cm
DBH > 14 cm
non sign.
14
2
10
2
12
3
8
5
11
12
2
CC
PC
CO
PC20
PC40
PC60

Figure 3

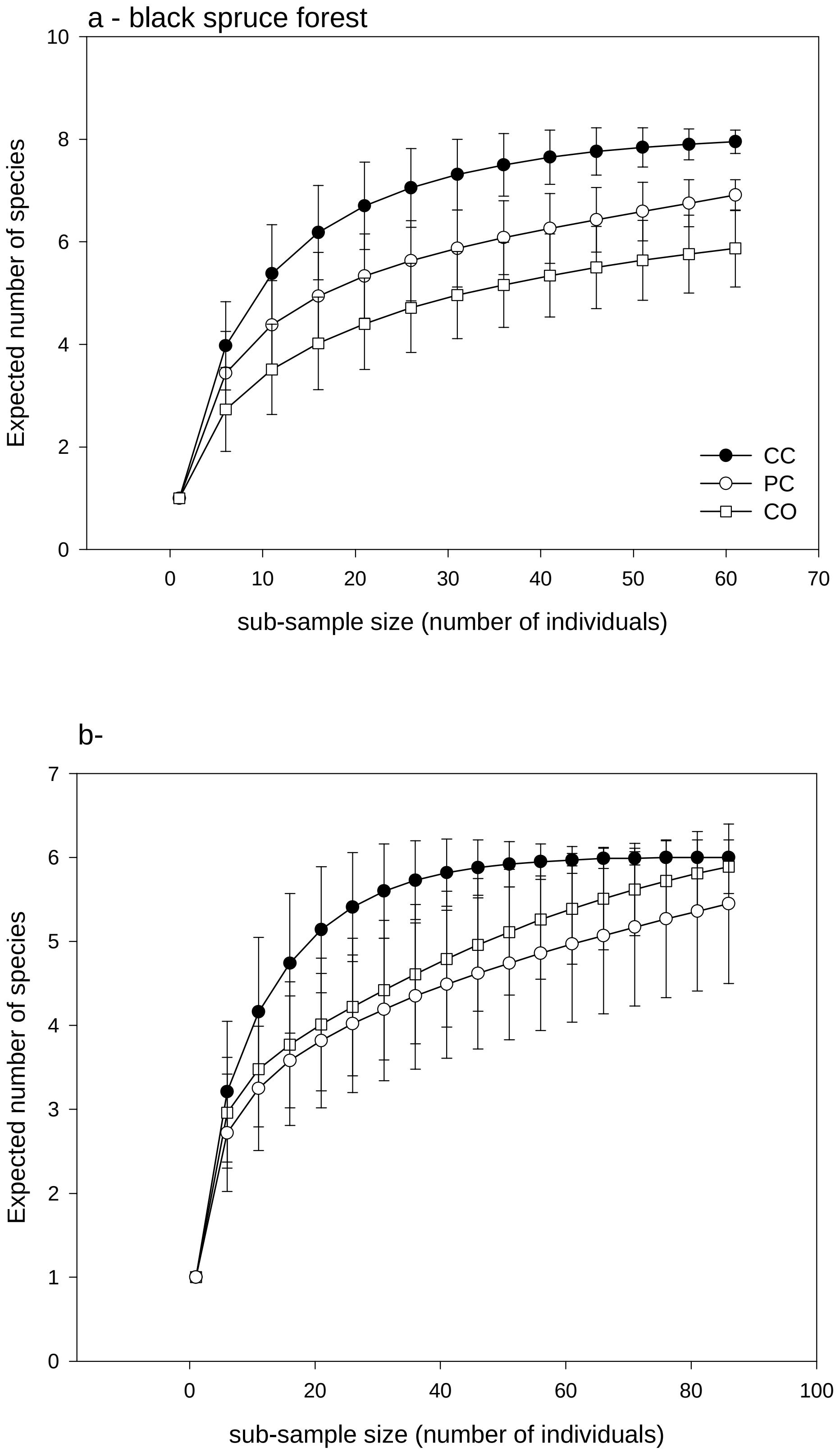
a - black spruce forest
Expected number of species
0
2
4
6
8
10
0
10
20
30
40
50
60
70
sub-sample size (number of individuals)
CC
PC
CO
b-
Expected number of species
0
1
2
3
4
5
6
7
0
20
40
60
80
100
sub-sample size (number of individuals)

Figure 4

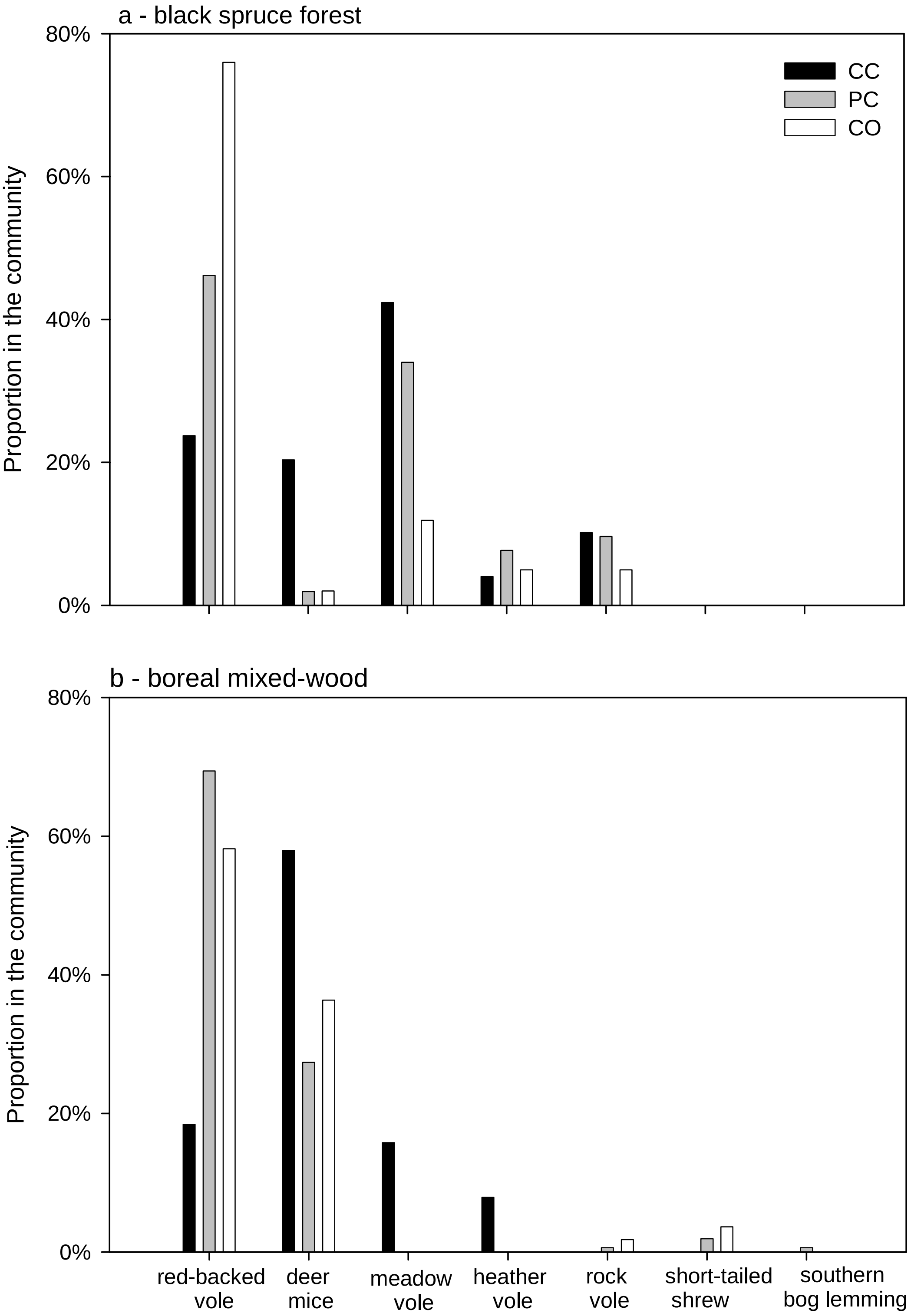
a - black spruce forest
b - boreal mixed-wood
Proportion in the community
80%
60%
40%
20%
0%
CC
PC
CO
red-backed vole
deer mice
meadow vole
heather vole
rock vole
short-tailed shrew
southern bog lemming

Figure 5

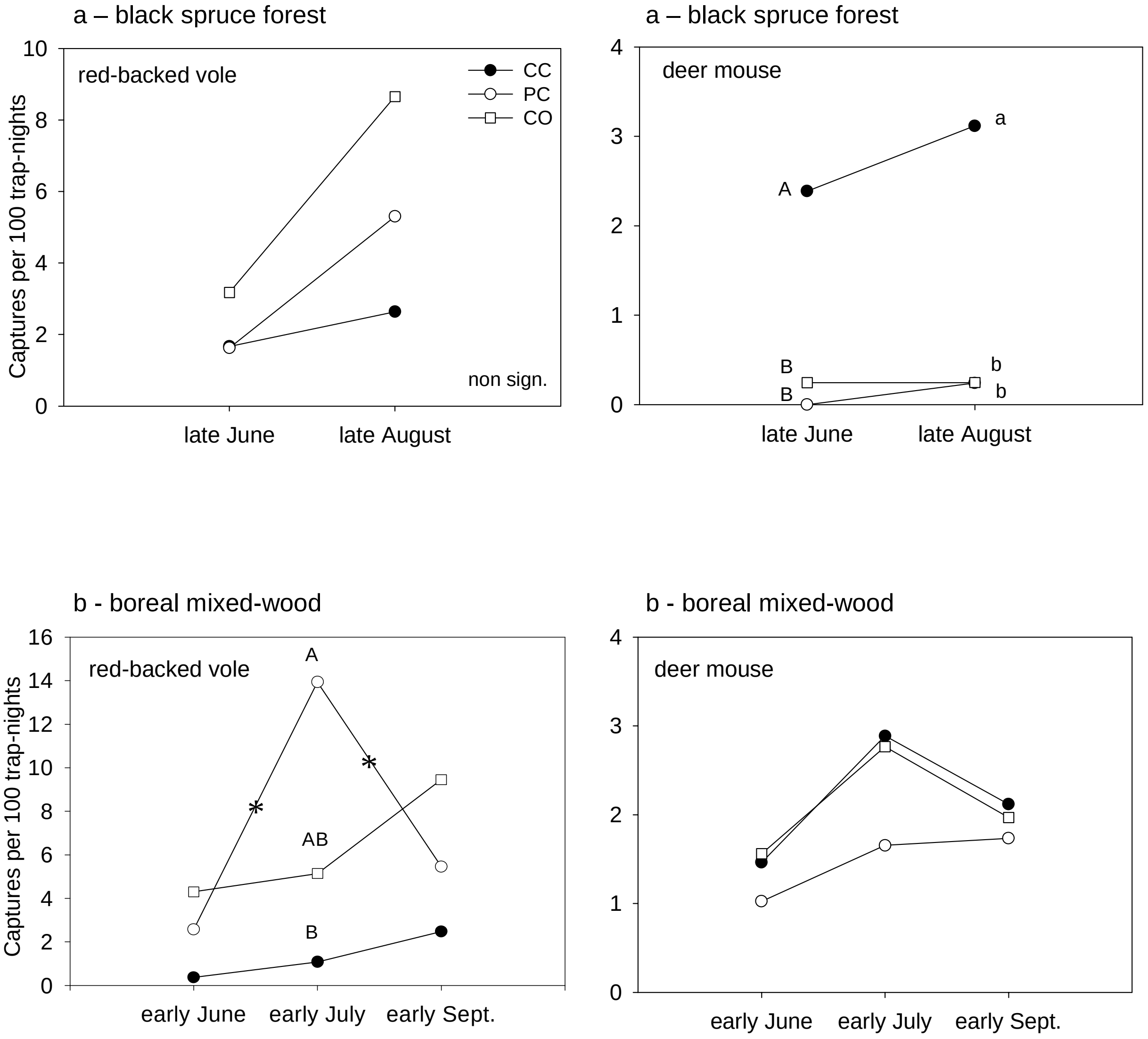
a – black spruce forest
Captures per 100 trap-nights
red-backed vole
CC
PC
CO
non sign.
10
8
6
4
2
0
late June
late August
a – black spruce forest
deer mouse
a
A
B
b
B
b
4
3
2
1
0
late June
late August
b - boreal mixed-wood
Captures per 100 trap-nights
red-backed vole
A
*
*
AB
B
16
14
12
10
8
6
4
2
0
early June
early July
early Sept.
b - boreal mixed-wood
deer mouse
4
3
2
1
0
early June
early July
early Sept.

Figure 6

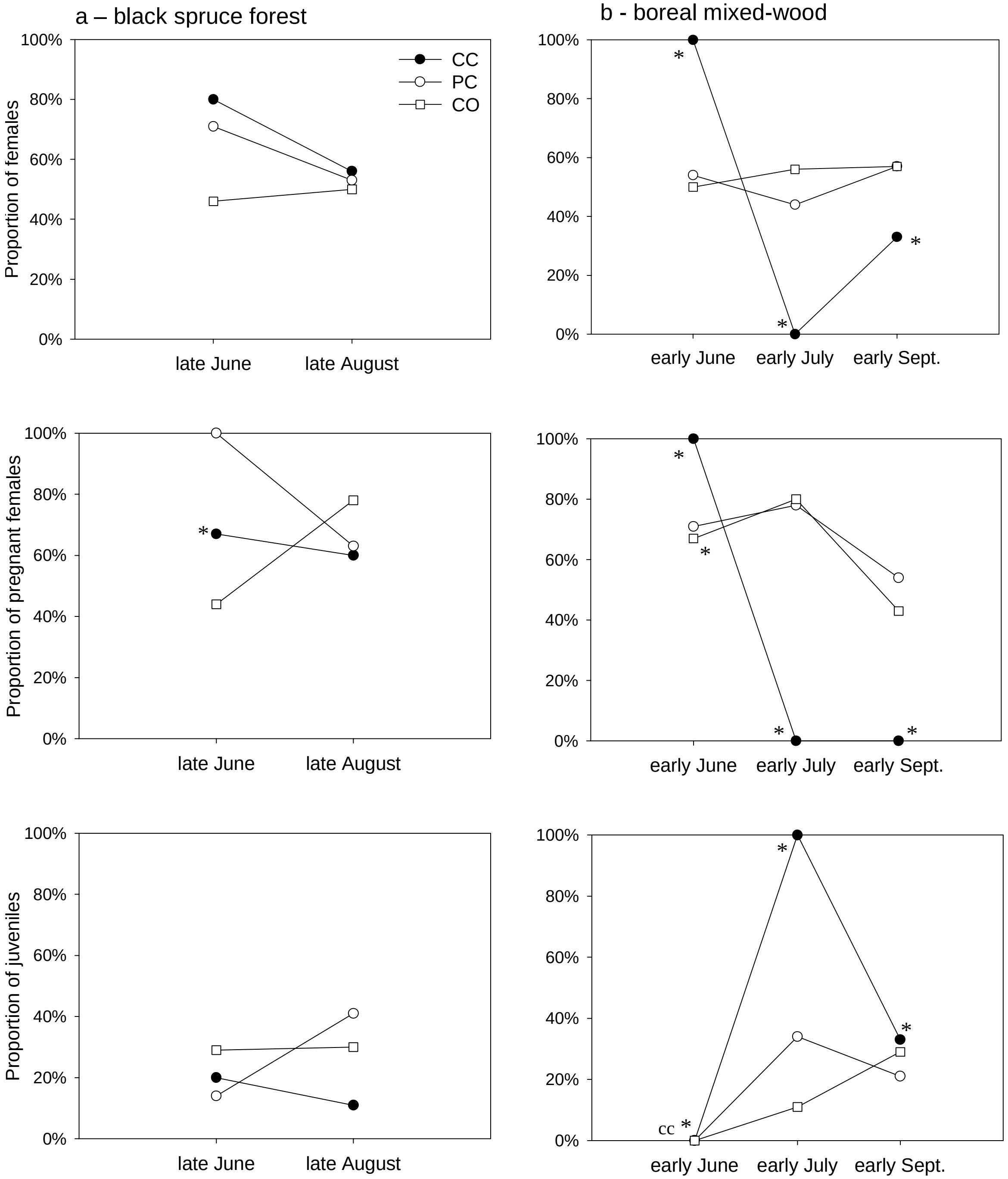
a – black spruce forest
b - boreal mixed-wood
CC
PC
CO
Proportion of females
Proportion of pregnant females
Proportion of juveniles
0%
20%
40%
60%
80%
100%
late June
late August
early June
early July
early Sept.
*
cc *

Figure 7

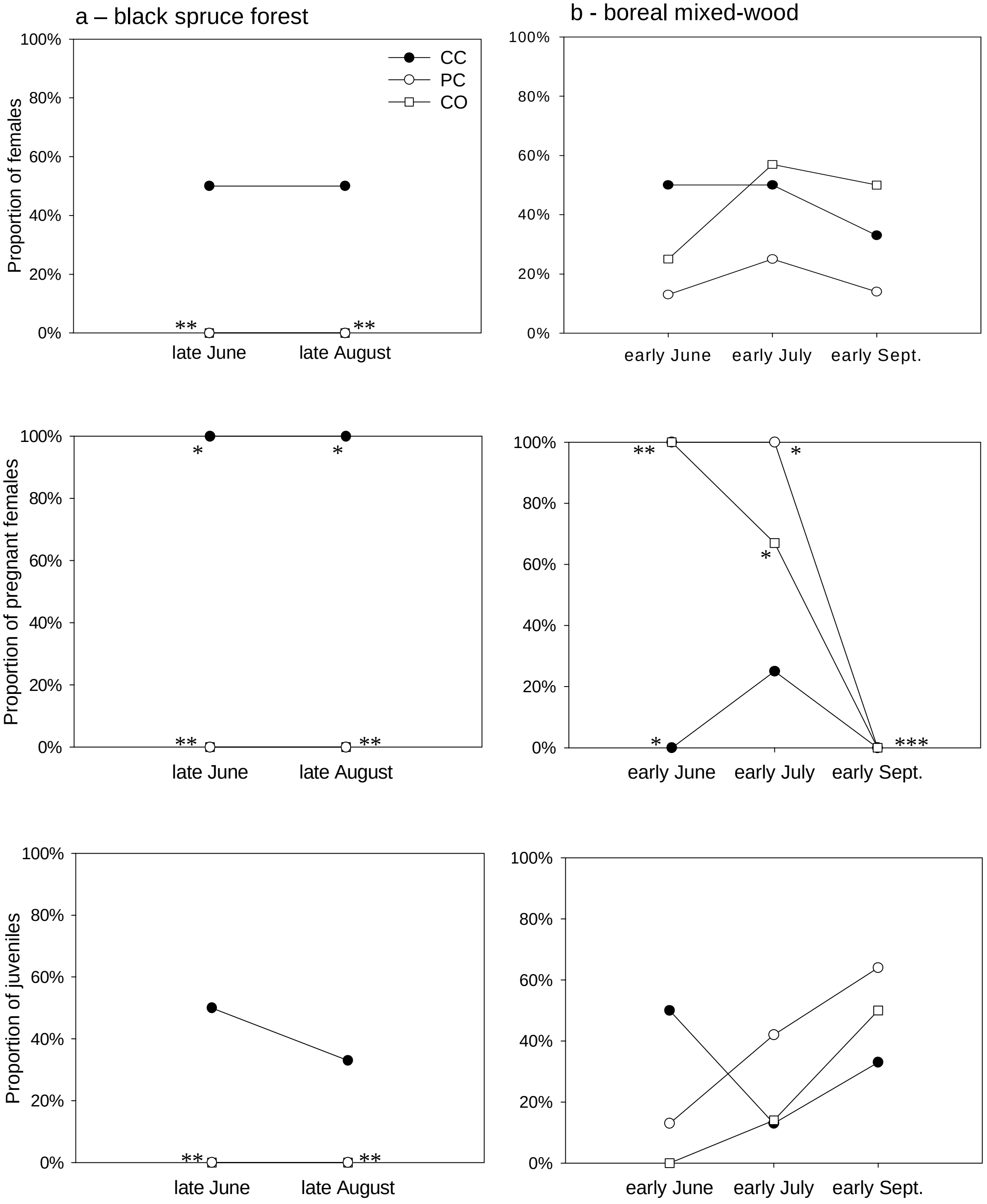
a – black spruce forest
b - boreal mixed-wood
CC
PC
CO
Proportion of females
Proportion of pregnant females
Proportion of juveniles
100%
80%
60%
40%
20%
0%
late June
late August
early June
early July
early Sept.
*
**
***

Figure 8

Table I : Mean percent cover of taxonomic groups below 1-m height in the three treatments and the two study areas. CC is for clear-cuts, PC partial cuts and CO control stands. Significant treatment differences ($P < 0.05$) are indicated by different letters.

			Mean percent cover		
	species	P	CC	PC	CO
Black spruce study area	ferns and allies	< 0.001	6.25^a	0.11^b	1.78^b
	forbs	0.087	6.67	3.78	6.29
	shrubs	0.023	34.25^a	20.78^b	32.60^a
	sedges	0.073	5.72	0.28	2.04
	deciduous trees	0.166	0.67	0.86	0.14
	Total vegetation cover below 1-m height	**< 0.001**	**58.47^a**	**34.83^b**	**44.72^b**
Mixed-wood study area	ferns and allies	0.085	0.50	3.31	7.56
	forbs	< 0.001	1.25^a	7.08^b	10.13^b
	shrubs	0.081	10.25	4.85	9.13
	sedges	0.358	0.13	1.63	0.13
	deciduous trees	0.002	2.13^a	1.90^a	6.50^b
	Total vegetation cover below 1-m height	**0.119**	**26.56**	**40.73**	**40.31**

Table II : Trapping effort and overall summer abundance (mean number per 100 trap-nights) of small mammals for the two trapping methods (traps and pit-falls) in clear-cuts, partial cuts and control stands, in the black spruce and the mixed-wood study areas. Diversity (Shannon-Wiener index), evenness and richness are shown for each treatment and each study area.

	Black spruce study area				Mixed-wood study area			
	Clear-cuts	Partial cuts	Control stands	**Total**	Clear-cuts	Partial cuts	Control stands	
Number of trap-nights	882	882	1764	**3528**	931	3037	1029	**4997**
Total abundance in traps	9.57	7.10	7.99	**8.16**	6.82	9.82	8.03	**13.16**
Number of pit-fall-nights	117	117	231	**465**	78	233	78	**389**
Total abundance in pit-falls	14.53	12.82	10.82	**12.26**	36.26	29.08	24.35	**24.42**
Diversity	6.23	4.62	3.25	**4.92**	4.13	3.22	3.57	**3.67**
Evenness	0.78	0.66	0.46	**0.62**	0.69	0.40	0.59	**0.37**
Richness	8	7	7	**8**	6	8	6	**10**

Note: Diversity, evenness and richness considered all species captured in traps and pit-falls.

Table III : Regression equations between response variables and vegetation variables in (a-) the black spruce and (b-) the mixed-wood study areas.

a -

Response variable	parameter	explanatory variables	P	R² adjusted
log (Red-backed vole abundance) =	0.28		**0.0496**	**0.2660**
	0.49	log (BA >16 cm)		
Meadow vole abundance =	0.44		**0.0004**	**0.7900**
	1.68	Deciduous trees	0.0018	
	0.24	Sedges	0.0054	
Masked shrew abundance in pit-falls =	1.81		**0.0437**	**0.2821**
	0.15	Total cover		

b -

Response variable	parameter	explanatory variables	P	R² adjusted
Red-backed vole abundance =	6.19		**0.0034**	**0.7473**
	0.48	Forbs	0.0203	
	-0.52	Shrubs	0.0112	
Deer mouse abundance =	1.81		**0.0044**	**0.6155**
	0.58	Deciduous trees		
Deer mouse recapture rate =	29.88		**<0.0001**	**0.8881**
	2.94	BA2-14 cm		

Table IV : Numbers of adult females, pregnant females, juvenile females, adult males and juvenile males in red-backed vole and deer mouse populations in clear-cuts (CC), partial cuts (PC) and control stands (CO), in the black spruce and the mixed-wood study areas.

		Numbers of adult females		Numbers of pregnant females		Numbers of juvenile females		Numbers of adult males		Numbers of juveniles males	
		Red-backed vole	Deer mouse	Red-backed vole	Deer mouse	Red-backed vole	Deer mouse	Red-backed vole	Deer mouse	Red-backed vole	Deer mouse
Black spruce study area	CC	8	5	5	5	1	1	4	2	1	4
	PC	12	0	9	0	2	0	4	1	6	0
	CO	32	0	22	0	6	0	23	2	17	0
Mixed-wood study area	CC	1	4	1	1	1	4	2	9	1	1
	PC	38	2	26	2	11	4	36	17	15	11
	CO	15	4	9	3	1	3	9	8	4	0

CONCLUSION

2.1. Cyclicité des petits mammifères en Amérique du Nord

Bien que diverses études aient avancé que les populations de petits mammifères ne connaissent probablement pas de fluctuations cycliques comme c’est le cas en forêt boréale fenno-scandinave (Boutin *et al.* 1995; Hansson & Henttonen 1985), on a disposé jusqu’à maintenant de peu de données pour confirmer ou infirmer cette hypothèse. Notre étude apporte des indications à l’effet qu’une dynamique cyclique des populations de proies (campagnols) et de prédateurs (chouettes) semble également avoir cours en forêt boréale de l’Est de l’Amérique du Nord. Nous avons montré que la nyctale de Tengmalm (*Aegolius funereus*) présente des cycles d’invasions hivernales de 4 ans au Québec. Ces invasions correspondent aux années de faible abondance d’une espèce de petits mammifères, le campagnol à dos roux (*Clethrionomys gapperi*). De plus, il existe une certaine synchronie entre les fluctuations de trois espèces de chouettes boréales (nyctale de Tengmalm, chouette épervière (*Surnia ulula*) et chouette lapone (*Strix nebolusa*)), à l’échelle de tout l’est de l’Amérique du Nord, au cours des 30 dernières années. Ces résultats indiquent l’existence d’une dynamique cyclique semblable à celle retrouvée en Scandinavie (Hanski *et al.* 1991) en forêt boréale de l’Est de l’Amérique du Nord. Ces chouettes qui sont des prédateurs spécialistes nomades, se déplacent vers le sud lorsque la densité de petits mammifères, leurs proies principales, est trop faible au nord (Korpimäki 1986). Ce phénomène à grande échelle influence certainement la dynamique de nombreuses espèces animales de la forêt boréale. Les chouettes ne sont pas la cause des cycles (Korpimäki & Norrdahl 1989; Norrdahl & Korpimäki 1995), mais elles se révèlent de très bons indicateurs des fluctuations d’abondance des petits mammifères.

2.2. Effets des coupes partielles sur les populations de petits mammifères

En second lieu, notre objectif consistait à évaluer les effets des coupes partielles sur les populations de petits mammifères. L’échantillonnage a donc été réalisé lors d’une année de forte abondance de petits mammifères. Les coupes partielles ont maintenu l’habitat forestier en conservant une végétation similaire aux forêts matures, c'est à dire couvert de protection et nourriture pour les petits mammifères. Elles ont également maintenu une communauté d'espèces similaire à celle retrouvée dans les sites témoins non-coupés, ainsi que des abondances de campagnols à dos roux et de souris sylvestres (les deux espèces les plus abondantes) à des niveaux plus proches des forêts naturelles. Enfin, les coupes partielles ont permis de conserver une structure de population de campagnols à dos roux similaire à la forêt naturelle, avec un ratio d'adultes/juvéniles montrant une persistance des adultes reproducteurs dans les peuplements aménagés similaire à celle des forêts non-coupées.

Les coupes totales actuellement utilisées à grande échelle transforment radicalement l'habitat (perte de couvert puis apparition de nouvelles espèces végétales) et modifient la composition en espèces de petits mammifères, en favorisant les espèces généralistes ou de milieu ouvert habituellement rares en forêt. De plus, elles ne permettent pas de soutenir les populations d'espèces forestières telles que le campagnol à dos roux. De même, les souris sylvestres, malgré une forte abondance dans les coupes totales, ont une faible activité reproductrice. Les coupes partielles semblent donc être une alternative intéressante aux coupes actuelles, moins compromettantes pour les populations de petits mammifères associées aux forêts matures et, par extension, pour tout le cortège de prédateurs qui s'en nourrit.

2.3. Recommandations

Bien que les petits mammifères aient à plusieurs reprises été proposés pour suivre les effets des pratiques forestières sur la diversité biologique, (Génier & Bergeron 1996; McLaren *et al.* 1998; Potvin *et al.* 1999), la reconnaissance d'une dynamique cyclique chez certaines espèces de petits mammifères nous incite à la prudence quand vient le temps d'utiliser ce groupe d'espèces comme indicateur de l'aménagement durable des forêts. La démographie des populations est complexe et peut comporter des cycles causés par les relations prédateurs-proies mais peut également être affectée par des facteurs densité-dépendants (Lidicker 1975; Van Horne 1981). Dans pareille situation, il devient nécessaire d'avoir des protocoles d'études qui comportent des témoins indépendants des traitements pour bien démarquer les fluctuations naturelles des populations des effets des pratiques d'aménagement.

Par ailleurs, nous avons montré que les études qui ne considèrent les effets des pratiques humaines que sur l'abondance des petits mammifères (comme l'avait déjà indiqué Van Horne (1983)) n'étaient pas à même de détecter les effets plus fins sur la structure des populations. La présence voire même l'abondance élevée de petits mammifères dans un milieu ne sont pas suffisants pour conclure sur sa qualité comme habitat, une connaissance plus approfondie de la structure des populations s'avère être une information incontournable pour statuer sur la survie à long terme de ces organismes dans le territoire aménagé. Pourtant, de nombreuses études ne traitent que de l'impact des pratiques sylvicoles sur l'abondance des différentes espèces (Bayne & Hobson 1998; Kirkland 1990; Lautenschlager *et al.* 1997; Monthey & Soutière 1985; Potvin *et al.* 1999).

D'autre part, plusieurs études ne considèrent que l'état des populations à la fin de l'été (août-septembre), soit au moment où les densités de populations atteignent des valeurs maximales. Cette période correspond également à la période de plus forte dispersion des juvéniles. Dans ce contexte, il est difficile de savoir si les habitats fortement occupés à ce moment le sont tout au long de la saison de reproduction ou seulement lors de la dispersion des jeunes (Génier & Bergeron 1996; Parker 1989; Potvin & Breton 1997; Verme & Ozoga 1981). Nous avons montré que les campagnols à dos roux ne fréquentaient les parterres de coupes totales qu'à la fin de l'été seulement et que durant tout le reste de l'été cet habitat n'était pas fréquenté (voir aussi Sullivan *et al.* 1999). Ainsi, des relevés qui ne sont réalisés qu'à la fin de l'été pourraient surestimer l'occupation des coupes totales par cette espèce et mener à des interprétations optimistes sur l'utilisation de ce type de forêt aménagée par une espèce associée aux forêts matures telle que le campagnol à dos roux.

2.4. Avantages des coupes partielles

Dans cette étude, les coupes partielles étudiées s'apparentaient à des CPPTM (coupe avec protection des petites tiges marchandes). La réalisation de ces coupes expérimentales, échelonnées sur plusieurs années, s'est améliorée avec le temps. Les opérateurs se sont en effet familiarisés avec le principe de la coupe à diamètre limite. Par exemple, l'impact visuel des coupes a été minimisé et les chemins sont devenus plus sinueux (chemins fantômes) dans les derniers essais qu'ils ne l'étaient au début de l'expérience (chemins rectilignes semblables à des coupes par bandes). Pour la diversité biologique, quelques éléments seraient encore à améliorer, tels que la conservation d'un certain nombre d'arbres de gros calibre et de chicots comme attributs d'habitats pour certaines espèces qui y sont inféodées (pics…), mais aussi afin de permettre un recrutement continu de gros débris ligneux. En effet, les débris ligneux sont considérés comme un élément essentiel de l'habitat du campagnol à dos roux (Bowman et *al.* 2000; Tallmon & Mills 1994) et de la souris sylvestre (Menzel et *al.* 1999). Un effort doit aussi être fait dans le choix de sites moins susceptibles au chablis, car la perte de surface terrière dans les années suivant la coupe partielle contribue à la rapprocher des coupes totales. Dans la pessière où les sols étaient sableux, le chablis s'élevait à près de 13% du volume résiduel seulement 1 an après le traitement (Morasse 2000).

Ce type de coupe semble particulièrement avantageux dans le domaine de la pessière à mousses. Les sols forestiers y sont recouverts de mousses et de lichens, organismes lents à s'installer après une perturbation (Coxson & Marsh 2001). De plus, ces groupes taxonomiques constituent une bonne part de l'alimentation des petits mammifères, notamment du campagnol à dos roux (Martell 1981). Les coupes partielles, qui protègent davantage la végétation au sol, permettront une recolonisation plus rapide par les différentes espèces végétales qui servent de couvert et de nourriture aux petits mammifères. Or, la sélection de l'habitat par ces espèces reflète les activités de recherche de nourriture et d'évitement des prédateurs (Yahner 1986). De plus, dans cette région, la croissance des arbres est lente (Ansseau *et al.* 1996) et la régénération en sous couvert faible, il est presque toujours nécessaire de replanter après une coupe totale. Les coupes partielles permettent donc d'éviter d'y avoir recours, car elles protègent les jeunes arbres qui n'ont pas encore atteint la maturité et permettent un retour plus rapide de la forêt. Cette pratique permet donc de conserver une certaine continuité dans le couvert forestier pour la faune. Enfin, les feuillus, presque totalement absents du paysage naturel de la pessière (Ansseau *et al.* 1996) ne réussiront pas à s'installer dans les coupes partielles, contrairement aux coupes totales, empêchant ainsi l'expansion de la souris sylvestre qui n'y est pas présente habituellement.

En forêt mixte, l'utilisation de cette pratique forestière permet essentiellement d'accélérer la succession forestière (Bergeron *et al.* 1999), en permettant de passer plus vite à une forêt principalement résineuse, alors que les coupes totales ramènent une forêt mixte ou feuillue (Harvey & Bergeron 1989). Le résultat sera alors le même que si les révolutions forestières étaient allongées. Les coupes partielles permettent donc de limiter l'enfeuillement de la région, causé par les perturbations anthropiques. Là encore, cette pratique empêchant la souris sylvestre de s'étendre alors que le campagnol à dos roux est l'espèce dominante en forêt mature.

2.5. Projets futurs

Nous avons étudié la dynamique cyclique à long terme des petits mammifères, ainsi que les effets à court terme des coupes partielles sur leurs populations. Nous pouvons alors nous demander quels sont les effets à long terme des coupes forestières en général, et plus particulièrement des coupes partielles sur la dynamique cyclique des petits mammifères et de leurs prédateurs. De même, quel serait l'effet du passage du régime forestier équien à révolution courte actuel, qui pourrait affecter la viabilité à long terme des populations de forêts matures à anciennes, à un régime mixte équien (coupes totales) et inéquien (coupes partielles), qui reproduit davantage les conditions naturelles des mosaïques forestières. Il faut aussi se demander comment se comportent les populations suivant un gradient d'âge des forêts : est-ce que la structure des populations de petits mammifères dans les forêts jeunes ou dans les forêts de 70 à 100 ans est similaire à celle des forêts anciennes. Si tel était le cas, alors le régime à courte révolution équien actuel pourrait ne pas avoir un effet si différent à long terme que les régimes naturels.

Il semble par ailleurs important d'établir un programme de suivi à long terme pour vérifier la présence de cycles chez le campagnol à dos roux, ainsi que l'absence de cycles chez les autres espèces de petits mammifères, en forêt boréale nord-américaine. Ce programme devrait être instauré en forêt boréale coniférienne, dans des peuplements non perturbés par l'homme. Étant donné la longueur des cycles, ce programme devrait s'étendre sur la durée d'au moins deux cycles, soit une dizaine d'années. D'autre part, il serait utile de vérifier si les hermines et les belettes jouent le même rôle dans la création des cycles d’abondance de petits mammifères, dans l’Est de l’Amérique du Nord qu’en Scandinavie.

Enfin, l’utilisation spatio-temporelle des parterres de coupes par les différentes espèces de petits mammifères reste encore inconnue. Comment s’effectue la dispersion des juvéniles qui sont forcés de quitter les meilleurs habitats forestiers vers des habitats de moindre qualité tels que les coupes.

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