UNIVERSITÉ DU QUÉBEC

DYNAMIQUE DES POPULATIONS DE LIÈVRES ET DE PETITS MAMMIFÈRES DU SUD-EST DE LA FORÊT BORÉALE NORD-AMÉRICAINE EN REGARD DE L'EXPLOITATION DES FORÊTS ET DES ANIMAUX À FOURRURE

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AVANT-PROPOS ET REMERCIEMENTS

Cette thèse constitue l'aboutissement de six années extrêmement enrichissantes d'expérience intellectuelle, morale et parfois même physique, outrageusement résumées dans les quelques pages qui suivent. Débuté en mai 1998 sous la forme d'une maîtrise, le défi s'est avéré complexe, certes, mais suffisamment vaste et scientifiquement robuste pour se transformer peu à peu en un doctorat, ô combien passionnant!

L'objet de la présente étude s'insère dans un programme de recherche, entamé en 1996, qui permit la formation de six personnes maintenant hautement qualifiées ou en voie de l'être. L'objectif principal de ce programme était de mieux comprendre le fonctionnement de l'ensemble de la chaîne trophique des petits mammifères dans une région écologique où il fut peu étudié, et dans un contexte où des activités humaines, telle que l'exploitation des forêts et des animaux à fourrure, sont susceptibles de l'affecter. Beaucoup d'organismes et de personnes ont contribué à cette entreprise et m'ont permis de mener à bien la partie qui m'a été confiée. En allouant argent, expertise, idées, patience ou, simplement, un peu d'amitié, tous ont su créer autour de moi des conditions motivantes et particulièrement propices à la réalisation de ce projet.

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RÉSUMÉ

Les mécanismes qui déterminent la dynamique des populations de lièvres et de petits mammifères sont encore mal définis, en particulier dans la zone de transition entre les forêts boréales et tempérées nord-américaines, où peu d'études ont été menées. Au sud du Québec, ces milieux sont soumis au piégeage des animaux à fourrure ainsi qu'à une intense exploitation de la matière ligneuse, deux types d'activités anthropiques dont l'influence sur la chaîne trophique des petits mammifères reste également mal connue.

Les objectifs de cette étude ont été de décrire la dynamique des populations de lièvres et de petits mammifères au sud-est du Québec et d'évaluer l'importance de la prédation dans cette dynamique. Nous voulions tester certaines prédictions découlant de l'hypothèse selon laquelle, dans ces milieux, l'ensemble des prédateurs régulariserait les populations de lièvres et de petits mammifères et les maintiendrait à faibles densités. Nous souhaitions également analyser leur réponse face au piégeage récréatif ou commercial des carnivores, en partant de l'idée que le piégeage des animaux à fourrure affecterait négativement l'abondance de l'ensemble des espèces exploitées et, qu'en conséquence, les densités et la survie des proies augmenteraient. Finalement, l'habitat des lièvres et des petits mammifères pouvant être grandement affecté par la coupe forestière, nous souhaitions étudier la dynamique des populations de ces espèces face aux perturbations de leur couvert protecteur engendrées par les pratiques forestières en vigueur dans cette région.

Pour atteindre ces objectifs, nous avons utilisé deux territoires potentiellement différents au niveau de l'abondance des prédateurs terrestres, le piégeage des animaux à fourrure étant autorisé dans l'un et interdit dans l'autre. Chacun de ces territoires était également géré pour la production du bois à l'aide de techniques telles que la CPRS (coupe avec protection de la régénération et des sols) ou l'ÉPC (éclaircie précommerciale). Ce dispositif a permis de mener une expérience dans laquelle le piégeage des animaux à fourrure fut considéré comme un moyen de contrôler l'abondance des prédateurs terrestres, alors que la CPRS et l'ÉPC ont été perçues comme des causes potentielles de dégradation du couvert protecteur des proies.

À l'intérieur des différents types d'habitats rencontrés dans les deux territoires, nous avons estimé l'abondance relative des prédateurs aériens et terrestres, ainsi que l'abondance et la survie des petits mammifères, incluant le lièvre pour lequel des précisions sur les causes de mortalité ont été obtenues. Enfin, nous avons mesuré les caractéristiques de la végétation dans chaque type d'habitat, afin d'estimer l'impact des CPRS et des ÉPC sur ces habitats et de faire un lien entre l'abondance des espèces proies et les caractéristiques des milieux qu'elles occupaient. Ces travaux ont fait intervenir des techniques de provocation vocale de prédateurs aériens, de pistage hivernal de prédateurs terrestres, de capture-marquage-recapture (CMR) de lièvres et de petits mammifères, de suivi télémétrique, et d'inventaire de végétation.

Nos indices d'abondance de prédateurs suggèrent que les lièvres aient fait face à une pression de prédation plus faible dans le territoire piégé que dans le territoire non piégé, alors que les petits mammifères auraient probablement subi une pression de prédation

davantage comparable entre les deux territoires. Nous avons également observé que les densités de lièvres et de petits mammifères sont restées relativement stables (non cycliques) et faibles durant cinq années. De plus, la prédation fut la principale cause de mortalité des lièvres adultes. La densité des lièvres fut deux fois plus élevée dans le territoire piégé que dans l'autre. Quant au recrutement des jeunes lièvres, il fut plus élevé dans le territoire piégé, alors que le taux de gestation a été similaire entre les deux territoires. Par contre, nous n'avons détecté aucune variation de densité ou de survie chez les petits mammifères. Ceci suggère que le piégeage des animaux à fourrure ait eu partiellement l'effet escompté. La survie des levrauts pourrait avoir été plus élevée en présence du contrôle de la prédation qu'en son absence, ce qui pourrait expliquer la différence de densité observée chez les lièvres des deux territoires. Nos résultats abondent donc dans le sens d'une régularisation des populations de proies par la prédation. Cependant, ils indiquent que les liens trophiques sont probablement plus complexes que nous pouvions le suspecter.

Les densités et la survie des lièvres et des petits mammifères ont répondu en conformité avec nos estimations de la pression de prédation. Ainsi, l'idée que le piégeage des animaux à fourrure puisse affecter négativement l'ensemble des espèces exploitées et, qu'en conséquence, les densités et la survie des proies auraient augmenté, s'est donc avérée trop simpliste. Le piégeage étant plus intense sur les carnivores de plus grandes tailles, il pourrait avoir provoqué un relâchement de la pression de prédation intra-guilde, à l'avantage des plus petits mustélidés qui semblent avoir exprimé une réponse numérique positive dans le territoire piégé. Ainsi, le piégeage des animaux à fourrure pourrait entraîner une altération des relations interspécifiques et causer des effets en cascade le long de la chaîne trophique sans pour autant que la dynamique des populations de certaines proies en soit grandement modifiée.

L'analyse des caractéristiques de la végétation indique que la CPRS a affecté les peuplements forestiers en diminuant la complexité structurelle de la canopée, et en augmentant celle du sous-étage végétal. Par la suite, l'ÉPC est venue réduire la complexité structurelle du sous-étage. Ces techniques ont donc considérablement modifié le couvert protecteur des proies. La réponse globale des lièvres et des petits mammifères en terme d'abondance relative et de richesse spécifique indique que durant les 10 ans qui suivent le traitement, l'ÉPC a vraisemblablement eu un effet plus négatif que les CPRS sur chacune des espèces étudiées. Suite à la CPRS, l'abondance estivale et le nombre d'espèces de petits mammifères se sont maintenus à des niveaux au moins comparables à ceux qui ont été observés dans les peuplements fermés. Les CPRS et les ÉPC pourraient donc avoir des impacts distincts sur la dynamique des proies, dus à leurs effets différents sur la disponibilité des refuges antiprédation.

Suite à ces résultats, les gestionnaires oeuvrant au sud de la forêt boréale nord-américaine devraient tenir compte de la possibilité d'une absence de cycle dans les populations de lièvres et de petits mammifères et du fait que la dynamique de ces espèces pourrait varier en fonction du risque de prédation associé à chaque type d'habitat. Ils devraient également intégrer le concept des interactions trophiques directes et indirectes dans la gestion des écosystèmes afin de pouvoir agir efficacement en évitant les réponses inattendues de la part de certaines de leurs composantes. Dans un soucis de conservation des populations de ces espèces ainsi que des processus écologiques qui en sont dépendants, nous pensons qu'au lieu de pratiquer l'ÉPC sur l'ensemble des peuplements susceptibles de subir ce traitement, il serait préférable de prévoir un délai dans le traitement de peuplements contigus, d'exclure certaines parcelles riches en gaulis, ou même de protéger certaines essences végétales pouvant offrir un bon couvert protecteur pour les proies.

Notre étude suggère que les interactions directes et indirectes existant entre les éléments d'un niveau trophique, ainsi qu'entre les niveaux trophiques eux mêmes, soient nombreuses et complexes, à cause de la diversité des espèces impliquées dans l'ensemble du réseau. Elle suggère également que l'écosystème puisse être relativement résiliant face à des perturbations d'origine anthropique comme les coupes et le piégeage des animaux à fourrure.

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INTRODUCTION GÉNÉRALE: DYNAMIQUE DES POPULATIONS DE LIÈVRES ET DE PETITS MAMMIFÈRES ET RÉPONSE DE CES ESPÈCES À L'EXPLOITATION DE LEUR HABITAT ET DE LEURS PRÉDATEURS

Dynamique des chaînes trophiques

Le nord-est de l'Amérique du nord présente trois zones écologiques distinctes qui, du nord vers le sud, appartiennent respectivement aux régions arctiques, boréales et tempérées de l'hémisphère nord (Ordre des Ingénieurs Forestiers du Québec, 1996). Pour expliquer la façon dont l'énergie se répartit entre les maillons des chaînes trophiques lorsque la productivité primaire des écosystèmes augmente, il existe deux hypothèses: la dominance trophique ascendante (bottom up) et la dominance trophique descendante (top down). Selon la première, l'énergie se répartit équitablement entre les niveaux trophiques (Polis et Strong, 1996), alors que selon la seconde la croissance en biomasse d'un niveau trophique va se faire en cascade le long d'un gradient nord-sud de productivité primaire (Oksanen et al., 1981). Cette hypothèse, nommée EEH (hypothesis of exploitation ecosystems; Oksanen et al., 1999) suggère qu'en allant du pôle nord vers des régions plus méridionales, on trouve d'abord une zone où seule une petite biomasse végétale peut survivre; et, plus vers le sud, les herbivores apparaissent, puis leur biomasse augmente progressivement jusqu'à ce qu'elle soit suffisante pour soutenir des carnivores. Dans ce dernier contexte, les végétaux abondent car les herbivores sont régularisés à faible densité par leurs prédateurs (Crête et Manseau, 1996) et gardés loin de la capacité de support, sauf si les prédateurs sont éliminés (Oksanen, 1988; Crête, 1999). Par contre, les carnivores et les plantes sont régularisés par la compétition. En supposant que les prédateurs déterminent l'abondance des herbivores, pour que le système soit stable, les populations de proies doivent être capables de trouver des habitats leur permettant d'échapper aux prédateurs (Predation-sensitive food hypothesis; Sinclair et Arcese, 1995). En accord avec le modèle des refuges (Wolff, 1981), le point d'équilibre du système tiendrait alors à la quantité d'habitats sûrs dans lesquels au moins une partie des herbivores serait en sécurité, les prédateurs y étant peu efficaces.

Prédation et régulation des populations de proies

Le rôle de la prédation dans la dynamique des populations de proies a fait l'objet de nombreux débats (voir revue de Solomon, 1949; Murdoch et Oaten,1975; Taylor, 1984; Sinclair, 1989). Durant plus de 70 années, la prédation fut alternativement perçue comme facteur limitant (Elton, 1927), comme facteur régulateur (Nicholson, 1933; Solomon, 1949), ou encore comme facteur secondaire, moins influent que le climat (Andrewartha et Birch, 1954) ou que la quantité de nourriture disponible pour les proies (Lack, 1954). Actuellement, alors que la régulation semble être une caractéristique commune à la dynamique de nombreuses populations de proies (Berryman et al., 2002), un consensus semble prédominer à l'effet que la prédation puisse en être parfois grandement responsable (voir revue de Priee, 1987; Newsome, 1990; Skogland, 1991). Plusieurs équipes de chercheurs ont démontré qu'à différentes densités de proies, les taux de prédation sont variables (e.g., Messier et Crête, 1985; Erlinge et al., 1988; Korpimäki et Norrdahl, 1989a; 1991; Sinclair et al., 1990; Korpimäki, 1993). La prédation peut donc être considérée comme un facteur régulateur des populations, son effet étant dépendant de la densité des proies.

La réponse des prédateurs à différentes densités de proies peut être numérique, lorsque l'abondance des prédateurs change, ou fonctionnelle, lorsque le taux de prédation change (Solomon, 1949). Une réponse numérique résulte d'un changement du taux de recrutement, de survie, d'immigration ou d'émigration (Readshaw, 1973) alors qu'une réponse fonctionnelle résulte d'un changement du taux d'attaque ou d'un changement de comportement pour aller vers des proies alternatives en fonction de leur abondance relative (Holling, 1959; Murdoch, 1969). L'effet combiné des réponses numériques et fonctionnelles des prédateurs pourrait donc être déterminant sur la dynamique des populations de proies.

Écologie du lièvre et des petits mammifères

Les lièvres et les petits mammifères représentent d'importantes proies pour de nombreux prédateurs terrestres et aériens (e.g.: Hörnfeldt et al., 1990; Keith, 1990;

Tannerfeldt et Angerbjörn, 1996). Selon les espèces, ils sont aussi consommateurs de plantes, de lichens, de champignons ou d'invertébrés (Ericson, 1977; Gebczynska, 1983; Hansson, 1988; Keith, 1990), disperseurs de graines et de spores (Kirkland, 1990; Ostfeld et al., 1997), et parfois même fouisseurs facilitant les échanges entre le sol et les autres composantes des écosystèmes (Hamilton et Cook, 1940). Certaines espèces, actives toute l'année et en densité parfois très élevée, sont susceptibles d'influencer considérablement la dynamique de leur milieu (e.g. Krebs et Myers, 1974; Boutin et al., 1995) en modifiant la croissance (Keith, 1974), la composition et la répartition des communautés végétales (Sullivan, 1979; Martell et Macaulay, 1981; Swan et al., 1984) et animales (Keith et al., 1977; Sullivan, 1979; Martell et Macaulay, 1981; Parker et al., 1983; Swan et al., 1984; Boutin et al., 1986; 1995; O'Donoghue, 1997). En conséquence, la prédation (Keith et al., 1984; Hik, 1995; voir revue de Lima, 1998; Beaudoin et al., 2004) et la competition interspécifique pour les ressources vitales (Löfgren, 1995; Morris and Lundberg, 1996) ont été identifiées comme des facteurs importants pour expliquer la distribution des petits mammifères et des lièvres à l'intérieur des paysages forestiers. La sélection de l'habitat par les petits mammifères devrait donc être fortement dépendante des composantes qui fournissent couvert (e.g.: refuge anti-prédateur), et nourriture (Hansson, 1982; Morris, 1996; Keith, 1990; Beaudoin et al., 2004) et devrait également refléter un taux de survie dépendant de ces composantes (Hansson, 1997).

Dynamique des populations de lièvres

Les populations de lièvres d'Amérique (*Lepus americanus*) sont connues pour leur dynamique particulière, montrant des fluctuations d'abondance dont l'amplitude et la régularité varient en fonction de la latitude. Dans les forêts boréales nordiques du Yukon, milieux relativement peu productifs, le lièvre exhibe des cycles de grande amplitude (jusqu'à environ 140:1; King et Schaffer, 2001), sur des périodes de 9 à 11 ans (Keith et Windberg, 1978; Krebs et al., 1995). Une interaction retardée entre la prédation et la raréfaction de la nourriture serait responsable de cette cyclicité (Keith et al., 1984; Krebs et al., 1995; King et Schaffer, 2001; Krebs et al., 2002). Vers le sud, de même que vers l'est de l'aire de répartition du lièvre, l'amplitude et la régularité des cycles semblent diminuer (Koehler, 1990; Keith, 1990), alors qu'au sud du fleuve Saint-Laurent et des Grands Lacs (Smith, 1983; Godbout, 1999), les cycles tendraient même à disparaître. Dans ces milieux plus productifs que la forêt boréale nordique, les populations de lièvres seraient relativement stables à faible densité (Buehler et Keith, 1982; Keith, 1990; Murray, 2000), bien qu'aucune série temporelle de données ne soit assez longue pour le démontrer clairement. L'absence de cyclicité chez les populations méridionales de lièvre d'Amérique serait attribuable à une interaction entre une importante pression de prédation et une répartition fragmentaire des habitats refuges. Ainsi, une forte prédation exercée sur des lièvres qui se dispersent hors des refuges (Wolff, 1981) ou bien sur des jeunes lièvres à l'intérieur des refuges (Wirsing et al., 2002), tendrait à stabiliser les populations.

Dynamique des populations de petits mammifères

La dynamique des populations des petits rongeurs pourrait également suivre un gradient nord-sud de cyclicité. En effet, dans les milieux nordiques eurasiens et nord-américains, les populations de campagnols suivent des cycles de trois à cinq ans (Hansson et Henttonen, 1988; Saitoh et al., 1998; Stenseth, 1999) au cours desquels la densité des populations peut varier d'un facteur 200 entre les pics d'abondance et les périodes de rareté (Boonstra et al., 1998). Plus au sud, les densités restent relativement stables, comme cela semble le cas dans le sud de la Scandinavie (Hanski et al., 1991). Sur l'île d'Hokkaido, au Japon, un patron comparable existe, avec des populations cycliques de campagnols vivant dans des conditions hivernales rigoureuses au nord de l'île, et des populations plus stables sous un climat plus doux, plus au sud (Bjørnstad et al., 1999). Cependant, l'agent de régulation n'est pas connu. Dans les forêts mixtes du centre de l'Ontario, les populations de petits mammifères subissent l'influence d'un agent régulateur non identifié et restent relativement stables (Fryxell et al., 1998).

Avant les années 1980, de nombreuses études avaient identifié que les prédateurs pouvaient être largement responsables des cycles de population observés chez les campagnols et les lemmings (e.g., Pearson, 1966; Fitzgerald, 1977; Goszczynski, 1977). La revue de littérature de Finerty (1980) indiquait que lorsque les populations de petits mammifères sont cycliques, la prédation n'en serait pas l'unique cause mais: (1) elle accentuerait la chute des populations déjà en déclin pour d'autres raisons (ex: manque de nourriture), (2) elle accentuerait l'amplitude des cycles en réduisant les populations de proies à de très faibles densités, (3) elle accroîtrait la période des cycles par persistance des prédateurs durant les bas de cycle (densité dépendance retardée), et (4) elle synchroniserait les cycles sur de larges étendues géographiques à cause de la grande mobilité de beaucoup de prédateurs. À l'époque, le principal argument contre l'hypothèse que la prédation soit le seul facteur responsable des cycles était que la prédation ne pouvait être mise en cause pour expliquer certains changements démographiques observés chez les proies, comme une réduction de fécondité ou une variation de taille corporelle selon les phases des cycles (voir la revue de Taylor, 1984). Cependant, durant les 15 dernières années, des biologistes Scandinaves ont développé des modèles de dynamique des populations de petits mammifères dans lesquels la prédation joue un rôle encore plus large. Dès lors, la plupart des écologistes se sont entendus pour dire que dans les régions nordiques, la cyclicité semble causée par une réponse numérique retardée, dépendante de la densité, de la part de carnivores spécialistes, alors que vers le sud, une forte réponse fonctionnelle de la part d'une communauté de prédateurs généralistes combinée à la présence de prédateurs spécialistes pourrait régulariser les populations (Turchin et Hanski, 1997; Hanski et al., 2001; Klemola et al., 2002).

Flux énergétique et causes de la stabilité des populations

L'idée d'un gradient nord-sud de cyclicité chez les populations de lièvres et de petits mammifères implique que plus les milieux deviennent productifs, plus la régularité et l'amplitude des fluctuations d'abondance diminuent. Ce patron pourrait s'expliquer par l'orientation du flux énergétique dans les écosystèmes. L'augmentation de productivité vers le sud pourrait permettre un accroissement de l'abondance et de la diversité des organismes, incluant celle des carnivores qui régulariseraient alors les herbivores à faible densité (Oksanen et Oksanen, 2000). Dans ce contexte, pourraient survivre une grande diversité de prédateurs spécialistes et généralistes, ainsi qu'un grand nombre de proies préférées et alternatives pour ces prédateurs. Les prédateurs spécialistes et généralistes semblent avoir un effet différent sur les populations de proies (Murdoch et Oaten, 1975; Erlinge et al., 1983; Hassell et May, 1986; Henttonen et al., 1987; Korpimäki, 1993). Les spécialistes résidents (ex: les petits mustélidés) semblent capables d'introduire de l'instabilité dans la dynamique des proies (Henttonen et al., 1987; Korpimäki et al., 1991), alors que les spécialistes nomades (e.g.: certains rapaces; Korpimäki et Norrdhal, 1991), qui possèdent un fort potentiel de régulation, pourraient avoir un effet stabilisant sur les populations de proies (Klemola et al., 2002). Les généralistes, quant à eux, peuvent amoindrir, voire étouffer la cyclicité (Hansson et Henttonen, 1988; Hanski et al., 1991; 2001; Turchin et Hanski, 1997) par d'importantes réponses fonctionnelles exprimées au gré des fluctuations d'abondance de leurs proies. De plus, l'effet stabilisant des prédateurs généralistes pourrait également se faire ressentir au travers d'une pression de prédation intra-guilde exercée sur les petits mustélidés (Korpimäki et Norrdhal, 1989b), qui sont source d'instabilité. Enfin, l'augmentation de productivité vers le sud entraînant un accroissement de l'abondance et de la diversité des organismes, aurait pour effet de complexifier le réseau trophique, ce qui le rendrait plus stable (Neutel et al., 2002).

Effet de l'exploitation des prédateurs sur les lièvres et les petits mammifères

Compte tenu du fait que la prédation peut jouer un grand rôle dans la dynamique des populations de nombreux herbivores, une disparition totale ou même partielle des prédateurs devrait avoir un effet important sur l'ensemble de la communauté affectée. Par exemple, un retrait ou une réduction substantielle des grands carnivores (e.g: loup (*Canis lupus*); ours (*Ursus sp.*)) dans la moitié sud de l'Amérique du nord a permis à la biomasse des cervidés de se multiplier au minimum par cinq (Crête, 1999). D'autres études ont également démontré qu'une diminution du nombre de prédateurs entraîne une augmentation de l'abondance des proies (e.g., Marcström et al., 1989; Newsome et al., 1989; Knowlton et Stoddart, 1992; Pech et al., 1992; Meserve et al., 1993; Boertje et al., 1996; Hayes et al., 2003). Chez le lièvre, l'exclusion des prédateurs terrestres a résulté en un accroissement de la survie et de la densité mais n'a pas empêché la cyclicité de se produire (Krebs et al., 1995). De même, l'exclusion totale des prédateurs de campagnols (*Microtus spp.*) conduisit à un accroissement d'abondance marqué, accompagné de fluctuations saisonnières (Norrdahl et al., 2002).

L'exploitation des prédateurs par le biais du piégeage récréatif ou commercial des animaux à fourrure exerce un retrait sélectif de carnivores terrestres intermédiaires ou de petite taille. Un piégeage soutenu des méso- ou petits carnivores devrait donc réduire la pression de prédation que subissent des espèces proies comme le lièvre ou les petits mammifères et, par conséquent, leur taux de mortalité devrait diminuer alors que leur densité devrait s'accroître. Cependant, bien que le piégeage soit relativement efficace à réduire l'abondance des prédateurs exploités (e.g., Hodgman et al., 1994; Frank et

Woodroffe, 2001; Johnson et al., 2001), ses conséquences sur l'abondance des animaux à fourrure eux-mêmes, et sur celle de leurs proies, restent très difficiles à prédire à cause des relations complexes, (incluant la prédation intraguilde; Fedriani et al., 2000), existant entre les nombreuses espèces de prédateurs et leurs proies.

Perturbations naturelles ou anthropiques des habitats forestiers

Les habitats du lièvre et des petits mammifères sont susceptibles d'être affectés par diverses perturbations d'origine naturelle ou anthropique (e.g.: feux, épidémies d'insectes, interventions forestières) qui influencent fortement la dynamique de leurs composantes. Les forêts du nord-est de l'Amérique du Nord ne sont que rarement affectées par les perturbations naturelles à grande échelle telles que les feux ou les tornades (Whitney, 1987; Frelich et Lorimer, 1991; Frelich, 1995), alors que les épidémies d'insectes, notamment celle de la tordeuse du bourgeon de l'épinette (*Choristoneura fumiferana*), sont beaucoup plus courantes (Irland et al., 1988). Par contre, dès l'arrivée des européens dans l'est de l'Amérique du Nord, des perturbations anthropiques de grande ampleur se sont installées avec, comme conséquences, une altération majeure des paysages (Palik et Pregitzer, 1992; Whitney, 1994; Mladenoff et al., 1994; Schneider, 1996). Avec le développement technologique et industriel, la pression anthropique s'est intensifiée, entraînant une réduction draconienne des superficies forestières, ainsi qu'un rajeunissement et une fragmentation des forêts (Whitney,1994; Frelich, 1995; Lorimer, 2001; OFBSL, 2003). D'importants changements ont également été observés au niveau de la composition végétale

(Whitney,1994; Frelich, 1995; Fuller et al., 1998; Orwig et Abrams, 1999). La récolte ayant été systématiquement orientée vers les espèces résineuses (Guay, 1942 ; Proulx, 1982), les forêts ont connu un "enfeuillement" progressif, dû au remplacement des essences de fin de succession par des essences pionnières, ou mieux adaptées à des perturbations à grande échelle (Whitney, 1994 ; Frelich, 1995 ; Fuller et al., 1998 ; Foster et al., 1998 ; Orwig et Abrams, 1999 ; Lorimer, 2001; White et Mladenoff, 2002) comme le peuplier faux-tremble ou l'érable rouge (Abrams et Scott, 1989 ; Whitney, 1994 ; Fuller et al., 1998 ; Lorimer, 2001). Depuis la dernière épidémie de tordeuse du bourgeon de l'épinette (1970-1980), grâce au contrôle des feux et aux pratiques forestières, la coupe totale est devenue la perturbation la plus fréquente dans les forêts du nord-est de l'Amérique du nord (Homyack, 2003).

Avec le temps, les techniques de l'industrie forestière ont évolué et, progressivement, l'exploitation est passée d'une récolte stricte de la ressource ligneuse à une gestion intégrée prenant en considération les besoins des autres utilisateurs (Rotherham, 1993). Depuis 1988, au Québec, il existe des lois provinciales visant à assurer le rendement soutenu de l'exploitation ligneuse tout en respectant sa durabilité ainsi que celle des autres formes d'utilisation (Génier et Bergeron, 1996). Les surfaces coupées d'un seul tenant ont diminué et la régénération préétablie ainsi que les sols forestiers sont mieux protégés. À partir de 1996, la coupe totale a été remplacée par la "Coupe avec Protection de la Régénération et des Sols" (CPRS) au Québec (Potvin et Breton, 1997), pratique maintenant obligatoire dans le règlement sur les normes d'intervention en milieu forestier (RNI). Actuellement, c'est la méthode de récolte la plus commune pour exploiter le bois et, à l'avenir, elle pourrait demeurer très répandue. La CPRS représente une perturbation majeure du milieu puisque la quasi-totalité des arbres est récoltée, mais c'est aussi le type de coupe qui se rapproche le plus des perturbations naturelles en forêt boréale. C'est donc le moins perturbateur pour les parcelles, les chemins de débardage y étant espacés et les tiges de faible diamètre sans valeur commerciale (Courtois et Potvin, 1994) ainsi qu'une partie de la végétation au sol étant laissées sur pied. La régénération est alors beaucoup plus rapide qu'avec d'autres méthodes (Potvin et Breton, 1997).

Une autre pratique sylvicole de plus en plus répandue, l'éclaircie pré-commerciale (ÉPC), contribue aussi à distinguer la succession végétale après les CPRS de celles suivant les perturbations naturelles. En effet, cette pratique vise à éliminer les tiges en surnombre dans un jeune peuplement dense de façon à réduire la compétition entre les arbrisseaux et concentrer la croissance sur un nombre restreint de plants d'avenir (Brissette et al., 1999). On pratique l'ÉPC une dizaine d'année (8 à 20 ans) après une perturbation (généralement après une CPRS) de telle sorte que le couvert près du sol (entre 0 et 3m) redevient très ouvert pendant quelques années. Suite aux grandes campagnes de coupes totales des années 1980-1990 succédant à la dernière épidémie de tordeuse du bourgeon de l'épinette, les années 1990-2000 ont connu un fort développement de l'ÉPC dans tout le nord-est de l'Amérique du nord (Canadian Council of Forest Ministers, 2002).

La forêt est l'habitat d'un grand nombre d'espèces animales qui sont susceptibles d'être affectées par des pratiques forestières telles que la CPRS et l'ÉPC (Ferron et al., 1994). La grande différence entre des perturbations naturelles et anthropiques tient au fait qu'après une perturbation naturelle, les arbres morts peuvent rester debout plusieurs années avant que le vent ne les renverse (Crête et al., 1995). À l'inverse, les coupes transforment les forêts en milieux ouverts, semblables à des steppes ou des prairies qui se reboisent progressivement. Les ÉPC, quant à elles, réouvrent partiellement les peuplements en régénération, dans le but d'accélérer les processus naturels de succession forestière (Homyack, 2003). Suite à ces pratiques, le couvert protecteur de certaines espèces devrait être considérablement modifié. La proportion d'habitats sûrs dans lesquels les prédateurs sont inefficaces devrait diminuer. La prédation jouerait alors un rôle prépondérant au cours de la période pendant laquelle les sites exploités se reboisent. La dynamique des populations de lièvres et de petits mammifères ainsi que la richesse en espèces pourraient donc en être affectées.

Effets des perturbations de l'habitat sur les lièvres et des petits mammifères

Le lièvre occupe des habitats très variés, mais préfère les parcelles de végétation au couvert arbustif dense, riches en nourriture et en couvert (Royar, 1986; Keith, 1990; Ferron et Ouellet, 1992). Les grandes forêts mûres ou surannées lui sont moins propices (Koehler, 1990a; 1990b) et il y devient dépendant de la distribution des ouvertures (Telfer, 1974). À court terme, les coupes et les ÉPC ont un effet négatif sur les densités (Telfer, 1974; Monthey, 1986; Thompson, 1988; Koehler et Brittell, 1990; Sullivan et Sullivan, 1988; Homyack, 2003) et sur le taux de survie du lièvre (Sievert et Keith, 1985; Keith, 1990) car elles affectent grandement l'une des principales composantes de son habitat, i.e. le couvert (Ferron et al., 1994; Homyack, 2003). La marginalisation du couvert ou la fragmentation de l'habitat sont susceptibles d'augmenter la mortalité (Sievert et Keith, 1985; Keith, 1990), entre autres, par accroissement des risques de prédation (Keith et al., 1993, Ferron et al., 1994). Cependant, quelques années après le traitement, l'abondance des lièvres croîtrait et atteindrait son maximum dans les peuplements âgés de 12 à 30 ans (Telfer, 1974; Monthey, 1986; Thompson, 1988; Koehler et Brittell, 1990; Homyack, 2003).

Les petits rongeurs et les insectivores sélectionneraient un habitat essentiellement en fonction de sa structure (e.g.: Miller et Getz, 1977; Pucek, 1983; Harmon et al., 1986; Kirkland, 1990; Batzli et Lesieutre, 1995; Ecke et al., 2001). Bien que les coupes et les ÉPC puissent modifier la composition et la structure des habitats (Ferron et al., 1994; Sullivan et al., 2001; Homyack, 2003), les populations de petits mammifères semblent résilientes face à ces perturbations. En fait, la composition et l'abondance des espèces de petits mammifères peuvent être influencées par les coupes et les éclaircies (Kirkland, 1990; Homyack, 2003), mais leur effet varie d'une espèce à l'autre (e.g.: Clough, 1987; Kirkland, 1990; Pagels et al., 1992; Homyack, 2003; Fuller et al., 2004). Globalement, l'abondance totale des petits mammifères tend à s'accroître dans les peuplements traités (voir revue de Kirkland, 1990; Homyack, 2003; voir la revue de Fuller et al., 2004), alors que leur réponse initiale en terme de diversité ou de richesse spécifique ne montre pas le même patron selon les cas étudiés (voir la revue de Kirkland, 1990; Pagels et al., 1992; Sekgororoane et Dilworth, 1995; Génier et Bergeron, 1996; Potvin et Breton, 1997).

L'incertitude qui ressort de toutes ces études pourrait s'expliquer par le fait qu'à court terme, comme une partie de la végétation est laissée sur pied (Courtois et Potvin, 1994) et que la régénération reforme un couvert protecteur rapidement, les coupes et à fortiori les CPRS sont probablement moins perturbatrices à l'échelle d'un petit mammifère qu'à celle d'un grand mammifère. Elles procureraient aux rongeurs une quantité suffisante de nourriture et un certain abri grâce à la régénération et aux débris de coupe, ou aux buissons, laissés sur place. L'abondance totale des petits mammifères serait donc peu affectée. Quant aux variations d'abondance spécifique, elles proviendraient des profondes modifications d'habitat causées par les pratiques forestières, rendant le milieu moins favorable au maintien de certaines espèces et plus propice à l'établissement de certaines autres.

Objectifs et intérêts de l'étude

De cet état des connaissances il ressort que, dans les forêts exploitées du nord-est de l'Amérique du nord, les mécanismes qui déterminent la dynamique des populations de lièvres et de petits mammifères sont encore mal définis. Au sud du Québec, comme la zone de transition entre les forêts boréales et tempérées constitue un milieu relativement productif, l'hypothèse EEH pourrait s'appliquer. Ainsi, la dynamique des populations de lièvre et de petits mammifères pourrait être dictée par le sommet de la chaîne trophique. La pression de prédation exercée par la grande diversité d'espèces prédatrices terrestres et aériennes présentes dans cette région devrait régulariser les populations de proies et les maintenir stables (non cycliques) à faible densité. Le point d'équilibre de ce système dépendrait de la présence d'habitats sûrs disponibles pour les espèces proies. Les milieux à l'étude sont également soumis à une intense exploitation forestière, et son influence sur la chaîne trophique des petits mammifères est, elle aussi, mal connue. En créant une ouverture du milieu, les pratiques forestières pourraient affecter la proportion d'habitats sûrs, ou refuges, en diminuant l'écran végétal protecteur des proies, ce qui conduirait à augmenter l'efficacité des prédateurs. De ce fait, l'ampleur et la nature même de la prédation pourraient être modifiées.

Le but de ce travail est, avant tout, d'étudier la dynamique des populations et l'importance de la prédation dans la chaîne trophique des petits mammifères au travers d'une expérience fortuite utilisant une activité récréative ou commerciale de piégeage des animaux à fourrure comme moyen de contrôler la prédation. Il est aussi de déterminer la réaction d'une partie de la communauté animale susceptible d'être affectée par le piégeage des carnivores et par la transformation du couvert protecteur due aux CPRS ou aux ÉPC, pendant l'intervalle de temps durant lequel le couvert arbustif se régénère.

Les objectifs spécifiques, faisant chacun l'objet d'un des articles scientifiques proposés dans ce document, sont au nombre de trois et se présentent comme suit:

- L'objectif du premier article (chapitre 2) est d'obtenir une meilleure compréhension du rôle de la prédation et du piégeage des prédateurs terrestres sur la dynamique des populations de lièvre d'Amérique, grâce à une estimation des densités et des taux de survie des lièvres de deux territoires qui différaient au niveau du piégeage des animaux à fourrure. Cette activité avait cours dans l'un des deux territoires, alors qu'elle était interdite dans l'autre.
- Le deuxième article (chapitre 3) vise à vérifier, à partir de cinq années de données, si les

populations de petits mammifères des forêt mixtes du nord-est de l'Amérique du nord pourraient être maintenues stables, à faible densité, et d'obtenir une meilleure compréhension du rôle de la prédation et du piégeage des prédateurs terrestres sur cette dynamique, grâce à une estimation de l'abondance et de la survie d'individus de différentes espèces à l'intérieur des deux mêmes territoires.

- Enfin, le troisième article (chapitre 4) a pour objectif d'examiner l'impact de la CPRS et de l'ÉPC sur les populations de lièvres et de petits mammifères en faisant un lien entre la structure des différents types d'habitats présents dans les deux territoires et l'abondance des individus pour les espèces ciblées.

L'intérêt de ce projet est d'essayer de décrire la dynamique des populations de lièvres et de petits mammifères et de mieux comprendre les facteurs qui l'influencent, dans la zone de transition entre les forêts boréales et tempérées du Nord-Est de l'Amérique du nord. Dans cette région, aucune étude de ce type n'a été réalisée auparavant, et aucun modèle n'a encore été proposé. L'intérêt est également de mettre en évidence l'impact des activités forestières sur l'écosystème et d'émettre les recommandations nécessaires, afin qu'à plus long terme, l'exploitation forestière puisse se poursuivre sans menacer la biodiversité.

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CHAPITRE II

POPULATION DYNAMICS OF SNOWSHOE HARES IN RELATION TO FURBEARER HARVEST[1]

Abstract

We studied the population dynamics of snowshoe hare in two areas of the southern boreal forest of eastern North America that differed with respect to furbearer harvest. We predicted that hare density and survival would be higher in the area with trapping (TRAP) than in the protected area (PROT) as a response to differential predator abundance. Indices of predator density suggested that predation risk was slightly higher in PROT than TRAP, particularly during the first year of our 3-year study. Predators killed 86% of the radio-marked hares (body mass >900 g) that died during the study (n =71). Hare density was higher in TRAP (56 ± 4 hares/100 ha) than PROT (30 ± 5 hares/100 ha). Furthermore, hare densities were relatively stable in both areas between 1998-2000. Additional data from the previous two years in TRAP indicated that hare density had remained relatively unchanged for five years. These findings were in agreement with regional trends in hunter harvests which were low and stable throughout the 1990s. Annual survival of radio-marked adult

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[1] Etcheverry, P., M. Crête, J.P. Ouellet, L.P. Rivest, M.C. Richer and C. Beaudoin, 2005. J. Wildl. Manage. in press.

hares (>900 g) were high in both areas but decreased during the study. Survival exhibited a sex*area interaction, and was lower for females in TRAP than PROT (46% vs. 76%) but higher for males in TRAP than PROT (64% vs. 37%); hare survival did not differ when sexes were combined. Differential survival of older hares could therefore not explain the difference in hare densities in the two areas. Gestation rates were similar in both areas but the numbers of young hares (300–900 g) entering the population and young: female ratios were higher in TRAP than PROT. Survival of young hares during their first summer was variable between time periods and tended to be higher in PROT than TRAP. Thus, it is likely that improved survival of juveniles (<300 g) soon after birth explains the increased hare density in TRAP. Study results show that managers cannot assume the existence of cyclicity in all hare populations and must be aware that complex trophic interactions can generate unexpected responses to perturbations.

Introduction

The partial or total removal of predators in terrestrial ecosystems can cause various effects in community dynamics. Removal or substantial reduction of top carnivores such as gray wolves (*Canis lupus*) and bears (*Ursus sp.*) in the southern half of North America has led to a minimum 5-fold increase in cervid biomass (Crête, 1999). Consequences of selective removal of medium or small terrestrial carnivores remain very difficult to predict, due to complex relationships between numerous predator and prey species including intraguild predation (Fedriani et al., 2000). In snowshoe hares (*Lepus americanus*), exclusion of terrestrial predators has resulted in increased survival and density but did not prevent cycling in one study (Krebs et al., 1995). Total exclusion of vole (*Microtus spp.*) predators has resulted in density increases with seasonal fluctuations (Norrdahl et al., 2002).

Although trapping can effectively reduce the abundance of harvested species (Hodgman et al., 1994; Frank and Woodroffe, 2001), the effects of trapping on furbearer numbers and their prey are poorly understood (Etcheverry et al., 2004). Regulation represents a common emerging property of many natural prey populations (Berryman et al., 2002) and density-dependence has been detected in some hare predators (Fryxell et al., 1999). Hare populations seem to exhibit a gradient of cyclicity according to latitude (Keith, 1990), with marked cycles in the north (Keith and Windberg, 1978; Krebs et al., 1995) and relatively stable and low densities in the south (Buehler and Keith, 1982; Keith, 1990; Murray, 2000; but see Hodges, 2000). Most authors suggest that predation is at least partly responsible for this particular dynamic (Wolff, 1981; Keith et al., 1984; Krebs et al., 1995; King and Schaffer, 2001; Krebs et al., 2002; Wirsing et al., 2002). Therefore predation plays a paramount role in population dynamics of snowshoe hares (Keith et al., 1984; Murray et al., 1997; Krebs et al., 2001). Accordingly, sustained harvests of furbearers should decrease predation pressure on hares unless avian predators fully compensate. As a result, hare density should increase in the presence of furbearer trapping because of reduced mortality.

Our objective of this study was to obtain a better understanding of the role of predation and furbearer trapping on the population dynamics of snowshoe hares.

Specifically, we compared 1) snowshoe hare density and survival and 2) the abundance of their predators between a trapped area (TRAP) and a protected area (PROT) located in the transition zone between mixed and boreal forests of northeastern North America. Trapping of furbearers occurred continuously in the TRAP area whereas it had been prohibited for over 20 years in the second PROT area. Assuming that trapping reduced the abundance of predators and that predation plays an important role in the population dynamics of snowshoe hares, we predicted that population density and survival of hares would be higher in TRAP than PROT.

Study area

We studied two forested blocks located 80 km apart and ≈250 km east of Québec City on the south shore of the St. Lawrence River. Furbearers had been continuously trapped in one area (TRAP; 47°36' N, 69°21' W; ≈800 km^2) but protected in the other area since the creation of a game reserve in 1977 (PROT; 48°08' N, 68°37' W; ≈270 km^2). Annual temperature averaged 2.5°C and annual precipitation varied between 900–1,200 mm, 33% of which was snow (Environment Canada, 1993). Snow cover generally persisted from early December to late April. Mixed forests typical of the transition zone between northern hardwood forest and boreal forest covered both areas (Marie-Victorin, 1995). Dominant species included balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), white cedar (*Thuja occidentalis),* paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), red maple (*Acer rubrum*) and sugar maple (*A.*

saccharum). Logging was conducted in both areas during the last century, which created a mosaic of forest stands of various ages. Deciduous, mixed and coniferous stands covered 22%, 20% and 24% of TRAP, respectively, compared to 5%, 18% and 41% of PROT. Lakes, rivers, wetlands and bogs made up the rest of the two areas. Young clearcuts (≤10 yr) were more common in TRAP (10%) than in PROT (1%). The two study areas offered comparable amounts of food and cover for snowshoe hares in winter (Beaudoin et al., 2004). Potential predators of snowshoe hare included coyotes (*Canis latrans*, since the 1970s, George, 1976), red fox (*Vulpes vulpes*), Canada lynx (*Lynx canadensis*), fisher (*Martes pennanti*), American marten (*M. americana*), red-tailed hawk (*Buteo jamaicensis*), barred owl (*Strix varia*) and great-horned owl (*Bubo virginianus*). Small predators that could hunt young hares included long-tailed weasel (*Mustela frenata*), ermine (*M. erminea*), northern saw-whet owl (*Aegolius acadicus*) and American kestrel (*Falco sparverius*).

Methods

Data collection

Hare population dynamics.— We monitored hares and estimated their density using a stratified random sampling technique based on 1:20,000 forest maps. In 1998–1999, we grouped all habitat types into three strata: recent clearcuts (≤10 years), established forest stands (>10 years) dominated by deciduous species and established forest stands dominated by conifers. In 1999–2000 and 2000–2001, we added a fourth stratum: stands treated with pre-commercial thinning (i.e., young stands in which stem density had been reduced to approximately 2,500 stems/ha).

We estimated hare density by combining stratified random sampling (Cochran, 1977) with the mark-recapture method. We allocated at least four mark-recapture grids to each stratum habitat for each area by randomly selecting forest stands, provided they were accessible on the ground and large enough to include a 300×400-m grid (Table 1). In each grid, we placed 20 Tomahawk traps that were systematically distributed along four lines at 100-m intervals. The effective grid size covered 23 ha and was calculated by adding half the mean distance between consecutive hare locations during a 24-hr period (135 m ±14 (SE), n = 180) at the periphery of trapping grids (Brooks et al., 1998). Traps were baited with a piece of apple and alfalfa and visited daily. We sexed captured hares and checked females for gestation by palpation (Keith et al., 1968). All individuals were marked with two tags between the hind-foot toes (Keith et al., 1968) and weighed. We discriminated between young and older hares based on body mass (young ≤900 g) to ensure that radio-collars did not exceed 4% of hare weight. The Animal Care Committee of the Université du Québec à Rimouski approved the handling protocol (# 09-20).

Because abundance was low in some grids, we used three types of trapping grids to maximize precision of density estimates: 1) grids trapped only once for one or three nights (n = 10); 2) grids trapped for one night during at least one growing season (n = 12); and 3) grids trapped for three nights during at least one growing season (n = 26). We tried to keep the same grids from year to year, but we had to relocate some of them because of logging or accessibility loss. Thus, the sample size was 28, 32, and 32 grids in 1998, 1999, and

2000, respectively. We conducted four trapping sessions in 1998 and three sessions in 1999 and 2000, each year between late May and early October, for total of ≈25,000 trap nights. We maintained six grids that had been used by Richer et al. (2002) in 1996 and 1997 in TRAP to extend density estimates to five years.

We radiocollared older hares (>900 g) in the various grids, and distributed collars equally among all strata in both TRAP and PROT. We then monitored hares weekly using 11- or 4-element Yagi antennae mounted on a pick-up truck or snowmobile, respectively. Radiocollars (Holohil Systems Ltd, model M1-2M[4]; ≈35 g) included a mortality switch. We classified mortality into six probable causes: predation by canids, felids, mustelids, avian predators, unknown predators, and other causes. We discriminated terrestrial predators from tracks and scats found around carcasses, by marks left on carcasses or collars, by dispersion of remains, or by locations where predators hid carcasses. Avian predation was concluded based on marks left on carcasses and mostly by feathers or pellets found around carcasses. We classified a death as unknown predator when insufficient signs were left. In some cases, we recovered entire carcasses which we necropsied in a laboratory to ensure predators had not made the kill.

Predator abundance.—To assess the predation risk in each area, we estimated the relative abundance of terrestrial predators using track counts in the snow along 56 permanent 800-m transects within hare capture grids (Table 1). Transects were equally distributed among strata in TRAP and PROT and were censused on snowshoes 3–5 times during January and February in 1999, 2000 and 2001. We noted the position of each predator track that crossed or came within 2.5 m of transects, and we then identified the species. We also recorded time elapsed since the last snowfall greater than 1 cm. We also estimated the harvest of furbearers in TRAP for the three years preceding and during the study by counting the number of pelts sold by trappers living around TRAP (1,265 km^2).

We surveyed nocturnal avian predators by playback recordings of vocalisations at sampling points that were systematically distributed along forest roads in each area (Takats et al., 2001; Table 1). We conducted the surveys three times in late spring and early summer each year from 1998–2000. We also estimated relative abundance of the diurnal red-tailed hawk and American kestrel using point counts (Ralph et al., 1993) and the same sampling points and sampling intervals as for owls.

Data analysis

Hare population dynamics.—We compared the number of hares captured with repeated-measures ANOVA to determine whether abundance varied between areas, strata, and years. We compared hare abundance using the number of different individuals captured because the probability of capture did not differ between areas or years based on the Chao estimator (Chao, 1987). Previous density estimates of snowshoe hares combining stratified random sampling with the mark-recapture method indicated that between-grid variability made up >99% of density variance, the remaining variability was associated with the correction factor (Caron, 1998; Richer et al., 2002). To increase sample size and precision of hare density estimates, we set some grids for one night only. For such grids, we calculated the number of different hares that would have been captured in grids trapped for one night if they had been trapped during three consecutive nights by fitting a Poisson regression to data collected on 3-night grids. We determined how the adjusted model fit the data by computing the R^2 between predicted and observed values. We used predicted or true numbers of hares captured after three nights to estimate hare density. We multiplied the mean number of individuals captured per grid by the correction factor (3.26 ±0.04 [SE]) and divided by the effective grid size (23 ha) and we estimated the standard error (SE) of the density according to the formula provided by Mood et al. (1974) for the product of two estimates.

To estimate the survival, we determined whether the daily probability of death (DPD) of radiotagged hares varied according to area, stratum, year, sex and season (spring = April–May; summer = June–September; fall = October–November; winter = December–March) with a likelihood-ratio test (Proc GENMOD, SAS Institute, 1999), assuming an exponential model. To test whether the exponential model was appropriate, we compared it to Weibull's model using a Lagrande multiple chi-squared test (Proc LIFEREG, SAS Institute, 1999). We estimated the SE of DPD using Proc GENMOD (SAS Institute, 1999). We then estimated seasonal and annual survival rates of radiocollared hares with the formula $(1\text{-DPD})^d$, where d represented the period length in days. We used the formula provided by Lamoureux et al. (2001) to calculate survival SEs. We compared areas for causes of mortality and tested for parity of sex-ratios with a χ^2 test.

We also estimated capture probabilities of young hares during their first summer using a log-linear model to describe capture histories in consecutive periods (Rivest and Lévesque, 2001), assuming the Mo model (Otis et al., 1978) due to small sample sizes. We then estimated survival of young hares between consecutive trapping periods during their first summer by fitting log-linear models for robust design (Rivest and Daigle, 2004).

Given that capture probabilities did not differ between TRAP and PROT for all testable periods, we compared survival of young hares using the Cochran-Mantel-Haenszel statistic (Agresti, 1996).

We analysed productivity and body mass of hares as complementary information. We utilized a log-linear model to analyze data on gestation rates using the area, stratum and year as explanatory variables. Given the imprecision of fitting log-linear models to tables lacking in data (Agresti, 1996:194), we set the significance level at $\alpha = 0.01$ when analyzing data. We also computed an annual young:female (>900 g) ratio for each grid by pooling all captures made during all trapping periods, given small sample sizes. We considered each grid as a random sample and used formulas provided for ratio sampling (Cochran, 1977:155). We estimated the number of young hares that would have been captured after three nights in grids trapped for one night only by fitting a Poisson regression to data from 3-night grids so that each grid had the same weight. We estimated overall young:female ratios for TRAP and PROT by taking the mean of annual estimates, and we estimated SEs by taking into account inter-annual covariance between grids that were trapped more than one year. We then compared overall young:female ratios between areas with a Z test. We compared body mass of young and older hares captured in the two areas were compared with the help of a factorial ANOVA, taking into account sex, stratum, year, and associated interaction terms.

Predator abundance.—We compared track density of terrestrial predators between the two areas using repeated-measures ANCOVA with time elapsed since the last snowfall as the covariate. Factors included area, stratum and year and their interactions. We square-root transformed data to normalize residuals. We then made post-hoc pair-wise multiple comparisons with protected least significant difference tests (LSD tests, option PDIFF, Proc LSMEANS, SAS Institute, 1999). We computed the mean number of avian predators seen or heard per sampling point per stratum for each survey and area, and we used a log-linear model (Proc GENMOD, SAS Institute, 1999) to determine the influence of area, stratum and year and included all interactions in the model. However, given that we had to interrupt some surveys due to weather conditions, we used the natural logarithm of observation days per sampling point to weight the data. Given the imprecision of fitting log-linear models to tables lacking in data (Agresti, 1996:194), we set the significance level at $\alpha = 0.01$ when analyzing data on birds of prey. All means are presented with associated SEs.

Results

Hare population dynamics

The number of hares captured per grid after one night varied between areas ($F_{1,31} = 6.30$; $P = 0.018$) and years ($F_{2,26} = 9.18$; $P = 0.001$) but not between habitat strata when excluding ($F_{2,31} = 2.38$; $P = 0.110$) or including pre-commercially thinned stands (1999 and 2000 only; $F_{3,32} = 1.79$; $P = 0.169$). The Poisson regression relating the number of captures after one and three nights provided a good fit ($R^2 = 0.70$) so all grids served to estimate density. The ANOVA comparing number of captures at three nights (observed and predicted combined) yielded similar results as that for one night, the number of hares differed between areas ($F_{1,31} = 6.55$; $P = 0.016$) and years ($F_{2,26} = 8.88$; $P = 0.001$) but not between strata ($F_{2,31} = 1.64$; $P = 0.209$). Density averaged (± SE) 45 (±5), 66 (±4), and 60

(±4) hares/100 ha in TRAP during summer 1998, 1999 and 2000 respectively, compared to 20 (±7), 33 (±5) and 41 (±5) hares/100 ha in PROT. Throughout the study, density was almost twice as high (t_{31} = 2.56; P = 0.016) in TRAP (56 ±4 hares/100 ha; n = 19) than PROT (30 ±5 hares/100 ha; n = 18). Hare density increased between 1998 and 1999 (P = 0.001) but was stable between 1999 and 2000 (P = 0.600). Over the three years of the study, we captured 79 males/100 females in TRAP (n = 350) and 116 males/100 females in PROT (n = 145); annual sex ratios did not differ from parity in either TRAP (χ^2_2 = 2.11; P = 0.348) or PROT (χ^2_2 = 0.18; P = 0.916).

We radiotagged 122 hares (58 males, 64 females). Survival of radiotagged hares (>900g) decreased during the study ($F_{2,375}$ = 3.93; P = 0.020) and the pattern differed between sexes ($F_{1,375}$ = 15.95; P <0.001). Females survival decreased faster than that of males in TRAP whereas the decline was similar for both sexes in PROT (Fig. 1). Overall, annual female survival was lower in TRAP (0.46 ± 0.11; n = 36) than PROT (0.76 ± 0.08; n = 28) and it tended to decrease in both areas, but more so in TRAP than PROT. In contrast, males showed a higher survival in TRAP (0.64 ± 0.11; n = 25) than PROT (0.37 ± 0.12; n = 33; P = 0.020). Moreover, females had a higher survival than males in PROT (χ^2_1 = 6.14; P = 0.013), whereas no difference occurred between sexes in TRAP (χ^2_1 = 1.35; P = 0.245). Survival did not differ between TRAP and PROT when combining sexes (χ^2_1 = 0.11; P = 0.745).

Among radiotagged hares, predators took 61 out of 71 individuals that died during the study. The other 10 hares died of various causes (e.g., 2 = shooting, 1 = collision, 7 =

other). Among the terrestrial predators, canids made the most kills (17), followed by mustelids (7) and finally lynx (3). Avian predators killed hares at a similar rate (18) as terrestrial predators (27: χ_1^2 = 0.86; *P* = 0.357). Causes of mortality were similar in both areas (χ_5^2 = 2.52; *P* = 0.774), and the type of predator could not be identified in 26% of predation cases.

We captured more young hares in TRAP than in PROT (Fig. 2). We were able to compare survival of young hares for the four intervals where we had captured specimens in both areas (Table 2). Survival of young hares varied greatly between periods, ranging from 0.25–0.52 in TRAP and from 0.16–0.85 in PROT. Overall, young hares tended to survive better in PROT than TRAP, but pair-wise comparisons yielded marginally- or non-significant results.

Palpation revealed a similar proportion of parturient females in TRAP (0.09 ±0.02; *n* = 460) and PROT (0.07 ±0.02; *n* = 200) over the study (χ_1^2 = 0.62; *P* = 0.429). Detection of gestation was higher in 1999 (0.14 ±0.02; *n* = 290) than in other years (1998 = 0.04 ±0.02, *n* = 118; 2000 = 0.08 ±0.02, *n* = 252: χ_2^2 = 11.91; *P* = 0.003). The number of young captured per female decreased from ≈0.3–0.5 in 1998 to ≈0.1–0.2 in 2000, and tended to be higher in TRAP than PROT each year (overall *Z* = 1.581; *P* = 0.057; Fig. 2).

Body mass of older hares (>900 g) did not differ between areas ($F_{1,33}$ = 0.02; *P* = 0.887) or among years ($F_{2,30}$ = 0.07; *P* = 0.933). At 900 g, snowshoe hares should have been approximately 60 days old (Keith et al., 1968) in our study area as they reached similar size (median 1.4 kg; 4% handled hares ≥2.0 kg) in Alberta (≈1.3–1.6 kg: Keith et al., 1984). Young hares (<900 g) weighed the same ($F_{1,18} = 0.01$; $P = 941$) in TRAP (0.58±0.16 kg; $n = 162$) and PROT (0.62±0.17 kg; $n = 64$), and only 6% of captures weighed <300 g.

Predator abundance

Coyote and red fox tracks followed similar patterns of abundance (area×year interaction: $F_{2,46} = 5.56$; $P = 0.007$ and $F_{2,46} = 9.64$; $P < 0.001$, respectively), being approximately 4 times less abundant in TRAP than PROT in 1999, but at similar levels in 2000 and 2001 (Fig. 3). Lynx tracks showed area × year × stratum interaction ($F_{1,46} = 3.77$; $P = 0.006$). This complex pattern indicated that lynx tracks were very rare in both areas, but increased in number in 2001, particularly in established coniferous stands of TRAP. Density of fisher tracks remained twice lower in TRAP (0.05 ±0.02 tracks/km) than PROT (0.12 ±0.03 tracks/km) during the whole study ($F_{1,48} = 4.22$; $P = 0.045$), whereas density of marten tracks did not vary according to area ($F_{1,48} = 1.71$; $P = 0.197$). Tracks of small mustelids also exhibited a significant area×year interaction ($F_{2,46} = 3.56$; $P = 0.036$), and tended to be more common in TRAP than PROT, particularly in 2001 where tracks were almost twice as abundant in TRAP thn PROT.

Except for Canada lynx, annual fur harvest per 1,000 km^2 declined for all commercially trapped species during the three years of the study period compared to the three preceding years: coyote = 27 versus 49; red fox = 103 versus 269; fisher = 63 versus 98; marten = 11 versus 50; ermine and weasel = 38 versus 81; Canada lynx = 6 versus 0 (there was a moratorium on lynx trapping between 1992–1997).

Playback response rates of great-horned owls showed a year×area interaction (χ^2_2 = 12.89; $P = 0.002$; Fig. 3); we detected fewer owls in TRAP than PROT during two years (1998: 2.71 ±1.10 vs. 12.05 ±2.76 birds/100 station•days, χ^2_1 = 10.25; $P = 0.001$; 2000: 7.42 ±2.09 vs. 19.99 ±3.88, χ^2_1 = 7.18; $P = 0.007$). Our data for barred owls exhibited an area×stratum interaction (χ^2_3 = 14.96; $P = 0.002$). Barred owls were almost absent from TRAP (< 0.020 birds/100 station•days), whereas we detected up to 9.19 ±3.01 (SE) birds/100 station•days in PROT, and this difference was particularly marked in pre-commercial thinning and coniferous stands. Response of northern saw-whet owls was similar in TRAP and PROT (χ^2_1 = 1.44; $P = 0.230$), and higher in 1999 than in the two other years (χ^2_2 = 14.46; $P < 0.001$). Observations of red-tailed hawks were low and relatively stable during the study, and between two and three times higher in TRAP than PROT for all three years (χ^2_1 = 5.50; $P = 0.019$), while American kestrels were detected at the same rate in both areas (χ^2_1 = 0.48; $P = 0.489$).

Discussion

In agreement with the hypothesis that predation plays a dominant role in the snowshoe hare population dynamics, hare density was almost twice as high in TRAP than PROT. However, contrary to our prediction survival of large hares (>900g) was not higher in TRAP than PROT and we must consider alternative mechanisms to explain the observed difference in density in the 2 areas. Although the survival of young hares (300–900 g, most

>30 days old based on body mass) was variable and precluded a firm conclusion, it tended to be higher in PROT than TRAP. The number of young hares entering the trapped populations and the young:female ratios were consistently higher in TRAP than PROT during the study. Hence, increased juvenile production and/or survival during the first month of life represent the most plausible reason explaining the higher density observed in TRAP.

Predation risk

Of the terrestrial predators, canids and mustelids killed most radiotagged hares in our two study areas, whereas Canada lynx killed only 4% of hares; lynx were rare during our study, particularly during the first two years. Trappers likely removed approximately 200 canids and mustelids from TRAP annually during the study whereas trapping was totally prohibited in PROT. Canid tracks were more abundant in PROT than TRAP during the first year of the study, and then decreased in PROT to similar levels as in TRAP for the last two years. Fisher tracks stayed lower in TRAP than PROT throughout the study whereas marten tracks were encountered at a similar rate in both areas.

Among large avian predators, we heard more great-horned owls and barred owls in PROT than TRAP. In contrast, we observed fewer red-tailed hawks in PROT than TRAP. Occurrence rates of the two smallest avian predators, northern saw-whet owl and American kestrel were similar in both areas. It is difficult to partition predation risk among avian predators but it is possible that the risk to hares was higher in PROT than TRAP.

Overall, our indices of both terrestrial and avian predator abundance suggest that snowshoe hares faced a slightly lower risk of predation in TRAP than PROT. Our census techniques provided only an index of predator density, however, and the relationship between the two variables may not be linear. In addition, trapping can bias the age structure of harvested populations towards young animals (e.g., Banci and Proulx, 1999), and young predators may be less efficient at hunting than adults. Furthermore, habitat types used by hares during the winter and summer of 1999 were consistent with the hypothesis of a higher risk of predation in PROT than TRAP (Beaudoin et al., 2004). At higher density, hares in TRAP occupied home ranges with less cover and more food than hares in PROT. This suggests that hares in TRAP responded to reduced predation risk by occupying more high risk areas than hares in PROT.

Besides trapping, the two study areas differed with respect to proportion of deciduous and coniferous stands, and carrying capacity could have been greater in TRAP than PROT. This is possible given the lack of replication of our study but we believe it is unlikely in terms of hare habitat. Density did not vary in summer among habitat strata (i.e. hares were uniformly dispersed within each area), whereas the two areas offered similar amounts of food and cover in winter (i.e., 11–15 g/m^2 of deciduous twigs and 64–89 g/m^3 of coniferous twigs (Beaudoin et al., 2004)).

Hare population dynamics

Survival of >900g hares.—We anticipated that furbearer trapping would reduce predation on large hares, which would have resulted in a higher density and survival in TRAP than PROT. Male survival of radiotagged hares was greater in TRAP than PROT, particularly during the last two years, whereas female survival followed the opposite trend. In addition, females lived longer than males in PROT; although survival did not differ between the sexes in TRAP. To our knowledge, this is the first instance where a sex-related difference in hare survival has been documented. Females may have been less mobile or occupied safer home ranges than males at the lower hare density in PROT, which would have lowered their encounter rate with predators (Lima and Dill, 1990). Female voles reduce their mobility to decrease predation risk (Norrdahl and Korpimäki, 1998). At the higher hare density in TRAP, some females could have been forced to occupy high risk home ranges. Agonistic behavior of female hares increases with group size during the non-reproductive season in enclosed conditions (Ferron, 1993). Overall annual survival of radiotagged hares averaged 0.58, which is much higher than that measured for cyclic populations, even during increase phases (Keith, 1990; Krebs et al., 2001). Some southern populations of hares have survival approaching those we measured (Hodges, 2000).

Survival of young hares.—In general, young hares (<900 g) began entering our traps when they weighed approximately 300 g (i.e., when they were about 25 days old; Keith et al., 1968). We always captured young hares at a higher rate in TRAP than PROT. Not surprisingly, young:female ratios in TRAP tended to exceed those in PROT. Estimated survival rates based on the mark-recapture technique exhibited much variability, and tended to be higher in PROT than TRAP although the difference was not clear. Thus the higher hare density observed in TRAP than PROT cannot be explained by increased survival of young hares between approximately 300 g and 900 g.

The palpation to estimate gestation rates we used proved to be difficult to apply, and we recorded low gestation rates even though snowshoe hares produce 3–4 litters/year (Cary and Keith, 1979). Overall, pregnancy rates appeared similar in both areas, although foraging conditions within ranges may have been superior in TRAP than PROT (Beaudoin et al., 2004). In the Yukon, food supplementation did not increase total reproductive output of experimental females compared to control females (O'Donoghue and Krebs, 1992). The only two published studies on leveret survival indicated that most juvenile mortality occured during the first five days of life when littermates still occupied natal nests (O'Donoghue, 1994; Krebs et al., 2002). On the mainland in the Yukon, red squirrels (*Tamiasciurus hudsonicus*) cause most mortality (O'Donoghue, 1994), whereas both coyotes and red squirrels kill leverets on Jacquot Island, in Lake Kluane (Krebs et al., 2002). Adult and especially leveret survival was higher on Jacquot Island than the mainland, which resulted in a much higher density on the island (130 hares/100 ha) than the mainland (70 hares/100 ha) over 25 years (Krebs et al., 2002). We did not radiotag leverets at birth so we cannot firmly conclude that higher leveret survival occurred in TRAP compared to PROT, and led to increased population density as in the Yukon, but our results are consistent with this hypothesis.

Stability of hare density.—We were able to extend our series of density estimates for TRAP to five years because Richer et al. (2002) had sampled the same area during the two previous summers. Between 1996 and 2000, annual hare density in TRAP averaged 49, 65, 45, 66, and 60 hares/100 ha and hence was relatively low and stable, as in non-cyclic southern populations. Densities were 5–10 times lower than the peak densities reached by cyclic populations (Keith, 1990), and although we observed some fluctuations in yearly survival, densities were relatively stable for five consecutive years. During similar intervals, densities of cyclic northern populations in Alberta (Keith and Windberg, 1978) and the Yukon (Krebs et al., 1986) exhibited much larger variations (i.e., 13–141-fold changes). Thus, our results are in agreement with the suggested gradient of cyclicity according to latitude (Keith, 1990). Moreover, hunter harvest rates of hares in the Bas-Saint-Laurent region, which includes our two study areas, also suggest that hare abundance was relatively stable between 1996–2000 (Fig. 4). This index of hare abundance shows that hare populations were relatively high between 1978 and 1984, decreased rapidly from 1987 to 1991, and stabilized at low levels in the 1990s. This index also coincides with the period when coyotes became well established in the region (Crête and Lemieux, 1996). Snowshoe hares represent a major food item for coyotes in northeastern North America (Ferguson et al., 1998) and coyotes may have influenced regional trends in hare numbers. The addition of a mortality factor for an animal population should result in lowered density if one assumes population regulation. The wide expansion of pre-commercial thinning during the same period, which negatively affects prime hare habitat (Beaudoin et al., 2004), could also have aggravated hare decline in the 1990s. Long-term studies of various predator assemblages will be necessary to fully understand the population dynamics of snowshoe hares in the south of their range; juvenile survival likely represents a key element within hare trophic interactions (Krebs et al., 2002).

Management implications

Our results showed that hare density can remain relatively stable and low in southern populations and that canids can dominate among terrestrial predators of large hares. Hence managers cannot assume the existence of cyclicity in all hare populations or the dominance of Canada lynx among predators. Our results also illustrated that furbearer trapping influence hare abundance. However, in a companion study (Etcheverry et al. 2004) we have shown that furbearer trapping in our study area did not affect the abundance of small rodents. Accordingly, managers must be aware that furbearer trapping may lead to different outcomes according to species due to complex interactions in multispecies assemblages.

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Table 1. Number of snow-tracking transects and sampling points used to estimate the relative abundance of hare predators (mammalian and avian), and summary of sampling grids used and number of hares handled and radio-tagged to estimate snowshoe hare density and survival, between trapped (TRAP) and protected (PROT, trapping prohibited) areas in 1998-2000, in southeastern Québec, Canada.

	1998–1999		1999–2000		2000–2001	
	TRAP	PROT	TRAP	PROT	TRAP	PROT
Furbearer transects	16	16	20	20	24	23
Avian predator sampling points	60	40	60	40	60	40
Sampling grids	14	14	16	16	15	17
1 or 3 nights (for 1 period only)	4	4	0	0	1	1
1 night (≥1 growing season)	4	4	4	4	3	5
3 nights (≥1 growing season)	6	6	12	12	11	11
Handled hares	132	44	220	101	173	82
Radio-tagged hares	31	18	27	30	3	13

Table 2. Daily probability of capture (DPC ± SE) and survival of young hares (<900 g) for several intervals during their first summer of life over 3 years (1998-2000) in 2 areas of southeastern Québec that differed with respect to furbearer trapping (TRAP = permitted; PROT = prohibited). Comparisons between TRAP and PROT could only be made for those intervals where we captured young hares in both areas (Figure 2).

			Survival			
Interval	Duration (days)	DPC	TRAP	PROT	CMH [a]	*P*[b]
July–September 1998	≈50	0.29±0.09	0.25	0.85	4.18	0.04
May–July 1999	≈80	0.15±0.05	0.30	0.75	0.03	0.87
July–October 1999	≈80	0.33±0.09	0.52	0.16	3.63	0.06
July–October 2000	≈80	0.26±0.09	0.37	0.72	0.86	0.35

[a] Cochran-Mantel-Haenszel statistic comparing survival rates between TRAP and PROT

[b] Probability that survival differed between areas

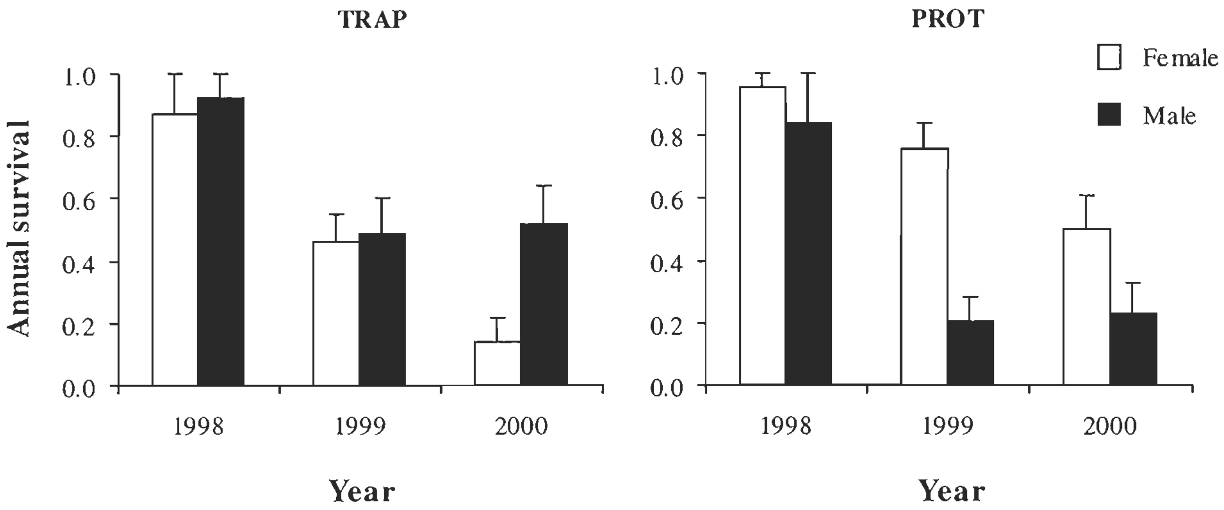

Figure 1. Mean annual survival (+ 1 SE) of 122 radiotagged male and female snowshoe hares monitored between 1998–1999 and 2000–2001 for 2 areas that differed with respect to furbearer trapping (TRAP = permitted; PROT = prohibited), southeastern Québec, Canada.

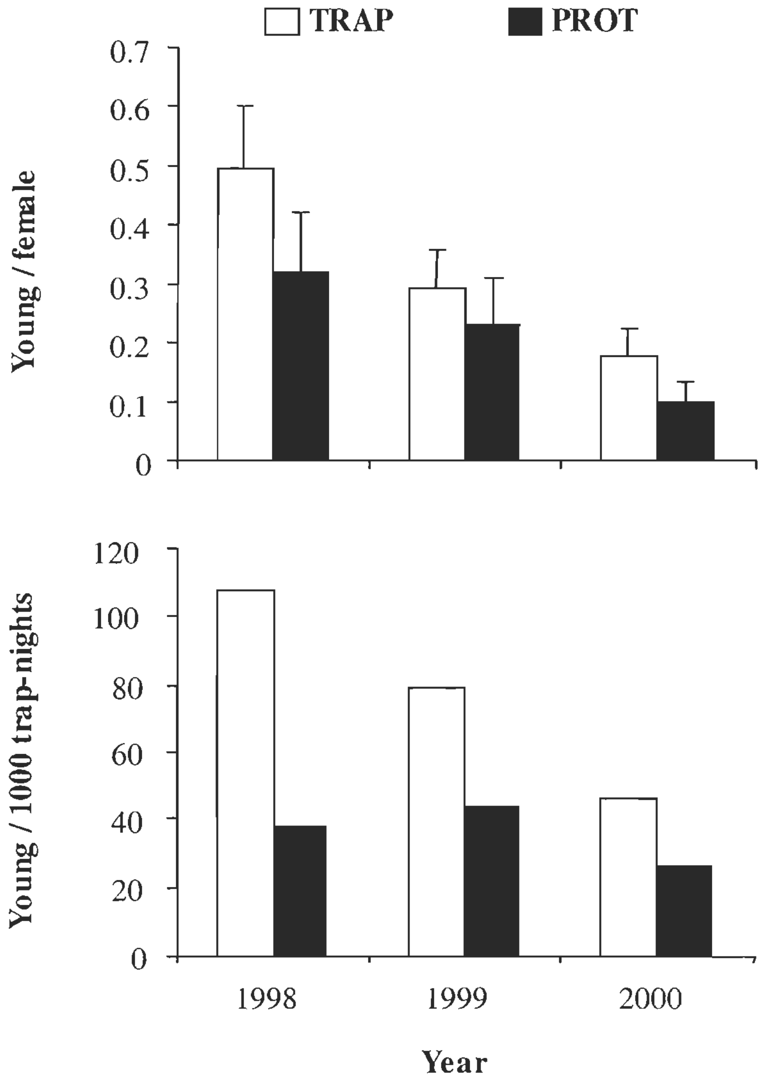

Figure 2. Mean snowshoe hare young:female ratios (+ 1 SE) and number of young hares (<900 g) captured per 1,000 trap-nights trapped during summers of 1998–2000 for 2 areas that differed with respect to furbearer trapping (TRAP = permitted; PROT = prohibited), southeastern Québec, Canada.

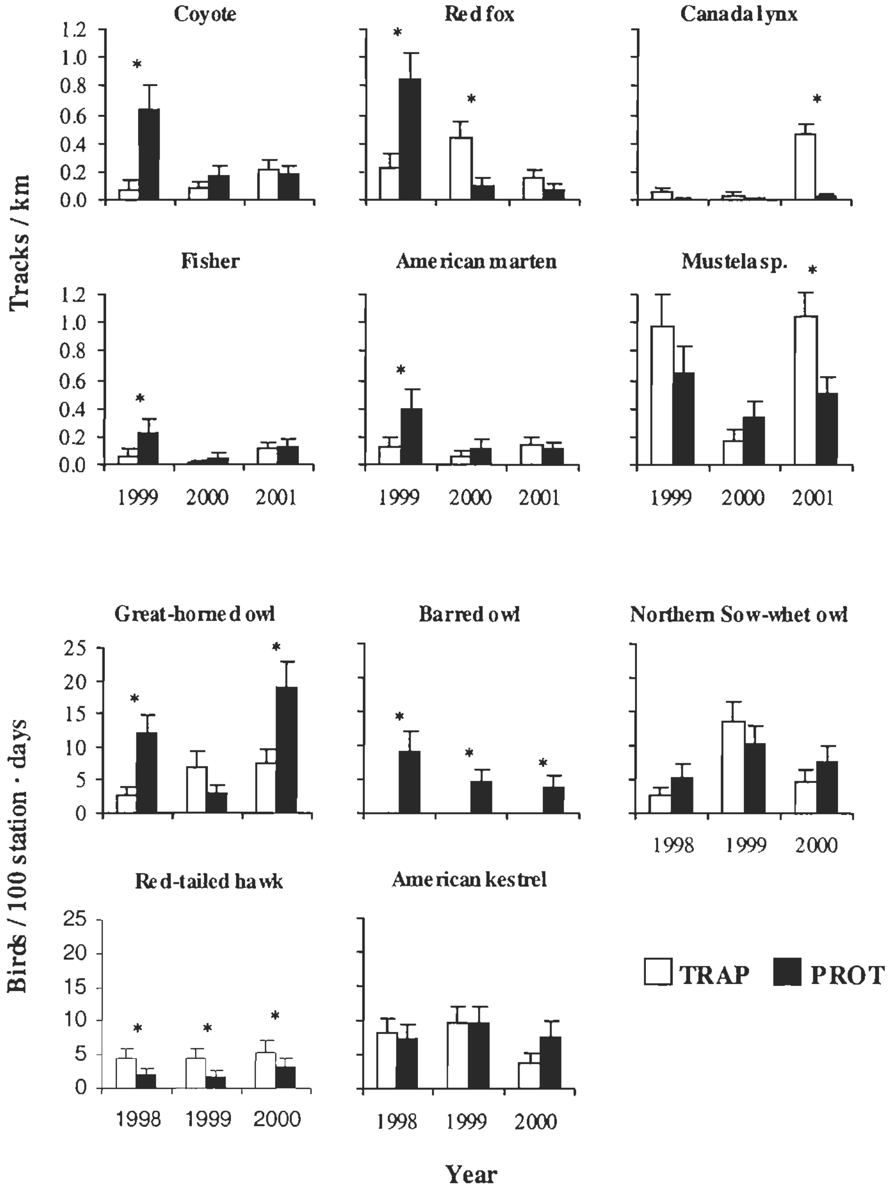

Figure 3. Mean annual index of abundance for terrestrial (estimated in winter) and avian predators (estimated in summer) of snowshoe hares between 1998-2000, for 2 areas that differed with respect to furbearer trapping (TRAP=permitted, PROT=prohibited), southeastern Québec, Canada. Asterisks denote a significant (*P*< 0.05) difference between TRAP and PROT.

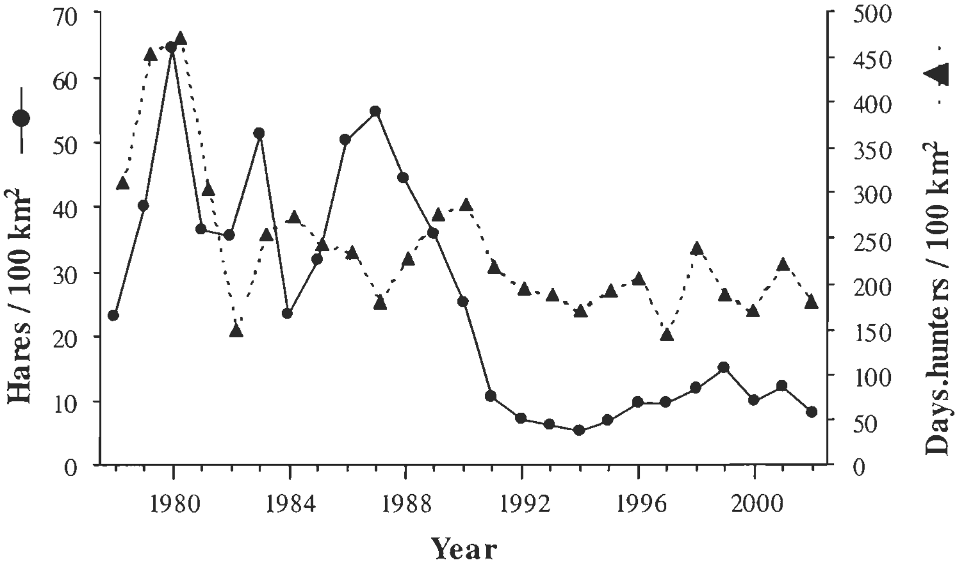

Figure 4. Annual hare harvest (circles) and hunting pressure (triangles) exerted by small game hunters in game reserves between 1978–2002 of the Bas-Saint-Laurent region of Québec, Canada (Société de la faune et des parcs du Québec, unpublished data).

CHAPITRE III

POPULATION DYNAMICS OF SMALL RODENTS IN THE SOUTHERN BOREAL FOREST AS INFLUENCED BY FURBEARER HARVEST[1]

Abstract

We tested four predictions derived from the hypothesis that the guild of avian and terrestrial predators should regulate small mammal populations at low densities in relatively productive ecosystems of the southeastern part of north American boreal forest. We estimated the density of two small mammal populations and the abundance of their predators for three years in two adjacent areas which differed with respect to trapping of furbearers. We predicted 1) that small mammal densities would not show multi-annual fluctuations in the two areas and 2) that densities would be much lower than peak densities reached by cyclic populations. Due to the harvest of furbearers in one area, we also predicted 3) that population densities and 4) survival of small mammals would be higher in the trapped than the protected area. In agreement with our first two predictions, densities of the two main small mammal species (southern red-backed vole, *Clethrionomys gapperi*,

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[1] Etcheverry, P., J.P. Ouellet, M. Crête and M.C. Richer, 2004. Écoscience, in press.

and deer mouse, *Peromyscus maniculatus*) showed little variation between 1998 and 2000 in both areas and additional data from the two previous years in the trapped area indicated that densities remained relatively stable and low over the five-year period. However, contrary to our last two predictions, densities of the two most abundant species did not vary between areas, nor did survival rate of red-backed voles, the only species for which this variable could be estimated. Our findings show that the effect of trapping did not cascade down to small mammals. We have some evidence based on snow tracking data that trapping, which focused on large generalist predators, may have relaxed intra-guild predation on small specialist predators and favored an increase in abundance of specialist predators. Accordingly, we can not reject the idea that a predation-based mechanism maintains small mammal densities at relatively low and stable levels in productive forests.

Introduction

Populations of small herbivores in northern latitudes exhibit large cycles over three to five years in the case of voles and lemmings (Hansson and Henttonen, 1988; Saitoh et al., 1998; Stenseth, 1999) and nine to eleven years for snowshoe hares (*Lepus americanus*; Keith and Windberg, 1978; Krebs et al., 1995). Further south, i.e. the south of the boreal region, populations seem to be more stable and occur at lower densities than those encountered to the north during cycle peaks, suggesting the presence of a cyclicity gradient according to latitude (small mammals:, e.g., Hanski et al., 1991; hare, e.g., Keith, 1990). Such a gradient has been described especially for voles in Fennoscandia (Hanski et al., 1991; Stenseth, 1999) and to a lesser extent on Hokkaido island, Japan (Saitoh et al., 1998; Bjørnstad et al., 1999) and in the U.K. (Southern, 1979; Lambin et al., 2000). This latitudinal difference could largely be due to predation (Korpimäki and Norrdahl, 1991; Korpimäki, 1993; Krebs et al., 2003). Most authors suggest that cycles in the north result from a delayed numerical response of specialist predators whereas in the south a strong functional response from generalist and specialist predators regulates small mammal populations without time lags (Turchin and Hanski, 1997; Hanski et al., 2001; Klemola et al., 2002). However, as cycles of abundance seem to be restricted to harsh environments (e.g.: northern environments) that exhibit long and severe winters (Stenseth, 1999; Klemola et al., 2002), some authors suggest that seasonality may also play a key role in the system (Hansen et al., 1999; Stenseth, 1999). Further south, in more productive areas, a relatively long summer (Hansen et al., 1999; Stenseth, 1999) coupled with an increased diversity and abundance of organisms, including carnivores (Oksanen and Oksanen, 2000), could regulate herbivores at low densities. Increasing complexity of the trophic web could result in a greater stability (Neutel et al., 2002).

In North America, the few long-term studies on small rodent populations suggest the presence of a gradient similar to that in Fennoscandian voles (Johnson et al., 2000). Cycles have been identified in lemmings in the northwest (Pitelka and Batzli, 1993) whereas 43 years of data indicated the existence of density-dependent regulation maintaining a relatively stable abundance of various species in mixed forests of Ontario (Fryxell et al., 1998). Further south, other time-series analyses also showed relatively stable populations that were punctuated by irregular eruptions which were free from multi-annual periodicity

(Garsd and Howard, 1981; Brooks et al., 1998; Getz and Hofmann, 1999). However, in those latter cases, as in other studies (e.g., Fryxell et al., 1998; Bjørnstad et al., 1999), the regulating factor was not identified. Although the results of North American studies suggest a predation-based mechanism of regulation (Johnson et al., 2000), no study has yet conclusively pinpointed the mechanism.

There is general agreement that predation plays an important role in the population dynamics of herbivores. One approach to testing the effects of predation consists of manipulating predator abundance, either by exclusion (e.g., Krebs et al., 1995; Korpimäki and Norrdahl, 1998; Carlsen et al., 2000; Huitu et al., 2003) or removal (Boertje et al., 1996; Henke and Bryant, 1999; Hayes et al., 2003). Recreative or commercial furbearer trapping has rarely been used as a tool to manipulate predation although trapping can effectively reduce the abundance of harvested species (e.g., Hodgman et al.,1994; Frank and Woodroffe, 2001). As found for ungulates (Boertje et al., 1996; Hayes et al., 2003), a reduction in predator density could result in increases in prey abundance. However, the effect of furbearer trapping on small mammal populations has not yet been investigated.

In this context, we estimated the abundance and survival of small mammal populations in two large blocks of mixed forests that differed with respect to trapping of terrestrial predators. Trapping occurred continuously in one area (TRAP) whereas it was prohibited in the second area (PROT). We tested four predictions derived from the hypothesis that the guild of terrestrial and avian predators maintains small mammal populations at relatively low and non-cyclic densities in productive ecosystems of the southeastern part of north American boreal forest. We predicted 1) that in both areas, densities of small mammals would not show multi-annual variations typical of cyclic populations; 2) that densities would be much lower than peak densities reached by cyclic populations; and finally, 3) that densities and 4) survival of small mammals would be higher in TRAP than PROT.

Methods

Study area

The study took place on the south shore of the St. Lawrence River (eastern Québec, Canada) in two large blocks of forest, 80 km apart. Furbearers were continuously trapped in TRAP (47°36' lat N, 69°21' long W; ≈800 km^2), whereas trapping had been prohibited in PROT (48°08' lat N, 68°37' long W; 271 km^2) since the creation of the Duchénier Game Reserve in 1977. Both areas are characterized by gently rolling hills and mixed forests typical of the transition zone between northern hardwood forest and boreal forest (Marie-Victorin, 1995). Altitudes vary between 220 and 610 m a.s.l. Annual temperature averages 2.5°C and precipitation varies between 900 mm and 1,200 mm, 33% of which falls as snow. Snow cover persists from early December to late April (Environment Canada, 1993).

Logging affected both areas during the last century and created both a mosaic of forest stands of various ages and a network of gravel roads and trails. Logging was more intense in TRAP than PROT, with larger clearcuts in the former than the latter. Similar tree species covered the two areas, but there were proportionally more coniferous stands in PROT than TRAP, due to a greater occurrence of white cedar (*Thuja occidentalis*) stands

(Beaudoin, 2001). Dominant tree species included balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), red maple (*Acer rubrum*) and sugar maple (*A. saccharum*).

Moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) black bear (*Ursus americanus*), American beaver (*Castor canadensis*) and snowshoe hare were common in both areas. Small mammals included northern flying squirrels (*Glaucomys sabrinus*), red squirrels (*Tamiasciurus hudsonicus*), eastern chipmunks (*Tamias striatus*), southern red-backed voles, meadow voles (*Microtus pennsylvanicus*), deer mice, woodland jumping mice (*Napaeozapus insignis*), northern short-tailed shrews (*Blarina brevicauda*), masked shrews (*Sorex cinereus*), smoky shrews (*S. fumeus*) and pygmy shrews (*S. hoyi*).

Carnivores preying on small mammals in our study areas included coyote (*Canis latrans*), red fox (*Vulpes vulpes*), Canada lynx (*Lynx canadensis*), fisher (*Martes pennanti*), American marten (*Martes americana*), ermine (*Mustela erminea*), long-tailed weasel (*Mustela frenata*), red-tailed hawk (*Buteo jamaicensis*), American kestrel (*Falco sparverius*), great-horned owl (*Bubo virginianus*), barred owl (*Strix varia*) and northern saw-whet owl (*Aegolius acadicus*). All the above mammalian species were targeted by trappers except Canada lynx. We estimated the relative abundance of terrestrial predators using track counts in the snow between 1999 and 2001, and that of avian predators by diurnal and nocturnal surveys carried out in summers 1998, 1999 and 2000. Snow tracking suggested that coyotes and fishers were less abundant in TRAP than PROT during the study (Table 1) whereas Canada lynx and *Mustela spp.* seemed to be more abundant in

TRAP. Among avian predators, great-horned owls and barred owls appeared more numerous in PROT than TRAP while red-tailed hawks showed the opposite trend (Etcheverry et al., 2005).

Abundance and survival of small mammals

To estimate the abundance and survival of small mammals, we used a random sampling design based on 1:20,000 forest maps prepared by the Ministère des ressources naturelles du Québec. In 1998, we grouped forest stands into three strata: recent clearcuts (≤10 years old; Clearcut), older forest stands dominated by deciduous species (Deciduous) and older forest stands dominated by conifers (Coniferous). In 1999 and 2000, we added pre-commercial thinning (PCThinning, the most widely implemented forest treatment in the region) as a fourth stratum because of its potential effects on small mammals.

We estimated the abundance of small rodents using capture-mark-recapture (CMR). We randomly allocated trapping grids to at least five forest stands (≥ 2 km apart) per stratum. Selected stands were used, provided they were accessible on the ground and large enough to include a 90 × 90-m grid (0.81 ha). We systematically placed 100 Sherman traps (229 x 89 x 76 mm) at 10-m intervals in a 10 x 10 grid square (Richer et al., 2002). The effective grid size (Brooks et al., 1998) covered 1.29 ha because the average distance between two consecutive captures during a three-night trapping period was 24.3 m ± 0.7 (± *SE*; $n = 903$) at the periphery of trapping grids. Traps were baited with a piece of apple and peanut butter and checked each morning. Captured animals were identified to species, weighed and sexed. All rodents were marked with a tag on each ear and released at the point of capture. The Animal Care Committee of Université du Québec à Rimouski approved the handling protocol (# 10-21).

Because abundance was low in some grids, we used three types of trapping grids to maximize precision of density estimates (see below): 1) grids trapped only once for one or three nights (*n* = 8); 2) grids trapped for one night during at least one growing season (*n* = 18); and 3) grids trapped for three nights during at least one growing season (*n* = 28). We tried to keep the same grids from year to year but we had to relocate some of them for various reasons (e.g. logging, loss of accessibility) during the study. Thus, the sample size was 40, 40 and 41 grids in 1998, 1999 and 2000 respectively. We trapped during four periods in 1998 and three in 1999 and 2000, each year between late May and mid-September. This totalled approximately 75,000 trap nights. We also used data from seven grids trapped in 1996 and 1997 by Richer et al. (2002) in two strata (Deciduous and Coniferous) of TRAP to extend density estimates in this site to five years.

Statistical analysis

We compared the number of small mammals captured with repeated-measures ANOVA to determine whether abundance varied between areas, strata and years, including the interactions between these factors (Proc MIXED, SAS Institute, 1999), after having square-root transformed data for each species to normalize residuals. We compared abundance of small rodents using the number of different individuals of each species captured because the probability of capture based on the Chao estimator (Chao, 1987) did not differ between areas (χ^2_2= 0.142, P = 0.931; χ^2_2= 0.909, P = 0.635) or years (χ^2_4= 0.271, P = 0.845; χ^2_4= 0.123, P = 0.915) for red-backed voles and deer mice, respectively.

The overall correction factor for three-night trapping averaged 2.021 (±0.003 (SE)) for red-backed vole and 2.308 (±0.026 (SE)) for deer mouse. In order to increase sample size when estimating density, we estimated the number of different small rodents we would have captured in grids that were trapped for one night if grids had been trapped for three consecutive nights by fitting a Poisson regression to data collected on three-night grids. We computed the R^2 value between predicted and observed values to determine how the adjusted model fit the data ($R^2 = 33\%$). We then conducted repeated-measures ANOVAs excluding or including predicted values, and the results were similar. We used predicted or true numbers of small mammals captured after three nights to estimate the density of each species by multiplying the average number of individuals captured over three nights per species and per grid by each species' correction factor and then dividing the product by the effective grid size (1.29 ha). We estimated the standard error of the density according to the formula provided by Mood et al. (1974) for the product of two estimates.

For grids trapped during at least three years (TRAP: n = 14; PROT: n = 12), we estimated the temporal variation in abundance of each species using an index of cyclicity (e.g., Hansson and Henttonen, 1985) with the formula:

$$s = \sqrt{\frac{\sum (\log \mathrm{N}_i - \overline{\log \mathrm{N}_i})^2}{n-1}}$$

where s is the index of cyclicity, N_i is the small mammal abundance in late summer-early autumn in year i, and n is the number of years.

We estimated the survival rate of red-backed voles between consecutive trapping periods by fitting a robust, open-population model with the help of a log-linear approach

(Proc GENMOD, SAS Institute, 1999; Rivest and Daigle, 2004). Due to small sample sizes, we had to restrict the analysis to 1999 and 2000 and pool strata. We used the chi-square test to compare estimates of survival rate between areas.

Results

Species captured

Red-backed voles (n = 2,349) and deer mice (n = 438) dominated among small rodent captures. The red-backed vole was the only species for which the sample size allowed us to estimate survival rates. We also captured 620 individuals from five other species (red squirrel, northern flying squirrel, eastern chipmunk, meadow vole and woodland jumping mouse), but low capture rates precluded any statistical analysis of abundance.

Abundance and survival

Numbers of red-backed voles per grid did not vary between areas ($F_{1,\,38} = 2.51$, $P = 0.121$) but differed between years ($F_{2,\,41} = 5.11$, $P = 0.010$; Table 2) and between strata, both when excluding ($F_{2,\,38} = 6.07$, $P = 0.005$) and including PCThinning (1999 and 2000 only: $F_{3,\,39} = 5.86$, $P = 0.002$). Over the three growing seasons, vole density was higher in coniferous stands than in other strata. Overall density remained stable from 1998 to 1999 ($t_{41} = -\ 0.71$, $P = 0.484$) but decreased slightly in 2000 ($t_{41} = 3.06$, $P = 0.004$). When including the data collected in TRAP during the two years preceding this study, vole density increased from 1996 to 1997 ($t_{11} = -\ 3.18$, $P = 0.009$; Figure 1) and remained relatively stable thereafter ($F_{4,\ 11} = 3.35$, $P = 0.050$). For this species, the mean index of cyclicity per grid averaged 0.33 ± 0.17 and 0.35 ± 0.18 in TRAP and PROT, respectively. Survival rates of red-backed voles did not differ between areas for any interval between small mammal trapping sessions (Table 3). In 1999, survival over the entire summer averaged 0.09 and 0.06 compared to 0.07 and 0.03 for 2000 in TRAP and PROT, respectively. The probability of surviving the winter of 1999-2000 averaged 0.03 in both study areas.

Deer mouse density exhibited an area × year interaction ($F_{2,\ 41} = 3.81$, $P = 0.031$), tending to be more common in PROT than TRAP, especially in 1999 ($t_{41} = 2.21$, $P = 0.033$;Table 2). For five consecutive summers in TRAP, deer mouse density varied between years ($F_{4,\ 11} = 5.27$, $P = 0.013$). Density was significantly higher in 1997 than 1996 ($t_{11} = -3.62$, $P = 0.004$) and 1998 ($t_{11} = -3.74$, $P = 0.003$) but did not differ from 1998 to 2000 (Figure 1). The deer mouse cyclicity index was 0.36 ± 0.11 in TRAP and 0.31 ± 0.19 in PROT. Throughout the study, deer mice used all strata equally whether including PCThinning ($F_{3,\ 39} = 0.60$, $P = 0.616$) or not ($F_{2,\ 38} = 1.02$, $P = 0.369$).

Discussion

We sampled two small rodent populations using 54 grids in two areas that covered at least several hundred km^2. We think that it was an appropriate scale for studying small mammal population dynamics with respect to predation. We tested four predictions derived from the hypothesis that the guild of terrestrial and avian predators maintains small mammal populations at relatively low and non-cyclic densities. Since the study areas were situated in the south of the boreal forest, a relatively productive area, we expected to find non-cyclic, low-density populations compared to those of northern latitudes. In addition, we predicted that small rodent densities and survival would be higher in TRAP than in PROT, due to furbearer trapping. In agreement with our first two predictions, red-backed vole and deer mouse densities were relatively low and stable during the study, but, contrary to our last two predictions, densities and survival rates did not differ between areas. Thus furbearer harvest in TRAP did not have a direct impact on the dynamics of small rodent populations. Based on the abundance of terrestrial carnivores in our study areas, we suggest that trophic links may be more complex than we expected. As a result, we can not reject the hypothesis of top-down trophic dominance through predation although some habitat differences between sites existed.

No evidence for cyclicity

From 1996 to 2000, deer mice and red-backed voles did not exhibit marked changes in numbers in TRAP. The cyclicity index of both species remained below 0.5, which suggests the absence of cycles (Henttonen et al., 1985), even though our time-series was only five years long. For deer mouse, this result is in accordance with the other studies, which described relatively stable populations of *Peromyscus*, even when vole populations were cyclic (Krebs and Wingate, 1985; Gilbert and Krebs, 1991). However, red-backed vole densities exhibited little fluctuation (amplitude ≈ 2 to 4:1) compared to the huge variations (e.g., 200:1) observed during the same time span in some cyclic populations (e.g., Boonstra et al., 1998). In addition, red-backed vole densities from both areas (≈ 15 to

20 ind/ha or ≈ 20 to 40 ind/1000 trap nights) were, on average, five to ten times lower than those observed during peaks in cyclic populations of closely related species (e.g., northern England, *Microtus agrestis* ≈ 150 to 200 ind/ha: Lambin et al., 2000; northwestern Finnish Lapland, *C. rufocanus* ≈ 100 to 260 ind/1000 trap nights: Hansen et al., 1999; northeastern Hokkaido, Japan, *C. rufocanus* ≈ 100 to 230 ind/1000 trap nights: Saitoh et al., 1998). On the other hand, densities were similar to those measured at low latitudes for populations exhibiting no multiannual cycles (e.g., Ontario, Canada, *C. gapperi* ≈ 10 to 50 ind/1000 trap nights: Fryxell et al., 1998; Bialowieza, Poland, *C. glareolus* ≈ 10 to 50 ind/ha: Jedrzejewski and Jedrzejewska, 1993; southwestern Hokkaido, Japan, *C. rufocanus* ≈ 10 to 60 ind/1000 trap nights: Saitoh et al., 1998).

Densities of the two most abundant species that we sampled did not fluctuate in parallel over time, and showed sporadic eruptions. A similar dynamic was found in Ontario (Fryxell et al., 1998) and in other regions of low latitude (e.g., Jedrzejewski and Jedrzejewska, 1996; Saitoh et al., 1998; Garsd and Howard, 1981; Brooks et al., 1998). Deer mice may have erupted in 1997 (Figure 1) as seen in neighboring New Brunswick ≈120 km further southeast (Bowman et al., 2000). The synchrony between deer mouse populations in Québec and New Brunswick suggests that a factor such as climate could play a role at the large scale.

Over the three growing seasons, vole density was highest in coniferous habitats whereas deer mice used all strata equally. If predation drives population dynamics of small mammals, it can be hypothesized (as suggested by Hansson (1997)), that the density of different species in various habitats reflected habitat-dependent survival. We will examine elsewhere how small rodent densities are related to habitat characteristics in our study areas.

Trapping effects and predation risk

In general, trapping reduces the abundance of harvested species (Hodgman et al., 1994; Frank and Woodroffe, 2001; Johnson et al., 2001) and consequently prey populations respond with increased density and survival (e.g., Krebs et al., 1995; Boertje et al., 1996; Hayes et al., 2003). Based on fur sales, we estimated that trappers removed approximately 250 animals /1000 km^2 /year in TRAP during the three years of our study (i.e., 27 coyotes, 103 red foxes, 63 fishers, 38 *Mustela spp.* and 19 individuals from other carnivore species). Although survival of red backed voles tended to be higher in TRAP than PROT during the late summer of 1999 and 2000 (Table 3), we did not find any evidence that furbearer trapping affected the vital rates of small rodents. This contrasts with findings on snowshoe hares in a companion study where predation was the main cause of mortality of hares and hare density was twice as high in TRAP than PROT (Etcheverry et al., 2005).

Our assumption that furbearer trapping would negatively affect the entire guild of terrestrial carnivores and result in higher survival and densities of small rodents may have been too simplistic. Among the 12 predator species inhabiting the study areas, six (coyote, red fox, Canada lynx, fisher, great-horned owl and red-tailed hawk) are relatively large in body size and are generalist predators or mostly feed on prey larger than small mammals or on berries (Table 1). The remaining species were either small mustelids or avian predators (American marten, long-tailed weasel, ermine, barred owl, northern saw-whet owl and

American kestrel) that prey primarily on small mammals (Table 1). In Fennoscandia, most vole mortality is due to small mustelids (Norrdahl and Korpimäki, 1995; Steen, 1995) or avian predators (Korpimäki and Norrdahl, 1991) that are considered nomadic specialists with a strong regulating potential (Korpimäki and Norrdhal, 1991). Since furbearer trapping mainly removed the large generalist carnivores, trapping could have relaxed intra-guild predation on small mustelids. Intra-guild predation has been identified as the major factor in population dynamics of some smaller carnivore species (e.g., Fedriani et al., 2000; Ray and Sunquist, 2001; Henke and Bryant, 1999) and has caused substantial mortality of monitored long-tailed weasel and ermines in our study areas (10 % over 37 days: St-Pierre, 2003). Weasels use more various habitats in TRAP than PROT (St-Pierre, 2003) and may have responded numerically to reduced intra-guild predation, based on snow tracking (Etcheverry et al., 2005; Table 1). We suggest that small mustelids compensated for the removal of large furbearers (such as coyotes and fishers) in TRAP and for the greater abundance of barred-owl in PROT (Table 1), so that the predation risk for small mammals was similar to that in PROT.

Although our results did not support our last two predictions, we can not reject the hypothesis that small mammal populations in our study areas were regulated at low densities by avian and terrestrial predators. Contrary to snowshoe hare (Etcheverry et al., 2005), partial exclusion of predators by trapping was not sufficient to demonstrate the top-down trophic dominance which predators are known to impose on populations of small rodents (Huitu et al., 2003). In addition, the low abundance of each small rodent and predator species reduced the statistical power of this study. Nevertheless, our study suggests that complex interactions existed among predator species and that the ecosystem exhibited resilience so that the presence of trapping in one area did not affect significantly the population dynamics of small rodents, which remained stable and at low densities, as in the untrapped area.

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Table 1:. Relative abundance and food habits (based on the literature) of the main avian and terrestrial predators in two areas of southeastern Québec that differed with respect to furbearer harvest (TRAP = trapped area; PROT = protected area).

Species	Type of predator	Abundance[a]	Proportion of small mammals in the diet
Coyote	Generalist	TRAP < PROT	Relatively low, depending on season and availability of other food sources (e.g., Leporids, Tetraonids, berries; Bekoff ,1982; Tremblay, Crête and Huot, 1998)
Red fox	Generalist	TRAP ≈ PROT	Relatively low, depending on season and availability of other food sources (e.g., Leporids, Tetraonids, berries; Samuel and Nelson, 1982)
Canada lynx	Hare specialist	TRAP > PROT	Generally low, depending on availability of Leporids (McCord and Cardoza, 1982)
Fisher	Generalist	TRAP < PROT	Relatively low, depending on season and availability of other food sources (e.g., Leporids, carrion; Strickland et al., 1982 a)
American marten	Semi-generalist	TRAP ≈ PROT	Relatively high, depending on season and availability of other food sources (e.g., Sciurids, berries; Strickland et al., 1982b)
Mustela spp.	Small mammal specialist	TRAP > PROT	50 to 94 % of diet (Svendsen, 1982)
Great-horned owl	Generalist	TRAP < PROT	7 to 23 % of diet, prefer larger prey (e.g., Leporids, Sciurids, Tetraonids; Houston, Smith and Rohner, 1998)
Barred owl	Semi-generalist	TRAP << PROT	30 to 98 % of diet, depending on season and availability of other prey species (e.g., Sciurids, birds; Mazur and James, 2000)
Northern saw-whet owl	Small mammal specialist	TRAP ≈ PROT	90 % of diet (Cannings, 1993)
Red-tailed hawk	Generalist	TRAP >> PROT	3 to 38 % of diet, prefer larger prey (e.g., Leporids; Preston and Beane, 1993)
American kestrel	Semi-generalist	TRAP ≈ PROT	15 to 79 % of diet, depending on availability of insects (Smallwood and Bird, 2002)

[a] Etcheverry et al., 2005.

Table 2. Mean small-mammal density per ha (± SE (n)) in two areas of southeastern Québec that differed with respect to furbearer harvest (TRAP = trapped area; PROT = protected area) during summers of 1998 to 2000.

Species	Year	TRAP	PROT
Red-backed vole	1998	16.52 ± 0.02 (21)	16.54 ± 0.02 (19)
	1999	20.46 ± 0.02 (20)	14.94 ± 0.02 (20)
	2000	14.74 ± 0.02 (20)	12.21 ± 0.02 (21)
Deer mouse	1998	2.33 ± 0.07 (21)	3.88 ± 0.09 (19)
	1999	4.43 ± 0.06 (20)	6.23 ± 0.03 (20)
	2000	2.80 ± 0.10 (20)	2.29 ± 0.08 (21)

Table 3. Survival rates (± SE) of red-backed voles in two areas of southeastern Québec that differed with respect to furbearer harvest (TRAP = trapped area; PROT = protected area) during five intervals between 1999 and 2000.

Interval (year)	Duration	TRAP	PROT	χ^2	*P*
May (1999) - July (1999)	~ 50 days	0.18 ± 0.08	0.30 ± 0.11	0.80	0.372
July (1999) - September (1999)	~ 50 days	0.50 ± 0.15	0.20 ± 0.07	3.17	0.075
September (1999) - May (2000)	~ 250 days	0.03 ± 0.01	0.03 ± 0.01	0.01	0.920
May (2000) - July (2000)	~ 50 days	0.26 ± 0.08	0.33 ± 0.10	0.27	0.605
July (2000) - September (2000)	~ 50 days	0.26 ± 0.10	0.10 ± 0.05	1.94	0.164

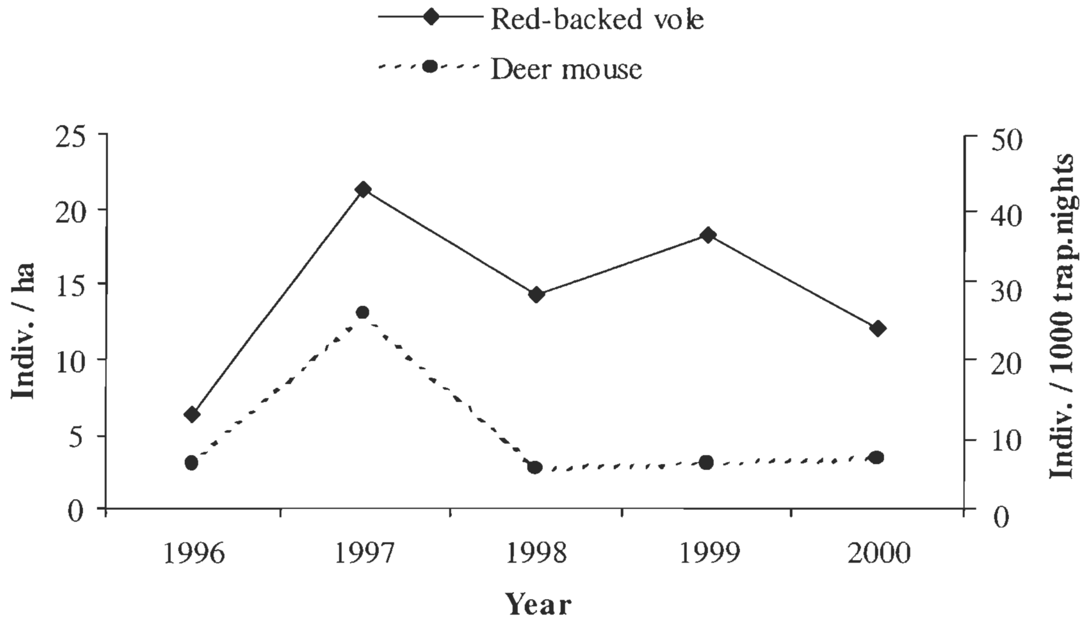

Figure 1. Red-backed vole and deer mouse density (individuals per ha, and individuals per 1000 trap nights) between 1996 and 2000 in seven trapping grids of TRAP, southeastern Québec.

CHAPITRE IV

RESPONSE OF SMALL MAMMALS TO CLEARCUTTING AND PRECOMMERCIAL THINNING IN MIXED FORESTS OF SOUTHEASTERN QUÉBEC[1]

Abstract

The impact of logging on habitat characteristics, species richness, and population dynamics of small mammals remains poorly understood. We studied the response of small mammal populations, including snowshoe hare, to two silvicultural treatments commonly used in northeastern North America, i.e., clearcutting with protection of advanced regeneration and soils (CPRS) and precommercial thinning (PCT). We thus compared stands recently harvested (≤ 10 years) by CPRS or PCT with established stands dominated by deciduous or coniferous tree species, in two large blocks of mixed forests. CPRS removes all merchandable trees in mature stands and minimizes soil disturbance and destruction of regenerating vegetation, whereas PCT reduces the density of young overstocked stands to accelerate growth of residual poles. We measured habitat components and abundance of snowshoe hares and other small mammals in the four stand types. Trees

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[1] Etcheverry, P., J.P. Ouellet and M. Crête, this article will be submitted for publication in an appropriate journal.

(DBH ≥9 cm) were very rare in CPRS and PCT stands whereas the structure and complexity of the understory were higher in CPRS while it was lower in PCT relative to closed stands. Our results indicated that small mammals responded to those perturbations in species-specific maner. The overall response in terms of relative abundance and species richness suggests that PCT had a greater negative impact on the small mammal community than CPRS, which had a more neutral effect compared to closed stands in our study areas. The negative impact of PCT likely results from the fact that this treatment, which normally follows CPRS by approximately 10 years, reduces structural heterogeneity and results in a simplification of the understory structure. Forest managers should thus exclude some stands from PCT after CPRS or natural perturbations, in order to maintain ecosystem diversity at the landscape level.

Introduction

Boreal populations of small mammals, including lagomorphs, tend to exhibit latitudinal gradients of cyclicity (rodents: Hanski et al., 1991; Stenseth, 1999; snowshoe hare (*Lepus americanus*): Keith, 1990; Murray, 2000) with predation playing a central role in this pattern (Hanski et al., 2001; Krebs et al., 1995). Small mammals, which represent the prey basis for many terrestrial and avian predators (Hörnfeldt et al., 1990; Keith, 1990; Tannerfeldt and Angerbjörn, 1996; Etcheverry et al., 2005), are both consumers of plants, lichens, fungi and invertebrates (Ericson, 1977; Gebczynska, 1983; Hansson, 1988; Keith, 1990) and dispersers of seeds and spores (Kirkland, 1990; Ostfeld et al., 1997).

Consequently, both predation and food supply have been identified as factors affecting small mammal habitat use within forested landscapes (Keith et al., 1984; Hik, 1995; Löfgren, 1995; Morris and Lundberg, 1996; reviewed by Lima, 1998; Beaudoin et al., 2004). Habitat selection by small mammals should therefore be strongly dependent on factors that provide cover (e.g., refuge against predators) and food sources (Hansson, 1982; Morris, 1996; Keith, 1990; Beaudoin et al., 2004) and could reflect habitat-dependent survival (Hansson, 1997; Beaudoin et al., 2004).

Habitat components are influenced by various natural and anthropogenic disturbances, including logging which has become the dominant perturbation in many parts of boreal and mixed forests over the last century. Clearcutting was the most widespread silvicultural practice over much of eastern Canada during recent decades (Homyack, 2003). However, since the adoption of new forest-harvesting standards in Québec in 1996, operators must use clearcutting with protection of advanced regeneration and soils (CPRS). Nevertheless, this sylvicultural treatment still represents a major disturbance since almost all trees are harvested. CPRS thus opens up the forest canopy and increases light levels in the shrub and ground layers but residual trees and shrubs provide residual cover for many species of terrestrial wildlife. Precommercial thinning (PCT), which reduces the density of young overstocked stands to accelerate growth of residual poles (Brissette et al., 1999), became rapidly widespread in Québec during the 1990s (Canadian Council of Forest Ministers, 2002). Between 1999 and 2003, approximately 1000 km^2 were subject to PCT annually (Parent and Fortin, 2003) and in some regions, almost all eligible stands were thinned. PCT takes place approximately 10 years (8 to 20 years) after a perturbation, mainly a CPRS, and partly reopens the cover close to the ground for some years. Because a large fraction of Québec forests is affected by these treatments, CPRS and PCT could significantly modify the habitat for many animal species, and could therefore influence species richness and population dynamics of small mammals.

Snowshoe hares occupy various habitats but prefer dense shrubby stands that are rich in food and cover (Keith, 1990; Ferron and Ouellet, 1992; Beaudoin et al. 2004), while small rodents and insectivores likely select habitat with respect to structure and abundance of woody debris, vegetation and cavities (e.g., Miller and Getz, 1977; Pucek, 1983; Harmon et al., 1986; Kirkland, 1990; Batzli and Lesieutre, 1995; Ecke et al., 2001). Clearcutting and PCT have the potential to modify the composition and structure of habitats (Ferron et al., 1994; Sullivan et al., 2001a; Homyack, 2003), but small mammal communities appear resilient to these disturbances. Although both species composition and abundance of small mammals may be influenced by these treatments (Telfer, 1974; Monthey, 1986; Sullivan and Sullivan, 1988; Thompson, 1988; Kirkland, 1990; Koehler et Brittell, 1990; Archambault et al., 1998; Hansson, 1999; Homyack, 2003), the effects vary from one species to another (Clough, 1987; Kirkland, 1990; Pagels et al., 1992; Darveau et al., 2001; Homyack, 2003; Fuller et al., 2004). In general, few years after perturbation, the overall abundance of small mammals tends to increase in treated stands (Telfer, 1974; Monthey, 1986; Thompson, 1988; Kirkland, 1990; Koehler et Brittell, 1990; Homyack, 2003; Fuller et al., 2004), while the initial response in terms of diversity or species richness does not show any consistent pattern among studies (reviewed in Kirkland, 1990; Pagels et al., 1992; Sekgororoane and Dilworth, 1995; Génier and Bergeron, 1996; Potvin and Breton, 1997;

Sansregret, 2000).

Small mammals are appropriate for examining the response of animal communities to forest management practices due to their multiple ecological roles. The impact of CPRS and PCT on habitat characteristics, species richness, and population dynamics of small mammals remains poorly understood. We thus studied snowshoe hare and small mammal populations in two large blocks of mixed forests in southeastern Québec that were heavily managed for timber production. We anticipated that both CPRS and PCT would have a negative effect on some species of small herbivores and insectivores. We aimed at 1) documenting how the two treatments affected forest habitats, 2) determining how the treatments affected species abundance and richness and 3) identifying which habitat components influenced species abundance. Lastly, we discuss our findings in light of forest management practices in northeastern North America with implications for maintenance of biodiversity at the local and landscape level.

Methods

Study area

This study was performed in two large forested blocks, located 80 km apart, on the south shore of the St. Lawrence River, Québec. Furbearers had been continuously trapped in the first study area (TRAP: 47°36’ lat N, 69°21’ long W; ≈800 km^2), whereas trapping had been prohibited in the other area (PROT: 48°08’ lat N, 68°37’ long W; ≈270 km^2) since the creation of the Duchénier Game Reserve in 1977. Trapping affected habitat use

(Beaudoin et al., 2004) and density of snowshoe hares (Etcheverry et al., 2005) due to reduced predation risk but had no obvious impact on abundance of other small mammal species (Etcheverry et al., 2004).

Both areas are characterized by gently rolling hills, with the altitude varying between 220 and 610 m ASL. Mixed forests typical of the transition zone between northern hardwood forests and boreal forests covered the two areas (Marie-Victorin, 1995). Annual temperature averages 2.5°C and precipitation varies between 900 mm and 1,200 mm, of which 33% falls as snow. Snow cover persists from early December to late April (Environment Canada, 1993). Spruce budworm (*Choristoneura fumiferana*) outbreaks and logging affected both areas extensively during the last century and created a mosaic of relatively young forest stands with a network of gravel roads and trails. Dominant tree species were similar in the two areas: balsam fir (*Abies balsamea*), red and white spruce (*Picea rubens; P.glauca*), paper and yellow birch (*Betula papyrifera; B. alleghaniensis*), trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), red maple (*Acer rubrum*) and sugar maple (*A. saccharum*).

Small mammals present in the two study areas essentially included snowshoe hare, northern flying squirrel (*Glaucomys sabrinus*), red squirrel (*Tamiasciurus hudsonicus*), eastern chipmunk (*Tamias striatus*), southern red-backed vole (*Clethrionomys gapperi*), meadow vole (*Microtus pennsylvanicus*), deer mouse (*Peromyscus maniculatus*), woodland jumping mouse (*Napaeozapus insignis*), northern short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*), smoky shrew (*S. fumeus*) and pygmy shrew (*S. hoyi*).

These small herbivores and insectivores were preyed upon by at least 12 species of avian and terrestrial carnivores (Etcheverry et al., 2004).

Vegetation sampling

We used a stratified random sampling design based on 1:20,000 forest maps. Over 95% of the stands in our study areas had been managed with various silvicultural treatments during the last century. Thus all forest stands were relatively young and could be grouped into four strata: ≤10 years since CPRS, ≤10 years since PCT, established forest stands dominated by deciduous species (Deciduous stands: DS >10 years since logging) and established forest stands dominated by conifers (Coniferous stands: CS >10 years since logging). The age varied among stands sampled but most of them were comprised in the 40-60 years old age class. We sampled the vegetation in 34 stands (17 in each study area) that were also used to trap hares and small mammals (Etcheverry et al., 2004, see below) during the summers of 1999 (20 stands) and 2000 (14 stands). Sampling plots were systematically distributed at 50-m intervals over the trapping grids used to estimate hare and small mammal abundance in each stand. In each sampling plot, we measured 21 habitat variables within four layers (tree, shrub, herb and forest floor) that could potentially provide cover (i.e., all vegetation restricting the visibility or movement of potential predators) or food for hares and small mammals.

We first laid out a 15-m linear transect, originating from each plot center and parallel with trapping lines (see below) to estimate canopy closure for deciduous and coniferous trees separately (trees >3 m high; in %). We then noted the presence of foliage over 10 points positioned at 1.5-m intervals along the transect. We estimated density of lateral cover at 3 m and 15 m for two height strata: 0-50 cm and 51-100 cm (in %), using a banner with 10, 10×10-cm black and white squares (Nudds, 1977; Wolfe et al., 1982). We also estimated tree density and basal area of deciduous and coniferous trees using a plotless method and a 2× metric prism (Grausenbaugh, 1952). We determined pole density (DBH = 1-9 cm) of all species by counting young stems within a 12.6-m^2 circular plot. We estimated the dry biomass (g) of all living plants between the ground and 1.5 m in height using simple and multiple regression models in which vertical and lateral coverage served as independent variables (Rouleau et al., 2002). We measured vertical and lateral coverage using a 2-m line transect placed over the plot center. Plants were identified to species and divided into seven sub-groups: foliage of conifers, including twigs above 50 cm; foliage of conifers, including twigs below 50 cm; foliage of deciduous shrubs and trees above 50 cm; foliage of deciduous shrubs and trees below 50 cm; ferns, lycopods and equisetaceae; herbs; and graminoids. We also estimated percent ground cover of litter, coarse woody debris (CWD; >10 cm) and other components (rocks, lichens, mosses, fallen branches, bare soil or sand) along the 2-m line transect.

Small mammal abundance and species richness

Abundance and species richness of small mammals, including snowshoe hares, were estimated using capture-mark-recapture (CMR) and removal trapping (for shrews) during the summers of 1998, 1999 and 2000 in 54 stands. All captured species were considered when estimating species richness. However, as our census techniques were not aimed to capture sciurids and small shrews, we focused on hare, red-backed vole, meadow vole, deer mouse, woodland jumping mouse and short-tailed shrew to estimate abundances. Trapping grids were randomly allocated to at least five forest stands in each of the four forest strata in each area. Selected stands were used provided they were accessible on the ground and large enough to include a 300×400-m grid. In each stand, we placed a grid of 20 Tomahawk traps systematically distributed at 100-m intervals along four lines in order to capture hares (n = 48 stands). Between the central two lines of Tomahawk traps, we also placed 100 Sherman traps at 10-m intervals in a 10 x 10 grid (Richer et al., 2002) to capture small rodents and shrews (n = 54 stands, i.e., 48 + 6 stands surveyed exclusively with Sherman traps). Effective grid sizes (Brooks et al., 1998) covered approximately 23 ha and 1.29 ha for hares and small rodents, respectively (Etcheverry et al., 2004; 2005).

Because abundance was low in some grids, we used three types of trapping grids to maximize precision of our estimates (see below): 1) grids trapped only once for one or three nights (hares: *n* = 10; rodents and insectivores: *n* = 8); 2) grids trapped for one night during at least one growing season (hares: *n* = 12; rodents and insectivores: *n* = 18); and 3) grids trapped for three nights during at least one growing season (hares: *n* = 26; rodents and insectivores: *n* = 28). We attempted to maintain the same grids from year to year but we were forced to relocate some grids because of logging or loss of access during the course of the study. Thus, the sample sizes were 28, 32 and 32 grids for hares and 40, 40 and 41 grids for rodents and insectivores in 1998, 1999 and 2000, respectively. We trapped during four periods in 1998 and three periods in 1999 and 2000, between late May and mid-September, for a total of approximately 100,000 trap nights.

Tomahawk traps were baited with a piece of apple and alfalfa, whereas peanut butter replaced alfalfa in Sherman traps. Both types of traps were visited daily. Captured hares and small rodents were identified to species, weighed, sexed, marked with tags (one tag between toes of each hind-foot for hares (Keith et al., 1968) and one tag on each ear for small rodents) and released at the point of capture. Shrews, when captured alive, were removed and released a few kilometres from trapping grids. The Animal Care Committee of Université du Québec à Rimouski approved the handling protocol (# 09-20 and # 10-21).

Statistical analysis

We performed factorial ANOVAs to compare habitat variables between areas and among strata. We assumed a Poisson distribution (Proc GENMOD, macro GLIMMIX, SAS Institute, 1999) when variables included many zeros, otherwise we used the normal distribution with log- or square-root transformations when appropriate. In a few cases, we used non-parametric ANOVA (Proc MIXED, SAS Institute, 1999).

We compared numbers of the three most common species captured, i.e., snowshoe hares, red-backed voles and deer mice, with repeated-measures ANOVA to determine whether abundance varied between areas, strata and years, including all interactions between these factors. We compared abundances using the number of different individuals captured per species after one night because the probability of capture based on the Chao estimator (Chao, 1987; Rivest and Daigle, 2004) did not differ between areas or years (Etcheverry et al., 2004; 2005). We then computed an overall correction factor for three-night trapping sessions for each species (hare = 3.259 ±0.038; red-backed vole = 2.021 ±0.003; deer mouse = 2.308 ±0.026; Etcheverry et al., 2004; 2005), in order to estimate the mean number of individuals per grid. When computing standard errors of means, we took into account the fact that our density estimates combined the CMR technique and stratified random sampling (Etcheverry et al., 2004; 2005). We also expressed abundance as number of individuals captured per 100 trap-nights to standardize measurements to those of three less common species (meadow vole, woodland jumping mouse and northern short-tailed shrew) for which we could not estimate densities using the CMR technique. For the rarest species, we compared abundance between areas, strata and years with log-linear models using the Poisson distribution (Proc GENMOD, macro GLIMMIX, SAS Institute, 1999) to take into account the possibility of dependence among repeated observations within a grid. We compared species richness between areas, strata and years with a factorial ANOVA (Proc GLM, SAS Institute, 1999).

We related the abundance of the four most common small mammals to habitat variables using multiple regression analyses for each species (Proc REG, SAS Institute, 1999). We performed a forward stepwise analysis and included only significant variables ($P < 0.05$) in the final model that increased the adjusted R^2-value by at least 1%. We also included interaction terms in the analysis to ensure that relationships were uniform between areas and strata. Lastly, we tested the fit of the final models by including relative abundance of other small mammal species. We related small mammal numbers to habitat variables only for those years when we had sampled vegetation in a given grid.

Means are presented ±1 SE and P-values less than 0.05 were considered statistically significant.

Results

Impact of CPRS and PCT on habitat characteristics

No habitat variable differed significantly between the two areas (PROT and TRAP), neither as the main factor nor in interaction terms, hence we pooled grids from both areas when comparing habitat components between forest strata. Forest canopy was almost completely closed in CS and DS, with coniferous cover dominating in CS (51 %) and deciduous cover in DS (83 %; Table 1). Tree density (536 vs. 386 trees / ha) and basal area of coniferous trees (24 vs. 17 m^2 / ha) were both significantly greater in CS than DS. CPRS removed most trees and opened up the canopy. Deciduous and coniferous trees were equally rare and canopy closure averaged approximately 7% in CPRS. Logging left only 27 trees / ha, corresponding to a basal area of approximately 1 m^2 / ha. Stands treated with PCT did not differ significantly from CPRS stands with respect to characteristics of the tree layer.

CPRS did not stimulate much the growth of shrub foliage whereas biomass drop after PTC was not great enough to be significant (Table 1). CPRS seemed to favour pole recruitment but pole density exhibited much variability and did not differ significantly among strata (Table 1). PCT reduced pole density to levels measured in established stands. CPRS was mostly performed in coniferous stands and stimulated the growth of deciduous shrubs whereas coniferous biomass did not change statistically following treatment. During PCT, operators select conifers over deciduous species, which was reflected in the low biomass of deciduous species measured in PCT stands. Density of lateral cover of the shrub layer at 3 m, which was comparable between CS and DS, increased following CPRS and remained elevated in PCT. Density of lateral cover at 15 m did not vary between strata and was almost 100%.

Biomass of herbs, ferns and graminoids increased after CPRS and remained high in PCT. Although the biomass of deciduous seedlings and low shrubs increased in both CPRS and PCT stands compared to CS, biomass of coniferous seedlings was three times higher in PCT stands than CPRS and CS stands. Lateral cover of the herbaceous layer at 3 m increased in both CPRS and PCT compared to CS and DS.

CPRS resulted in increased proportion of CWD compared to PCT and DS but did not differ significantly from CS. Litter cover was intermediate in CPRS and PCT stands compared to DS and similar to that in CS.

Small mammal abundance and species richness

During the entire study, we trapped 752 snowshoe hares, 2,349 southern red-backed voles, 438 deer mice, 33 meadow voles, 48 woodland jumping mice, 442 northern short-tailed shrews and 991 individuals from six other species (squirrels, chipmunks and shrews). The number of hares captured per grid differed between areas ($F_{1,31} = 6.55$; $P = 0.016$) and years ($F_{2,26} = 8.88$; $P = 0.001$) but not between strata when excluding ($F_{2,31} = 1.64$; $P = 0.209$) or including PCT (1999 and 2000 only; $F_{3,32} = 1.79$; $P = 0.169$). Overall hare abundance was almost twice as high in TRAP than PROT ($t_{31} = 2.56$; $P = 0.016$). Number of hares increased between 1998 and 1999 ($P = 0.001$) but remained stable between 1999 and 2000 ($P = 0.600$). Although the difference was not significant, hares tended to be more abundant in CS and CPRS than in other strata (Fig. 1).

Numbers of red-backed voles did not vary between areas ($F_{1,\,38} = 2.51$, $P = 0.121$) but differed between years ($F_{2,\,41} = 5.11$, $P = 0.010$) and between strata both when excluding ($F_{2,\,38} = 6.07$, $P = 0.005$) and including PCT (1999 and 2000 only: $F_{3,\,39} = 5.86$, $P = 0.002$). Overall red-backed vole abundance remained stable from 1998 to 1999 ($P = 0.484$) but decreased in 2000 ($P = 0.004$) and was higher in CS and CPRS than in other strata (Fig. 1). Deer mice exhibited an area × year interaction ($F_{2,\,41} = 3.81$, $P = 0.031$), tending to be more common in PROT than TRAP, especially in 1999 ($t_{41} = 2.21$, $P = 0.033$). Abundance of deer mice did not differ between strata ($F_{2,\,38} = 1.02$, $P = 0.369$) throughout the study (Fig. 1).

Abundance of meadow voles and woodland jumping mice were low during the three years of our study (Fig. 1). Numbers captured per 100 trap-nights did not vary between areas (meadow voles: $\chi_1^2 = 0.21$; $P = 0.644$ and woodland jumping mice: $\chi_1^2 = 0.11$; $P = 0.739$), years ($\chi_2^2 = 1.65$; $P = 0.438$ and $\chi_2^2 = 2.73$; $P = 0.256$, respectively) or strata ($\chi_2^2 = 3.96$; $P = 0.138$ and $\chi_3^2 = 4.59$; $P = 0.204$, respectively). Since no meadow voles were captured within CS, we omitted this stratum from the statistical analysis for this species. Meadow voles tended to be more abundant in CPRS ($P = 0.011$) and PCT ($P = 0.053$) than in DS, whereas woodland jumping mice tended to be more abundant in DS than CPRS ($P = 0.135$), CS ($P = 0.064$) and PCT ($P = 0.028$; Fig. 1). Numbers of short-tailed shrews differed between years ($\chi_2^2 = 26.51$; $P < 0.001$) and exhibited an area × stratum interaction ($\chi_3^2 = 20.57$; $P < 0.001$). Over the study period, short-tailed shrews decreased significantly each year and were more abundant in closed (DS and CS) than in open stands (CPRS and PCT) in PROT, whereas the opposite occurred in TRAP (Fig. 1).

The index of species richness differed between strata ($F_{3, 39} = 4.60$, $P = 0.006$) with a higher number of different species captured per 100 trap-nights in DS and CPRS and fewer species in CS and PCT (Fig. 2).

Models predicting the abundance of small mammals

We developed reasonably well-adjusted models (Adjusted $R^2 = 0.24$ to 0.35; Table 2) to predict abundance of snowshoe hares, red-backed voles, deer mice and short-tailed shrews according to habitat characteristics and abundance of other mammal species. However, we could not adjust regression models for meadow voles or woodland jumping mice, likely due to their rarity.

Snowshoe hare and red-backed vole abundance were positively associated with coniferous trees in the canopy. Biomass of coniferous foliage above 50 cm was also related to hare abundance while the presence of woodland jumping mice also increased the probability of encountering hares. Besides coniferous canopy closure, red-backed vole abundance was positively related to presence of short-tailed shrews. Deer mouse abundance was positively related to CWD coverage and to presence of red-backed voles. Finally, we detected an interaction between abundance of short-tailed shrews and habitat strata ($F_{3, 33} = 4.48$, $P = 0.006$). Overall, short-tailed shrews tended to be more abundant in DS and PCT, and least abundant in CS. We found no other habitat variables to be significantly related to shrew abundance but presence of red-backed voles had a positive influence on shrew abundance.

Discussion

Forest management has been intensive in southeastern Québec during the last few decades so that the age class 0-30 years comprised 41% of forest stands, with very few mature and old-growth stands in our study area (OFBSL, 2003). The objective of this study was to document how two common sylvicultural treatments, CPRS and PCT, affected abundance and species richness of small mammals in treated stands compared to established mid-age or mature forest stands. Characteristics of the four types of stands differed markedly with respect to several variables from the canopy to the ground layer. Small mammals responded species-specifically to habitat differences between stand groups. The overall response in terms of relative abundance and species richness suggests that PCT had a greater negative impact on the small mammal community than CPRS, which had a more neutral effect compared to mature stands. Moreover, our regression models showed positive relationships between small mammals and some habitat components as well as positive associations between some small mammal species.

Effects of CPRS and PCT on habitat characteristics

CPRS substantially opened up the forest canopy and reduced both tree density and basal area. Increased light in the understory stimulated vegetation growth, particularly for the herbaceous layer. Lateral cover was therefore denser in CPRS than CS or DS. CPRS operations increased CWD and structural complexity of the understory during the first 10 years following disturbance. Other studies in similar forests have also revealed that clearcutting substantially increased woody debris (Ferron et al., 1994; Génier and Bergeron, 1996) and light intensity on the ground (Génier and Bergeron, 1996) and thereby favoured development of herbs, shrubs and seedlings. Thus, in addition to producing residual material that increased food availability, such as tree seeds and invertebrate prey (Monthey and Soutiere, 1985), stands treated with CPRS offered an improved structural complexity to small mammals living close to the ground.

In our study areas, PCT occurred on average 10.8 ±1.8 (*n* = 12) years after CPRS. Although thinning may increase stem diameter (Brissette et al., 1999; Pothier, 2002) and crown size (Brissette et al., 1999; Sullivan et al., 2001b), PCT tended to lower both pole density and plant biomass between the ground and 1.5 m in height to similar levels as those measured in DS and CS. Moreover, we observed a reduction in proportion of CWD in PCT compared to CPRS. Since no operations were performed to remove woody debris, this reduction was likely due to natural degradation. Our results support those of Homyack (2003), indicating that the application of PCT resulted in a reduction in structural complexity of the understory. As the total plant biomass in the 0-0.5 m height stratum remained high during the growing season, we believe that PCT did not negatively affect the availability of food for small herbivores, but rather the efficiency of stands to protect small mammals from predators was reduced, particularly during the dormant season. In our study areas, hares used tall herbs in conjunction with balsam fir as cover during summer, but only conifer twigs during winter (Beaudoin et al., 2004). Thus, over a relatively short period of time, CPRS and PCT represent two major perturbations that could potentially have opposite effects on small mammal population dynamics due to their inverse effects on refuge availability.

Effects of CPRS and PCT on small mammals

Snowshoe hare abundance was twice as high in TRAP than PROT due to a higher predation pressure in the latter area (Beaudoin et al., 2004; Etcheverry et al., 2005) but hare abundance remained relatively uniform between all strata in the two areas during summer. These findings indicate that vegetative characteristics within all strata were sufficient to maintain hares, which are generalists in habitat requirements during summer (Wolff, 1980; O'Donoghue, 1983) when food is widespread and cover is not limiting (Wolff, 1980; Litvaitis et al., 1985; Beaudoin et al., 2004). We found that hare abundance was related to biomass of coniferous foliage in the understory, which agrees with results of a detailed study on hare habitat in the study area (Beaudoin et al., 2004).

Red-backed voles occupied all strata and thus appeared to be generalists, as found in other parts of eastern North America (Fuller et al., 2004). However, this species exhibited a positive association with coniferous canopy closure and a marked preference for CS and CPRS, the two strata with high proportions of CWD. Our results are consistent with other studies which recognize red-backed voles as residents of coniferous forests and report positive relationships between voles and CWD or density of understory cover, two habitat components that most likely offer protection against predators (Maser et al., 1978; Clough, 1987; Nordyke and Buskirk, 1991; Lachowski, 1997; Bowman et al., 2000). PCT was less favourable for red-backed voles than CPRS. This agrees with findings from Wyoming

(Nordyke and Buskirk, 1991) but contradicts results from Maine where PCT stands supported higher densities of voles than clearcuts (Homyack, 2003).

Deer mice used all strata equally and we did not detect any influence of CPRS or PCT on their abundance, however deer mouse abundance was associated with presence of CWD. Fuller et al. (2004) suggested that CWD provides adequate cover for this species. Vickery (1981) found increased numbers of deer mice in stands with dense ground- and mid-story cover in Québec, in line with findings that this species can respond positively to clearcutting (Martell and Radvanyi, 1977; Martell, 1983; Kirkland, 1990) or partial harvesting (Fuller et al, 2004). Deer mice may respond minimally to PCT (Sullivan et al., 2001b; Homyack, 2003), as was the case in our study.

Abundance of meadow voles and woodland jumping mice were very low during the three years of our study. Although the trend was not statistically significant, meadow voles tended to be more abundant in CPRS and PCT than in older stands and this species was practically absent in CS. Meadow voles prefer grassland habitats (Adler and Wilson, 1989) so their presence in the two opened strata was presumably associated with an increased biomass of graminoids and herbaceous plants within those habitats, a pattern also observed elsewhere (Kirkland, 1990; Moses and Boutin, 2001). The abundance of woodland jumping mice did not vary significantly between strata although this species sometimes responds positively to clearcutting (Kirkland, 1990).

Captures of short-tailed shrews decreased significantly over the study period, likely due to the removal trapping, and we observed an area × stratum interaction. In PROT, short-tailed shrews were most abundant in DS, which is consistent with the usual preference of this species (Monthey and Soutiere, 1985). Because short-tailed shrews attempt to avoid desiccation, their distribution seems to be limited by moisture levels (Getz, 1961). Thus, deciduous stands with deep leaf litter should provide sufficient ground moisture and be favourable to this species. On the other hand, short-tailed shrews were most abundant in PCT and CPRS in TRAP, which also seems normal because shrew densities are generally associated with a complex understory consisting of dense herbaceous vegetation (Miller and Getz, 1977; Healy and Brooks, 1988; Kirkland 1990). We could not detect any relationship between abundance of this species and measured habitat variables. Thus, in our study, the response of short-tailed shrews to CPRS and PCT was not clear and its abundance is likely related to variables we did not measure. DS and PCT appeared to offer conditions favourable to short-tailed shrews in our study areas.

Heterogeneous environments generally enhance species richness (Kerr and Parker, 1997). Both CPRS and PCT improve heterogeneity at the landscape scale and thus could increase species richness (e.g., Carey and Johnson, 1995; Sullivan and Sullivan, 2001; Ecke et al., 2002). At the scale of forest stands, our results indicated that species richness, as estimated with 12 species of small mammals, remained relatively high in CPRS whereas richness decreased in PCT compared to CS and DS. CPRS, which removes the tree canopy but increases structural complexity of the understory, creates heterogeneity within stands at the scale of small mammals. On the contrary, PCT (which normally follows CPRS by approximately 10 years) reduces structural heterogeneity of the stand and results in a simplification of understory structure (Homyack, 2003), particularly during the dormant season. We found several positive associations among species of small mammals in our study areas once habitat variables had been taken into account, which suggests that certain habitat components (e.g., cover) influence the presence of several species in the same manner. Future studies should investigate which variables explain the positive associations we observed between pairs of small mammal species.

Management implications

The observed response of small mammals to CPRS and PCT in southeastern Québec was species-specific, as previously observed elsewhere (Clough, 1987; Kirkland, 1990; Pagels et al., 1992; Homyack, 2003; Fuller et al., 2004). However, the overall response in terms of relative abundance and species richness indicates that, in the short term, PCT had more negative effects on the small mammal community than CPRS, which had a more neutral impact compared to mature stands. By increasing structural complexity of the understory immediately above the ground, CPRS may have simultaneously increased cover against avian and terrestrial predators and provided additional food sources, whereas PCT reduced cover protection for several years. PCT thus may produce within-stand habitat conditions that were less favourable to small mammals than CPRS (Bujold, 2004; but see Homyack, 2003). Moreover, PCT likely also impacts other trophic levels through the multiple ecological roles that small mammals play in forest ecosystems, particularly as a prey base for carnivores. To maintain ecosystem diversity at the landscape level, forest managers should thus exclude some stands from PCT. This could prove to be particularly important because stands with high pole density are a common feature of mixed and boreal forests following natural disturbances.

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Table 1. Characteristics ($\overline{X}$ ± SE) of four forest strata sampled during summers 1999 and 2000 in two areas of southeastern Québec. CS = mid-aged, mature coniferous stands; DS = mid-aged, mature deciduous stands; CPRS = clearcut with protection of advanced regeneration and soils (≤ 10 years previously); PCT = precommercially thinned stands (≤ 10 years previously).

Variable		CS	DS	CPRS	PCT	Test statistic	P
Tree layer:							
Canopy closure (%):	Coniferous[1]	51^a ± 4	10^b ± 4	6^b ± 4	5^b ± 7	$F_{3,26} = 28.32$	< 0.001
	Deciduous[1]	29^b ± 5	83^a ± 6	8^c ± 5	7^c ± 9	$F_{3,26} = 39.24$	< 0.001
Tree density (# / ha):	Coniferous	461^a± 3	63^b ± 3	10^c ± 3	9^c ± 3	$F_{3,26} = 25.58$	< 0.001
	Deciduous	74^b ± 2	322^a± 2	17^c ± 2	$35^{b,c}$ ± 3	$F_{3,26} = 14.58$	< 0.001
Basal area (m^2 / ha):	Coniferous	19.6^a ± 2.0	2.9^b ± 0.9	0.3^b ± 0.2	0.4^b ± 0.1	$\chi^2_3 = 13.69$	0.003
	Deciduous	4.3 ± 1.1	14.4 ± 3.2	0.9 ± 0.3	1.4 ± 0.5	$\chi^2_3 = 7.21$	0.065
Shrub layer (%):							
Leaf biomass (g/m^2):	Coniferous	24.6 ± 5.8	17.5 ± 6.1	25.9 ± 6.1	12.4± 3.9	$\chi^2_3 = 2.05$	0.562
	Deciduous	3.7 ± 1.5	8.9± 2.1	13.8± 4.3	3.0± 0.8	$\chi^2_3 = 6.15$	0.104
Pole density (stems/ha)		4058 ± 557	6287± 1592	8515± 1512	5173± 318	$\chi^2_3 = 6.09$	0.108
Lateral cover at 3m (%): 50 to 100 cm high[1]		42^b ± 7	36^b ± 8	62^a ± 7	73^a ± 13	$F_{3,26} = 3.70$	0.024

Lateral cover at 15m (%): 50 to 100 cm high[1]		89± 42	90± 42	92± 37	100± 70	$F_{3,26} = 0.70$	0.560
Herb, seedling and low shrub layer:							
Leaf biomass (g/m^2):	Coniferous	$3.6^{b} \pm 0.8$	$0.4^{c} \pm 0.2$	$3.0^{b} \pm 1.1$	$11.8^{a} \pm 1.4$	$\chi^2_3 = 7.81$	0.050
	Deciduous	$2.3^{b} \pm 0.4$	$4.5^{a} \pm 0.7$	$5.0^{a} \pm 0.8$	$5.0^{a} \pm 0.9$	$\chi^2_3 = 8.69$	0.034
Ferns, lycopods and equisetaceae		3.6± 0.8	4.3 ± 1.4	6.8 ± 1.4	3.1 ± 0.7	$\chi^2_3 = 3.52$	0.318
Herbs		$4.5^{b} \pm 1.1$	$3.3^{b} \pm 0.8$	$8.9^{a} \pm 1.9$	$7.3^{a,b} \pm 3.0$	$F_{3,26} = 5.10$	0.006
Graminoids[2]		0.4 ± 3.3	0.0 ± 0.1	1.1 ± 5.6	1.4 ± 6.7	-	-
Lateral cover at 3m (%): 0 to 50 cm high[1]		$70^{b} \pm 5$	$62^{b} \pm 5$	$89^{a} \pm 5$	$95^{a} \pm 8$	$F_{3,26} = 8.78$	< 0.001
Lateral cover at 15m (%): 0 to 50 cm high[1]		96 ± 20	96 ± 20	99 ± 18	98 ± 34	$F_{3,26} = 0.49$	0.695
Floor layer:							
Coarse woody debris (%)		$12^{a,b} \pm 2$	$4^{c} \pm 1$	$16^{a} \pm 3$	$8^{b} \pm 1$	$\chi^2_3 = 9.79$	0.020
Litter (%)[1]		$65^{b} \pm 5$	$90^{a} \pm 5$	$74^{b} \pm 5$	$75^{a,b} \pm 8$	$F_{3,26} = 4.85$	0.008
Other components (%)		23 ± 2	6 ± 1	10 ± 1	17 ± 2	$\chi^2_3 = 2.56$	0.683

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[1] Parametric and non-parametric tests provided similar results.

[2] Absent from 93 % of plots, which precluded any statistical analysis.

[a,b,c] Different letters refer to strata that were significantly different ($P<0.05$) for each variable.

Table 2. Linear regression models predicting abundance of four small mammal species according to habitat variables (coniferous canopy closure (CCC), biomass of coniferous foliage above 50 cm (BCSup), coarse woody debris (CWD)) and relative abundance of other animal species (snowshoe hare (Hare), southern red-backed vole (RBVole), deer mouse (DMouse), northern short-tailed shrew (NSTShrew) and woodland jumping mouse (WJMouse)) within two areas (TRAP and PROT) of southeastern Québec. For northern short-tailed shrews, the final model varied between habitat strata. CS = mid-aged, mature coniferous stands; DS = mid-aged, mature deciduous stands; CPRS = clearcut with protection of advanced regeneration and soils; PCT = precommercially thinned stands.

Species	Model	Adj. R^2
Hare	$y = 0.476 + 0.217 \times CCC + 0.020 \times BCSup + 2.313 \times WJMouse$	0.35
RBVole	$y = 1.996 + 0.240 \times CCC + 0.157 \times NSTShrew$	0.25
Dmouse	$y = 0.633 + 2.031 \times CWD + 0.40 \times RBVole$	0.24
NSTShrew	$y = (CS: 0.127; DS: 0.759; CPRS: 0.296; PCT: 0.738) + 0.091 \times RBVole$	0.29

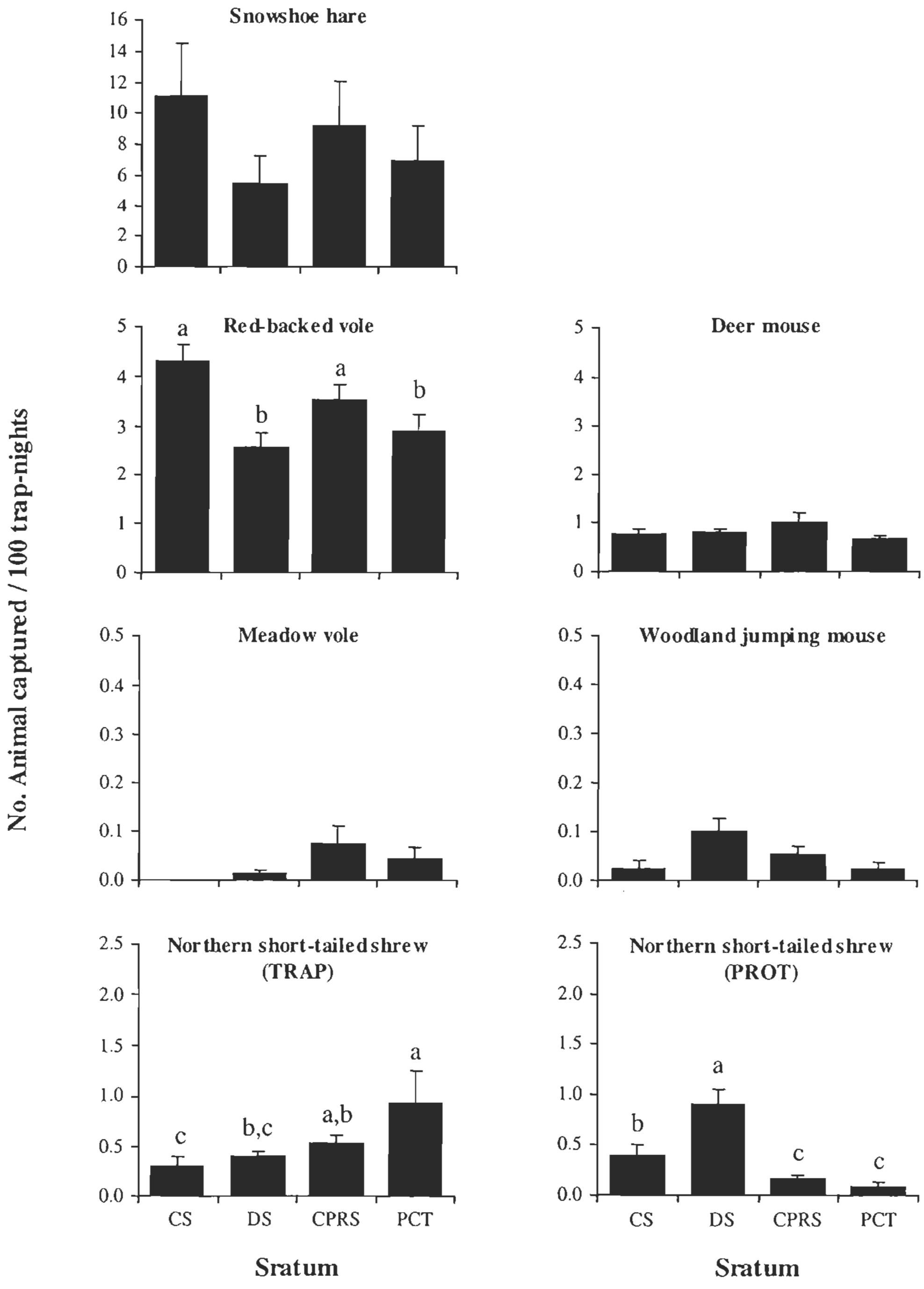

Figure 1. Index of abundance (number animals captured / 100 trap-nights +SE) of small mammals and hares according to forest strata (CS = mid-aged, mature coniferous stands; DS = mid-aged, mature deciduous stands; CPRS = clearcut with protection of advanced regeneration and soils; PCT = precommercially thinned stands) in two areas (TRAP, PROT) of southeastern Québec. Different letters refer to strata that were significantly different (*P*<0.05).

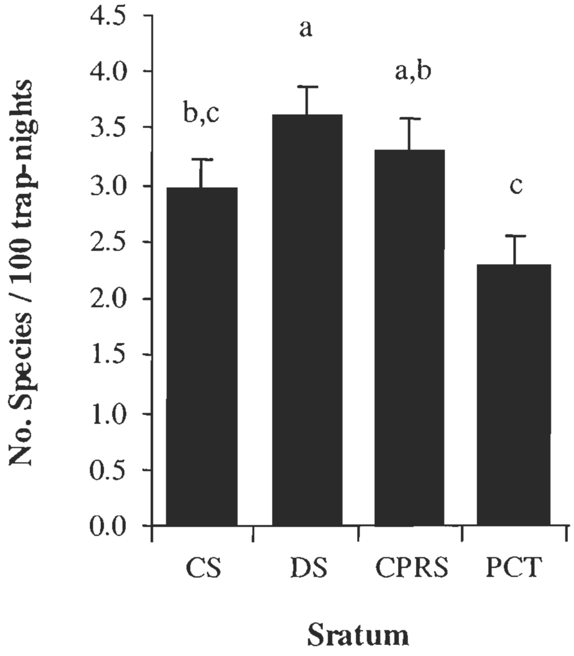

Figure 2. Mean number of different small mammal species (including snowshoe hare, northern flying squirrel, red squirrel, eastern chipmunk, southern red-backed vole, meadow vole, deer mouse, woodland jumping mouse, northern short-tailed shrew, masked shrew, smoky shrew and pygmy shrew) captured per 100 trap-nights (+SE) within four forest strata (CS = mid-aged, mature coniferous stands; DS = mid-aged, mature deciduous stands; CPRS = clearcut with protection of advanced regeneration and soils; PCT = precommercially thinned stands) in two areas of southeastern Québec. Different letters refer to strata that were significantly different ($P<0.05$).

CHAPITRE V

CONCLUSION GÉNÉRALE

Les principaux objectifs de ce travail étaient de décrire la dynamique des populations de lièvres et de petits mammifères de la zone de transition entre les forêts boréales et tempérées de l'est de l'Amérique du nord, et d'évaluer l'importance de la prédation dans cette dynamique. Nous souhaitions également analyser la réponse des lièvres et des petits mammifères au piégeage récréatif ou commercial des carnivores. Enfin, comme l'habitat de ces espèces peut être considérablement modifié par des pratiques forestières telles que la CPRS (coupe avec protection de la régénération et des sols) ou l'ÉPC (éclaircie précommerciale), nous voulions évaluer leur réaction face à ces perturbations.

Pour atteindre ces objectifs, nous avons utilisé deux territoires forestiers du sud-est du Québec, potentiellement différents au niveau de l'abondance des prédateurs terrestres. En effet, dans le premier (≈800 km^2), le piégeage des animaux à fourrure était autorisé de longue date, alors que dans le second (≈270 km^2) les animaux à fourrure étaient protégés depuis 1977. Chacun de ces territoires était également intensivement géré pour la production du bois et la CPRS ou l'ÉPC y étaient largement pratiquées. Ce dispositif nous a permis de mener une expérience dans laquelle le piégeage des animaux à fourrure fut considéré comme un moyen de contrôler l'abondance des prédateurs terrestres, alors que la

CPRS et l'ÉPC ont été perçues comme des causes potentielles de dégradation du couvert protecteur des proies. À l'intérieur des deux territoires nous avons classé les habitats en quatre strates (CPRS <10 ans, EPC <10 ans, forêts fermées > 10 ans à dominance de feuillus et forêts fermées > 10 ans à dominance de résineux) facilitant l'étude de l'effet des pratiques forestières sur l'habitat et la dynamique des populations de lièvres et de petits mammifères, en plus de permettre un échantillonnage aléatoire stratifié pour l'ensemble des inventaires que nous avons menés.

Afin d'évaluer le risque de prédation à l'intérieur de chaque territoire, nous avons estimé l'abondance relative des prédateurs aériens et terrestres. Pour ce faire, dans chaque territoire nous avons établi des stations de provocation vocale de rapaces diurnes et nocturnes systématiquement réparties le long des chemins forestiers. Chaque station a été inventoriée cinq à 12 fois par année, pendant trois années (1998, 1999 et 2000). En complément, à l'intérieur de chaque strate d'habitat, nous avons sélectionné aléatoirement au moins cinq peuplements dans lesquels nous avons effectué jusqu'à 16 campagnes de pistage hivernal, réparties sur trois années (1999, 2000 et 2001).

Dans chacun des peuplements sélectionnés aléatoirement, nous avons également effectué jusqu'à 10 campagnes de Capture-Marcage-Recapture (CMR) de lièvres et de petits mammifères, réparties en trois saisons estivales, afin d'en estimer les densités et la survie. Pour obtenir des précisions sur le taux de survie et les causes de mortalité des lièvres dans les deux territoires, nous avons marqué certains individus capturés en CMR avec des émetteurs radio et nous les avons suivis sur une base hebdomadaire, pendant deux ans.

Enfin, nous avons réalisé des inventaires de végétation à l'intérieur de parcelles systématiquement réparties dans 34 des peuplements utilisés pour les captures de lièvres et de petits mammifères, dans le but d'estimer l'impact des CPRS et des ÉPC sur les habitats et de faire un lien entre l'abondance des espèces proies et les caractéristiques de la végétation des milieux qu'elles occupaient.

Dans les sections qui suivent, nous présentons une analyse du dispositif de contrôle de la prédation, nous résumons les principaux résultats obtenus et discutons de leur contribution à l'avancement des connaissances sur la dynamique des populations de lièvres et de petits mammifères, et sur la réponse de ces espèces face à l'exploitation de leurs prédateurs et de leurs habitats. Nous discutons également de l'implication de nos observations pour la gestion des espèces et des habitats ciblés par ce projet, ainsi que des perspectives de recherche qui en découlent.

Dispositif de contrôle de la prédation

À partir des données recueillies lors des 470 km de pistage hivernal et de 595 heures de provocation vocale, nous avons estimé l'abondance relative des prédateurs terrestres et aériens. Les indices d'abondance montrent que les prédateurs de plus grande taille (i.e.: coyote, renard, pékan, martre, grand-duc et chouette rayée) ont été légèrement moins abondants dans le territoire piégé que dans le territoire non piégé, alors que ce fut l'inverse pour les mustélidés les plus petits (*Mustela spp.*) et la buse à queue rousse. Quant au lynx, il fut rare, mais en augmentation durant toute l'étude. L'abondance de la petite nyctale ainsi que celle de la crécerelle d'Amérique, deux prédateurs de petite taille, furent similaires dans les deux territoires.

Compte tenu de l'importance relative que chaque espèce de prédateur a vis-à-vis de chaque espèce proie, ces indices d'abondance suggèrent que les lièvres aient fait face à une pression de prédation plus faible dans le territoire piégé que dans le territoire non piégé (chapitre 2). Par contre, aucune évidence n'indique que cette situation ait aussi prévalu pour les petits mammifères. Ainsi, ces derniers auraient probablement subi une pression de prédation davantage comparable entre les deux territoires (chapitre 3).

Dynamique des populations de lièvres et de petits mammifères

Au sud de la forêt boréale nord-est américaine, au niveau de la transition vers les forêts tempérées, les milieux sont relativement productifs et, conformément à l'hypothèse EEH (Oksanen et al., 1999), la prédation exercée par une communauté abondante et diversifiée de prédateurs spécialistes et généralistes devrait régulariser les populations de proies et les maintenir stables, à faible densité. Selon cette perspective, la présence d'une activité de piégeage des animaux à fourrure réduisant l'abondance des prédateurs devait provoquer une augmentation des densités et de la survie des lièvres et des petits mammifères.

Notre dispositif de CMR nous a permis de capturer 752 lièvres et quelques 4300 individus provenant de 11 espèces de petits mammifères, pour un effort de ≈ 100 000 nuits-piège. Chez les petits mammifères, notre attention s'est essentiellement portée sur les espèces les plus abondantes, soit le campagnol à dos roux, la souris sylvestre et la grande musaraigne. Parallèlement, grâce à 26 369 jours-lièvre de suivi télémétrique réalisés sur 122 individus, nous avons obtenu des précisions sur le taux de survie et les causes de mortalité des lièvres adultes (>900g).

Nos données indiquent que les densités de lièvres (chapitre 2) et de petits mammifères (chapitre 3) sont restées relativement stables durant une période de trois ans dans chacun des territoires inventoriés, et même sur cinq ans (de 1996 à 2000) dans l'un de ces territoires (les années 1996 et 1997 provenant des travaux de Richer et collaborateurs (2002)). De plus, durant toute l'étude, les densités sont restées beaucoup plus faibles que celles observées dans d'autres régions plus nordiques lors d'un pic d'abondance chez des populations cycliques i.e.: 30-56 (chapitre 2) vs. 180-1,086 lièvres/100 ha (Keith, 1990) et 20-40 (chapitre 3) vs. 100-260 *Clethrionomys* spp./1000 nuits-piège (Hansen et al., 1999), et comparables à celles observées chez des populations non cycliques (Keith, 1990; Murray, 2000; Fryxell et al., 1998; Saitoh et al., 1998). Les populations de lièvres et de petits mammifères sont donc restées relativement stables, à faibles densités, durant cinq années. Ces résultats sont en accord avec l'hypothèse d'un gradient nord-sud de cyclicité dépendant de la latitude, suggérée tant chez les lièvres (Keith, 1990) que chez les petits rongeurs (Hanski et al., 1991).

Dans les faits, nos données montrent qu'au moins 12 espèces de prédateurs généralistes et spécialistes, résidents ou nomades, étaient susceptibles de stabiliser les populations de lièvres et de petits mammifères de notre région. Les indices d'abondance de ces prédateurs ainsi qu'une analyse de l'utilisation de l'habitat (Beaudoin et al., 2004), indiquent que le lièvre a vraisemblablement subi une pression de prédation plus faible dans le site contrôlé, alors que ce ne fut pas nécessairement le cas pour les petits mammifères. Parallèlement, nous avons observé 1) que la prédation était la principale cause de mortalité des lièvres adultes (>900 g) ayant été responsable de 86% des 71 cas de mortalités de lièvres marqués de radio-émetteurs; 2) que la densité des lièvres était deux fois plus élevée dans le territoire piégé que dans l'autre (56 ± 4 vs. 30 ± 5 lièvres/ 100 ha); 3) que la survie des lièvres femelles fut significativement plus élevée dans le territoire protégé que dans le territoire piégé alors que l'inverse fut observé chez les mâles, suggérant qu'à plus haut risque de prédation, les femelles seraient moins mobiles ou occuperaient des habitats plus sûrs, diminuant ainsi leur taux de rencontre avec les prédateurs; et 4) que le nombre de jeunes lièvres et le rapport jeunes/femelle adulte ont été plus élevés en présence de piégeage des animaux à fourrure qu'en son absence, alors que les taux de gestation ont été similaires. Ceci suggère que la survie des levrauts fut probablement plus élevée en présence du contrôle de la prédation qu'en son absence, et explique vraisemblablement la différence de densité observée entre les deux territoires (chapitre 2). Par contre, nous n'avons détecté aucune variation de densité ou de survie chez les petits mammifères (chapitre 3).

Par conséquent, malgré la difficulté à évaluer les risques de prédation et malgré le manque de réplication dans notre étude, il semble que le contrôle des animaux à fourrure ait eu partiellement l'effet escompté. Nos résultats abondent donc dans le sens de l'hypothèse d'une dominance trophique descendante et indiquent que les liens trophiques sont probablement plus complexes que nous pouvions le suspecter.

Impact du piégeage des carnivores sur les lièvres et les petits mammifères

En général le piégeage réduit l'abondance des espèces exploitées (Hodgman et al., 1994; Frank et Woodroffe, 2001; Johnson et al., 2001), entraînant un accroissement de la densité et de la survie des proies (Krebs et al., 1995; Boertje et al., 1996; Hayes et al., 2003). Dans le territoire où le piégeage avait lieu, les trappeurs exerçaient une forte pression sur les prédateurs de plus grande taille (193 coyotes, renards et pékans prélevés /1000 km^2 / an), les plus petits étant moins recherchés (57 martres, visons, belettes et hermines prélevés /1000 km^2 / an). Nos indices d'abondance indiquent que les prédateurs terrestres les plus grands étaient légèrement moins abondants en présence de piégeage qu'en son absence alors que ce fut l'inverse pour les mustélidés les plus petits, suggérant que le lièvre a vraisemblablement subi une pression de prédation plus faible dans le territoire piégé que dans l'autre, alors que ce ne fut pas nécessairement le cas pour les petits mammifères. Les densités et la survie des lièvres et des petits mammifères semblent avoir répondu en conformité avec nos estimations du risque de prédation. De fait, l'idée que le piégeage des animaux à fourrure puisse affecter négativement l'ensemble des espèces exploitées et, qu'en conséquence, les densités et la survie des proies auraient augmenté, s'est donc avérée trop simpliste.

Le piégeage étant plus intense sur les carnivores les plus grands, il pourrait avoir provoqué un relâchement de la pression de prédation intra-guilde, reconnue comme un facteur d'importance majeure dans la dynamique des populations des petits carnivores (Henke et Bryant, 1999; Fedriani et al., 2000; Ray et Sunquist, 2001). Bien qu'exploités par le piégeage, les plus petits mustélidés (belettes et hermines) pourraient avoir exprimé une réponse numérique positive en réaction à une réduction de la prédation intra-guilde dans le territoire piégé. Ainsi, le piégeage des animaux à fourrure pourrait entraîner une altération des relations interspécifiques et causer des effets en cascade le long de la chaîne trophique (Henke et Bryant, 1999; St-Pierre, 2003) sans pour autant que la dynamique des populations de certaines espèces proies (e.g.: les petits rongeurs, chapitre 3) en soit grandement modifiée.

Impact des CPRS et des ÉPC sur les lièvres et les petits mammifères

Selon le modèle du refuge élaboré par Wolff (1981) pour expliquer la stabilité présumée dans les populations méridionales de lièvres, dans un système où les prédateurs détermineraient l'abondance des proies, le point d'équilibre tiendrait à la quantité d'habitats sûrs dans lesquels au moins une partie des herbivores pourrait échapper aux prédateurs, les individus en surplus étant forcés de se disperser vers des habitats plus risqués. Ce modèle implique que la structure de l'habitat serait un paramètre crucial, capable d'influencer le mécanisme qui détermine l'abondance et la survie des espèces proies. De fait, à cause de leur impact potentiel sur la structure de l'habitat, les perturbations comme la CPRS ou l'ÉPC sont susceptibles d'influencer la dynamique des populations de proies.

À partir des inventaires de végétation effectués dans 240 parcelles équitablement réparties entre les strates de chacun des territoires, nous avons pu analyser les caractéristiques des peuplements utilisés pour les estimations d'abondance de lièvres et de petits mammifères (chapitre 4). Globalement, les plus grandes abondances de lièvres et de petits mammifères et la plus grande richesse spécifique ont eu tendance à se retrouver dans les habitats qui offraient la plus grande complexité structurelle. Plus spécifiquement, nous avons observé que la CPRS affectait les peuplements forestiers en diminuant la structure et la complexité de la canopée, mais qu'elle augmentait celles du sous-étage végétal. Par la suite, l'ÉPC venait affecter le sous-étage en diminuant sa structure et sa complexité. Les lièvres et les petits mammifères ont répondu à ces modifications de façon différente selon les espèces, comme ce fut le cas dans d'autres études (Clough, 1987; Kirkland, 1990; Pagels et al., 1992; Homyack, 2003; Fuller et al., 2004). Cependant, la réponse globale en terme d'abondance relative et de richesse spécifique indique que durant les 10 ans qui suivent le traitement, l'ÉPC a vraisemblablement eu un effet plus négatif que les CPRS sur chacune des espèces qui composent la communauté des petits mammifères. Les CPRS, quant à elles, semblent avoir été plus neutres puisqu'elles ont maintenu l'abondance estivale et le nombre d'espèces de petits mammifères à des niveaux au moins comparables à ceux qui ont été observés dans les peuplements fermés.

En ouvrant la forêt, les CPRS permettent à la lumière de gagner les strates herbacées et arbustives, stimulant la croissance de la végétation basse, source de nourriture pour les herbivores. Elles produisent également des résidus qui accroissent la disponibilité en ressources alimentaires comme les graines d'arbres et les invertébrés (Monthey et Soutiere, 1985). Cependant, les arbres de faible diamètre, sans valeur commerciale, ainsi qu'une partie de la végétation basse sont laissés sur pied. Couplés aux résidus de coupe et à l'accroissement de la biomasse végétale près du sol, ces éléments augmentent la complexité structurelle du sous étage, durant les 10 années qui suivent le traitement. Ainsi, les CPRS offriraient aux petits mammifères des conditions d'habitat leur procurant une certaine abondance de refuges contre les prédateurs terrestres et aériens.

L'ÉPC accroît le diamètre des tiges laissées sur pied (Brissette et al., 1999; Pothier, 2002), ainsi que la taille de la courrone résiduelle (Brissette et al., 1999; Sullivan et al., 2001), mais elle réduit la complexité structurelle du sous-étage (Homyack, 2003). Nos résultats indiquent cependant qu'après l'ÉPC, la biomasse végétale proche du sol peut rester élevée. Nous croyons donc que l'ÉPC n'affecterait pas la disponibilité en nourriture pour les lièvres et les petits mammifères au cours de l'été, mais plutôt qu'elle réduirait l'efficacité protectrice des peuplements traités en diminuant la proportion de refuges antiprédateurs. Ainsi, pendant les 10 années de régénération qui suivent le traitement, l'ÉPC fournirait des conditions d'habitat intra-peuplement moins favorable aux lièvres et aux petits mammifères que les CPRS. En conclusion, les CPRS et les ÉPC pourraient avoir des effets opposés sur la dynamique des proies dus à leurs effets inverses sur la disponibilité des refuges.

Implications pour la gestion de ces espèces et de leurs habitats

Dans les milieux relativement productifs du sud de la forêt boréale, les densités de lièvres et de petits mammifères peuvent rester relativement stables et faibles. Nous avons également observé que les canidés pouvaient occuper une place de choix parmi les prédateurs de lièvres adultes. De fait, dans ces régions, les gestionnaires devraient tenir compte de la possibilité d'une absence de cycle dans les populations de lièvres et de petits mammifères et de ses répercussions sur les populations d'animaux à fourrure. De même, ils ne devraient plus prendre pour acquis la dominance du lynx parmi leurs prédateurs du lièvre.

Dans l'habitat des lièvres et des petits mammifères, la disponibilité des refuges est susceptible d'être grandement affectée par d'importantes perturbations comme la CPRS et l'ÉPC. Les populations de ces espèces devraient donc être suivies dans différents types habitats, car leur dynamique pourrait varier en fonction du risque de prédation associé à chaque type d'habitat. Ces informations aideraient les gestionnaires à la prise de décision.

À cause de son impact sur l'habitat, l'ÉPC a vraisemblablement eu un effet plus négatif que la CPRS sur les lièvres et les petits mammifères. Par conséquent, dans un soucis de conservation des populations de ces espèces ainsi que des processus écologiques qui en dépendent, nous pensons qu'au lieu de pratiquer l'ÉPC sur l'ensemble des peuplements susceptibles de subir ce traitement, il serait préférable d'appliquer des mesures de mitigation. Par exemple, les gestionnaires pourraient prévoir un délai de plusieurs années dans le traitement de peuplements contigus, ou même exclure certaines parcelles riches en gaulis des superficies à traiter. Ils pourraient également prévoir de protéger certaines essences végétales, comme les arbrisseaux (e.g.: bleuet, chèvrefeuille, etc), qui peuvent offrir un bon couvert protecteur.

Dans l'hypothèse d'une dominance trophique descendante, les végétaux abondent car les herbivores sont régularisés à faible densité par leurs prédateurs (Crête et Manseau, 1996) et gardés loin de la capacité de support, sauf si les prédateurs sont éliminés (Oksanen, 1988; Crête, 1999). Cependant, notre étude suggère que les interactions directes et indirectes existant entre les éléments d'un niveau trophique, ainsi qu'entre les niveaux trophiques eux mêmes, soient nombreuses et complexes, à cause de la diversité des espèces impliquées dans l'ensemble du réseau. Elle suggère également que l'écosystème puisse être relativement résiliant face à des perturbations d'origine anthropique. Les gestionnaires devraient toutefois intégrer le concept des interactions trophiques directes et indirectes (Schmitz et al., 2004) dans la gestion des écosystèmes afin de pouvoir réagir efficacement face à des réponses inattendues de la part de certaines de leurs composantes.

Perspectives de recherche

Suite à ce travail, certaines questions perdurent alors que d'autres apparaissent. Bien que nous ayons apporté certains éléments de réponse, l'importance de la prédation demeure hypothétique dans la dynamique des populations de lièvres et de petits mammifères. D'autres expériences de contrôle des prédateurs devraient être menées dans le même genre de milieu. Ces expériences pourraient également être orientées vers l'obtention de différents assemblages de prédateurs de manière à pouvoir évaluer l'importance relative et l'effet des prédateurs terrestres et aériens, des généralistes et des spécialistes, des résidents et des nomades, sur la dynamique des populations de différents types de proies (carnivores, herbivores et insectivores). Elles pourraient également mieux nous renseigner sur les relations directes et indirectes existant entre toutes ces espèces.

Si la prédation joue bien un rôle prépondérant dans la dynamique des proies, la quantité et la qualité des refuges anti-prédation devient un élément crucial pour leur survie. Faire varier artificiellement la quantité de refuges dans différents types d'habitats et vérifier l'impact de ces variations sur la dynamique des proies, serait une autre façon d'évaluer l'importance de la prédation dans le système.

L'hypothèse d'un gradient nord-sud de cyclicité chez les proies demeure, elle aussi, en suspens car aucune étude portant sur les populations méridionales de lièvres ou de petits mammifères boréaux américains ne possède d'assez longues séries temporelles de données pour statuer sur la présence ou l'absence de cycles, dans le sud de la forêt boréale nord-américaine. Il est donc important de poursuivre les estimations de densité des proies à plus long terme.

Chez le lièvre, il serait important d'investiguer davantage la survie des levrauts, en particulier durant leur première semaine de vie, car ce facteur semble déterminant pour la dynamique des populations de cette espèce. De même, il serait particulièrement intéressant d'analyser la survie des adultes afin de vérifier l'interaction entre le sexe des individus et le risque de prédation et d'en comprendre la raison.

Il serait également bénéfique de profiter de la mise en place des mesures d'atténuation de l'impact des ÉPC sur la petite faune, pour en mesurer l'effet sur la structure forestière ainsi que sur la dynamique des populations des proies. Finalement, mener ces expériences à différentes échelles spatiales et temporelles permettrait d'obtenir les informations utiles à la mise en place de mesures de gestion visant la conservation des espèces et des processus écologiques qui leur sont reliés.

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