UNIVERSITÉ DU QUÉBEC À MONTRÉAL

SÉLECTION D'HABITAT ET DÉMOGRAPHIE DU PIC À DOS NOIR DANS LES FORÊTS BRÛLÉES DE LA FORÊT BORÉALE

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DU DOCTORAT EN BIOLOGIE

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ANTOINE NAPPI

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À Méa, Éli et Ève, mes plus belles réussites,
et à Julie, pour en avoir été la source ...

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Pierre Drapeau, professeur, directeur de thèse, Département des sciences biologiques, Université du Québec à Montréal;

Timothy Work, professeur, président du jury, Département des sciences biologiques, Université du Québec à Montréal;

Sylvie Gauthier, chercheure scientifique, Service canadien des forêts, Centre de foresterie des Laurentides, Ressources naturelles du Canada;

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RÉSUMÉ

Le feu constitue un élément clé de la dynamique forestière naturelle et de la biodiversité en forêt boréale. À court terme, le feu génère une combinaison de conditions qui sont favorables à de nombreuses espèces fauniques et floristiques. En particulier, le feu représente, à l'échelle régionale, une source importante de bois mort pour plusieurs espèces de vertébrés et d'invertébrés qui dépendent de cet attribut d'habitat. Cette thèse vise à approfondir nos connaissances sur l'utilisation du bois mort et des forêts brûlées par les pics en forêt boréale. Plus spécifiquement, l'objectif de cette thèse est de mieux comprendre les processus écologiques à la base de l'utilisation des forêts brûlées par le pic à dos noir et d'évaluer la contribution de cet habitat dans la dynamique des populations de cette espèce en forêt boréale. La thèse est divisée en deux parties réparties sur quatre chapitres.

La première partie de la thèse, composée du chapitre 1, décrit l'écologie alimentaire de six espèces de pics qui nichent dans les forêts mixtes et résineuses de la forêt boréale de l'est. Les résultats révèlent que le bois mort constitue un substrat alimentaire important pour cinq espèces de pics soient le pic à dos noir, le pic à dos rayé, le pic chevelu, le pic mineur et le grand pic. Ce volet de la thèse décrit également les spécialisations de chaque espèce quant à son utilisation du bois mort, notamment en ce qui a trait aux stades de dégradation des arbres et aux types de proies. Le pic à dos noir était l'espèce qui montrait la plus forte association au bois mort pour son alimentation. Cette espèce sélectionnait principalement les conifères récemment morts, une préférence qui s'explique par sa spécialisation pour certains insectes saproxyliques (i.e. Cerambycidae) présents en grandes densités dans les premiers stades de dégradation des conifères. Ces résultats montrent que le pic à dos noir dépend du recrutement d'arbres morts pour son alimentation, qu'ils soient issus de la mortalité individuelle des arbres ou de perturbations naturelles de grande ampleur tel que le feu.

La deuxième partie de la thèse (chapitres 2 à 4) traite plus spécifiquement de la sélection d'habitat et de la démographie du pic à dos noir dans les forêts brûlées. Dans le chapitre 2, la sélection des arbres pour l'alimentation et la nidification a été étudiée de manière à déterminer les facteurs qui influencent la qualité de cet habitat pour l'espèce. Les résultats indiquent que les caractéristiques des arbres de nidification (i.e. feuillus, chicots dégradés) sont passablement différentes de celles des arbres d'alimentation (conifères, récemment morts, modérément brûlés). Ces résultats montrent que la combinaison des conditions présentes avant feu (i.e. composition, structure et âge des forêts) et de la sévérité du feu influence la qualité des forêts brûlées comme habitat pour cette espèce.

Dans le chapitre 3, j'examine le temps d'occupation des forêts brûlées et le succès reproducteur d'une population de pic à dos noir pendant une période de trois ans après feu. Ce volet de la thèse démontre clairement que les forêts brûlées peuvent représenter un habitat de nidification de haute qualité pour cette espèce. Cette occupation est cependant éphémère, étant limitée dans notre étude aux deux premières années suivant le feu. Le succès reproducteur a été évalué sur plus d'une centaine de nids au cours des trois années. Celui-ci diminuait en fonction des années depuis la perturbation et variait en fonction des conditions présentes dans le paysage brûlé. Le succès reproducteur était notamment plus élevé dans les peuplements matures que dans les peuplements jeunes brûlés et plus élevé à proximité de la bordure des forêts non brûlées. Ces résultats viennent corroborer ceux concernant la sélection d'habitat et démontrent l'importance des conditions de la matrice forestière avant feu ainsi que des patrons spatiaux dans la sévérité du feu sur la qualité de l'habitat pour l'espèce. Une évaluation du statut source-puit suggérait que ces forêts brûlées représentaient un habitat source pour les deux premières années suivant le feu et que ce statut se maintenait plus longtemps dans les habitats à dominance de forêts matures brûlées.

Le dernier chapitre a permis d'aborder l'influence de la sévérité du feu sur l'occupation à long terme des forêts brûlées par les insectes saproxyliques et les oiseaux qui s'alimentent sur ces derniers, en particulier le pic à dos noir. Les résultats montrent qu'une sévérité légère peut prolonger le temps d'occupation des forêts brûlées par les espèces d'insectes et d'oiseaux généralement associées aux premières années après feu. Dans cette étude, les secteurs brûlés légèrement étaient associés à une mortalité différée des arbres, ce qui a probablement contribué à la présence plusieurs années après feu d'insectes saproxyliques typiquement associés aux arbres récemment morts. À l'échelle des peuplements, certains insectes saproxyliques (ex. scolytes) ainsi que les oiseaux prédateurs de ces insectes (pic à dos rayé et grimpereau brun) étaient plus abondants dans les peuplements légèrement brûlés. À l'échelle de l'arbre, la sévérité du feu a eu un effet important sur la présence d'*Arhopalus foveicolis*, le Cerambycidae le plus important 8 à 11 ans après feu. La plus grande abondance de cet insecte dans les arbres légèrement brûlés a probablement contribué à la forte abondance du pic à dos noir dans ces vieux brûlis.

Les résultats de cette thèse montrent que le recrutement de bois mort, en particulier par le feu, constitue un élément clé du maintien et de la dynamique des populations du pic à dos noir en forêt boréale. Bien que la qualité des forêts brûlées soit variable et éphémère, cette thèse supporte l'hypothèse que ces forêts peuvent constituer des habitats sources pour les populations de cette espèce en forêt boréale. La récupération des forêts brûlées de même que le rajeunissement de la matrice forestière causé par l'aménagement forestier, par son effet indirect sur la qualité des conditions post-feu, ont un impact négatif sur la quantité et la qualité de cet habitat pour le pic à dos noir. L'intégration de certains résultats de cette thèse dans le développement de stratégies d'aménagement des forêts brûlées permettrait de mieux assurer le maintien d'habitats adéquats pour le pic à dos noir ainsi que pour plusieurs autres espèces qui sont associées aux forêts brûlées.

Mots-clés : forêt boréale, feu, bois mort, pic à dos noir, sélection d'habitat, succès reproducteur.

ABSTRACT

Fire is a key determinant of natural forest dynamics and biodiversity in the boreal forest. In the short-term, fire generates habitat conditions that are favourable to a diversity of fauna and flora. In particular, at the regional scale, fire represents an important source of dead wood for many species that depend on this habitat attribute. The aim of this thesis is to increase our knowledge on the use of dead wood and burned forests by woodpeckers in the boreal forest. More specifically, the objective of this thesis is to better understand the ecological processes underlying the use of burned forests by the black-backed woodpecker and to evaluate the contribution of this habitat to the population dynamics of this species in the boreal forest. The thesis is divided in two parts which cover a total of four chapters.

Chapter 1 describes the foraging ecology of six woodpecker species present in eastern boreal mixedwood and conifer forests. Results show that dead wood is an important foraging substrate for five woodpecker species: the black-backed woodpecker, the American three-toed woodpecker, the hairy woodpecker, the downy woodpecker and the pileated woodpecker. This part of the thesis also describes how each species specializes in their use of dead wood, in particular with regards to tree degradation stage and prey types. Of all the species studied, the black-backed woodpecker showed the strongest association with dead wood with respect to foraging. This species selected mainly recently dead conifers, a preference explained by its specialization for specific saproxylic insects (i.e. Cerambycidae) present in high densities in the first stages of conifer tree degradation. These results show that the black-backed woodpecker relies on the recruitment of recent snags for foraging, which can result from individual tree mortality or from large-scale natural disturbances such as fire.

The second part of the thesis (Chapters 2 to 4) addresses more specifically habitat selection and demography of the black-backed woodpecker in burned forests. In Chapter 2, tree selection for foraging and nesting was studied to identify the factors that influence post-fire habitat quality for this species. Results indicate that nest tree characteristics (i.e deciduous trees, pre-fire degraded snags) differ markedly from foraging tree characteristics (i.e. conifers, recently dead trees, moderately burned trees). These results show that pre-fire forest conditions (i.e. forest age, structure and composition) together with fire severity influence the quality of burned forest habitats for this species.

In Chapter 3, I examine the temporal occupancy and the reproductive success of a black-backed woodpecker population over a 3-year period after fire. This chapter shows that burned forests likely represent a high-quality habitat for this species. However, occupation of burned forests in this study was temporally limited to the first 2 years after fire. Reproductive success was evaluated based on more than a hundred nests over the 3-year period. Reproductive success decreased with years since fire and varied as a function of post-fire forest conditions. Reproductive success was higher in mature burned forests that in young burned forests and also in proximity to unburned forests. These results support those found in Chapter 2 and demonstrate the importance of pre-fire forest conditions and fire severity patterns in determining habitat quality for this species. A source-sink evaluation indicated that these burned forests likely functioned as source habitats for the first 2 years post-fire, in particular in portions of the burn dominated by mature burned forests.

The last chapter examines the influence of fire severity on the long-term occupancy of burned forests by bark-foraging birds, in particular the black-backed woodpecker, and saproxylic insects. The results indicate that low-severity fire can favour the long-term persistence of species typically associated with recently burned forests. In this study, burned stands of lower severity provided delayed tree mortality that likely contributed to the presence, many years after fire, of saproxylic insect species typically associated with recently dead trees. At the stand scale, saproxylic insects such as bark beetles (i.e. scolytinae) and associated bark-foraging predators (American three-toed woodpecker, brown creeper) were more abundant in burned stands of lower severity. At the tree scale, fire severity greatly influenced the presence of *Arhopalus foveicollis*, the most abundant Cerambycidae found 8 and 11 years after fire. The higher abundance of this insect in lightly charred trees likely contributed to the high abundance of the black-backed woodpecker in these old burns.

The results of this thesis show that dead wood recruitment, in particular by fire, represents a key determinant in the maintenance and population dynamics of black-backed woodpeckers in the boreal forest. Although post-fire habitat quality is temporally limited and may vary greatly within burns, this thesis supports the hypothesis that burned forests may represent source habitats for populations of this species in the boreal forest. Post-fire logging but also landscape-level decrease in forest age caused by forest management, because of its indirect effect on post-fire habitat conditions, negatively affect the quantity and the quality of such habitat for the black-backed woodpecker. Integrating the results of this thesis in post-fire forest management practices would help maintain suitable habitats for not only the black-backed woodpecker but a host of other species associated with post-fire habitats.

Keywords: boreal forest, fire, dead wood, black-backed woodpecker, habitat selection, reproductive success.

INTRODUCTION GÉNÉRALE

Le feu et ses effets sur l'avifaune en forêt boréale

En forêt boréale, comme dans un grand nombre d'écosystèmes forestiers nord-américains, le feu constitue une perturbation naturelle majeure et un élément clé de la dynamique forestière (Brown et Smith 2000, Conner *et al.* 2001, Saab et Powell 2005). Bien que variant en intensité, en fréquence et en superficie, le régime de feu de la forêt boréale est typiquement caractérisé par des feux de couronne qui couvrent de grandes superficies et qui induisent des changements importants dans la structure des peuplements forestiers (Brown et Smith 2000, Bergeron *et al.* 2002). Ces feux façonnent le paysage forestier boréal depuis des millénaires en influençant la composition, la structure d'âge et la configuration des mosaïques forestières (Bergeron 2000, Bergeron *et al.* 2001, 2004, Carcaillet *et al.* 2001).

Outre son importance dans le façonnement des paysages forestiers, le feu génère également à court terme des conditions fort différentes de celles retrouvées dans les forêts non brûlées. En effet, bien que le feu élimine en grande partie le couvert forestier et modifie les conditions abiotiques et biotiques qui y sont associées, il génère en contrepartie une combinaison de conditions - ouverture de la canopée, grande densité d'arbres morts, combustion de la matière organique au sol, réduction de la compétition, luminosité et chaleur accrue - qui est unique aux forêts brûlées (Wikars 1992, Ahnlund et Lindhe 1992, Kaila *et al.* 1997, Drapeau *et al.* 2003, Greene *et al.* 2005). Bien que certaines de ces conditions soient peu propices aux espèces inféodées aux forêts fermées, plusieurs espèces sont adaptées à celles-ci (Smith 2000, Saab et Powell 2005). La colonisation des forêts brûlées par la faune et la flore est bien documentée dans la littérature scientifique. Certaines espèces d'insectes, considérées comme « pyrophyles », sont notamment adaptées pour repérer les feux afin de tirer profit des conditions qui s'y trouvent (Evans 1966, Schütz *et al.* 1999, Schmitz *et al.* 2000, Suckling *et al.* 2001). D'autres espèces animales ou végétales sont tout simplement présentes en plus forte abondance dans les forêts brûlées, dû à la présence de conditions d'habitat auxquelles elles sont associées ou dépendantes. Ces espèces ont été qualifiées par les différents auteurs comme des espèces associées au feu (Hannon et Drapeau 2005), spécialistes du feu (Saab et

Powell 2005), favorisées par le feu (Wikars et Schimmel 2001) ou restreintes au feu (Hutto 1995).

Les études menées en forêt boréale canadienne montrent que plusieurs espèces de plantes, d'invertébrés et de vertébrés sont présentes exclusivement ou en plus grande abondance dans les forêts brûlées que dans d'autres types de forêts naturelles ou aménagées (Nguyen-Xuan *et al.* 2000, Saint-Germain *et al.* 2004a, Hannon et Drapeau 2005, Schieck et Song 2006, Buddle *et al.* 2006, Larrivée *et al.* 2008). Une des particularités les plus frappantes des communautés d'espèces présentes dans les forêts brûlées est la forte abondance d'invertébrés et de vertébrés qui sont associées ou qui dépendent du bois mort. Les brûlis récents constituent, en effet, des forêts d'arbres morts qui sont typiquement colonisées par une multitude d'espèces d'insectes saproxyliques (i.e. insectes qui dépendent du bois mort pour au moins une partie de leur cycle vital; Saint-Germain *et al.* 2004b, Boulanger et Sirois 2007). Chez les vertébrés, plusieurs espèces d'oiseaux qui se nourrissent de ces insectes ainsi que celles qui nichent dans les cavités sont également favorisées par les nouvelles conditions générées par le feu (Hutto 1995, Drapeau *et al.* 2002, Morissette *et al.* 2002, Hannon et Drapeau 2005, Saab et Powell 2005, Schieck et Song 2006).

Les pics constituent un groupe d'oiseaux qui est particulièrement favorisé par cette forte abondance de substrats d'alimentation et de nidification (i.e. arbres morts brûlés). Les fortes abondances de certaines espèces de pics à la suite de perturbations naturelles majeures telles le feu (Blackford 1955, Hutto 1995, Murphy et Lehnhausen 1998, Covert-Bratland *et al.* 2006) ou les épidémies d'insectes (Crockett et Hansley 1978, Goggans *et al.* 1989) sont d'ailleurs bien documentées, notamment pour les espèces du genre *Picoides*. En réponse à l'abondance élevée des ressources alimentaires, les densités de pics dans ces forêts peuvent être de 40 à 80 fois supérieures aux densités observées dans les forêts non perturbées (Fayt *et al.* 2005). De par les liens entre le bois mort, les insectes saproxyliques, les pics et les utilisateurs secondaires de cavités, les forêts brûlées ne constituent pas seulement un habitat propice aux espèces utilisatrices d'arbres morts, mais elles sont également à la base d'un réseau trophique complexe et dynamique.

Bien que l'effet du feu sur l'avifaune en Amérique du Nord soit un sujet qui a reçu beaucoup d'attention dans la littérature scientifique (Smith 2000, Saab et Powell 2005), les études menées jusqu'à présent ne permettent, pour la plupart, que de dresser un portrait général (ex. abondance, occurrence) de la réponse de ces espèces au feu (Saab et Powell 2005). En contrepartie, nous en connaissons relativement peu sur l'écologie et la démographie des espèces qui utilisent les forêts brûlées. Ces lacunes font en sorte qu'il est difficile de déterminer le rôle et l'importance de ce type de perturbation dans la dynamique des populations de ces espèces en forêt boréale. Pour les pics, une meilleure compréhension de l'utilisation des forêts brûlées repose préalablement sur une connaissance adéquate de l'écologie alimentaire de ces espèces, de leurs degrés de dépendance au bois mort ainsi que de leurs patrons d'utilisation de ce substrat. En outre, il est primordial d'avoir une meilleure compréhension des facteurs qui influencent la qualité des forêts brûlées ainsi que leur occupation par les pics, ce qui repose entre autres sur des études traitant de la sélection d'habitat et quantifiant les paramètres démographiques des populations (ex. succès reproducteur).

Portrait des pics et de leur association au bois mort

Les pics (famille Picidae, sous-famille Picinae) comptent près de 180 espèces réparties à travers le monde, dont 22 sont présentes en Amérique du Nord (Winkler *et al.* 1995). En forêt boréale de l'est, sept de ces espèces nichent de façon régulière. Il s'agit du pic maculé (*Sphyrapicus varius*), du pic mineur (*Picoides pubescens*), du pic chevelu (*Picoides villosus*), du pic à dos rayé (*Picoides dorsalis*), du pic à dos noir (*Picoides arcticus*), du pic flamboyant (*Colaptes auratus*) et du grand pic (*Dryocopus pileatus*). Pour toutes ces espèces, à l'exception du pic à dos rayé et du pic à dos noir, la forêt boréale correspond à la limite nord-est de leur aire de répartition. Pour le pic à dos rayé et le pic à dos noir, principalement associés aux forêts résineuses, la forêt boréale représente le cœur de leur aire de répartition.

Les pics jouent plusieurs rôles fonctionnels importants dans les écosystèmes forestiers. Une des fonctions les mieux documentées est la production de cavités dans les arbres. Celles-ci constituent des sites de reproduction et d'abri importants et limitants pour une panoplie d'espèces d'oiseaux, de mammifères, d'amphibiens, de reptiles et d'insectes qui les utilisent (Brawn et Balda 1988, Newton 1994, Martin *et al.* 2004). Au Québec par exemple, plus d'une trentaine d'espèces d'oiseaux et de mammifères utilisent ces cavités (Drapeau *et al.* 2005). Les pics jouent donc un rôle d'espèces « clés de voûte » (« keystone species ») en rendant ainsi disponible tout un réseau de cavités pour les utilisateurs secondaires, qui ne sont pas en mesure de creuser eux-mêmes leurs cavités (Martin et Eadie 1999, Martin *et al.* 2004). Ce rôle d'excavateur est d'autant plus important dans les peuplements résineux boréaux puisque les cavités naturelles y sont rares (Vaillancourt 2006).

Les pics peuvent également jouer un rôle important en rendant disponibles certaines ressources alimentaires. Par exemple, le pic maculé génère, pour son alimentation, tout un réseau de trous permettant l'écoulement de la sève et qui seront utilisés par plusieurs autres espèces d'oiseaux comme le colibri à gorge rubis (Southwick et Southwick 1980). Étant donné la prédation que peuvent exercer les espèces de pics sur les insectes perceurs d'écorce tels les scolytes (Coleoptera, Scolytinae), il a également été suggéré que les pics pourraient jouer un rôle important dans la régulation des populations de ces insectes (Fayt *et al.* 2005). Finalement, par les cavités qu'ils creusent tant pour la nidification que pour l'alimentation, les pics contribueraient à la décomposition du bois en favorisant la dispersion des champignons saprophytes (Jackson et Jackson 2004, Farris *et al.* 2004).

Peu d'espèces d'oiseaux sont aussi fortement associées au milieu forestier que les pics. Cette affinité avec la forêt repose essentiellement sur leur dépendance aux arbres qu'ils utilisent à la fois comme substrats de nidification, d'alimentation et de communication. Le bois mort, en particulier, est généralement considéré comme un attribut d'habitat important pour les pics. Ce constat relève en grande partie des études menées pour caractériser les substrats de nidification des oiseaux qui nichent dans des cavités (Mannan *et al.* 1980, Raphael et White 1984, Martin *et al.* 2004). En effet, ces études montrent généralement une forte utilisation des arbres morts ainsi que des arbres vivants mais partiellement dégradés comme substrat de nidification. En contrepartie, l'utilisation du bois mort pour l'alimentation semble être moins prononcée et plus variable entre les espèces de pics (Mannan *et al.* 1980, Raphael et White 1984, Bull *et al.* 1986). Pour les espèces qui dépendent du bois mort cependant, la disponibilité de cette ressource peut être beaucoup plus limitante pour l'alimentation que pour la nidification en raison de la quantité d'arbres ou des caractéristiques qui sont requises (Weikel et Hayes 1999, Imbeau et Desrochers 2002).

L'essentiel de nos connaissances actuelles sur l'écologie alimentaire des pics provient de plusieurs travaux menés de la fin des années 1960 au début des années 1980, en Amérique du Nord et en Europe. Ces études, menées à partir du cadre théorique de la partition des niches (ex. MacArthur 1958, Stallcup 1968), ont porté plus spécifiquement sur le partitionnement intra et inter-spécifique des niches alimentaires des pics. Indirectement, ces travaux ont permis de quantifier et de comparer plusieurs aspects de l'alimentation des pics tels que les habitats, les substrats d'alimentation, les comportements alimentaires ainsi que les types de proies utilisés (ex. Jackson 1970, Hogstad 1971, Conner 1981, Török 1990). Bien que plusieurs de ces études aient quantifié l'utilisation de bois mort comme substrat de nidification, peu d'entre elles permettent de conclure quant à la sélection effective (utilisation vs disponibilité, Johnson 1980) du bois mort comme substrat d'alimentation. D'autre part, peu d'études ont examiné de façon précise les patrons de sélection des arbres pour l'alimentation des pics.

En forêt boréale, nous possédons relativement peu de connaissances sur l'écologie des pics. Jusqu'à présent, la plupart des connaissances sur cette famille proviennent d'études sur l'occupation d'habitats (données d'occurrence et d'abondance; ex. Imbeau *et al.* 1999, Drapeau *et al.* 2000, Hoyt et Hannon 2002, Morissette *et al.* 2002, Drapeau *et al.* 2003, Schieck et Song 2006). Bien que ce genre d'étude soit essentielle afin de déterminer les types d'habitats fréquentés par chacune des espèces, elles ne nous renseignent qu'indirectement sur les exigences écologiques de celles-ci en matière de nidification ou d'alimentation. Les quelques études menées en forêt boréale sur l'écologie alimentaire des pics ne traitent généralement que d'une seule espèce ou ont été menées dans des forêts sévèrement brûlées où seuls des arbres morts sont disponibles (Murphy et Lehnhausen 1998, Imbeau et Desrochers 2002, Nappi *et al.* 2003). Ces études ne permettent donc pas d'évaluer la sélection du bois mort par ces espèces pour leur alimentation.

Utilisation des forêts brûlées par le pic à dos noir

Le pic à dos noir est l'espèce de pic qui est la plus abondante dans les forêts résineuses brûlées de la forêt boréale (Nappi 2000, Hoyt et Hannon 2002, Koivula et Schmiegelow 2007). Cette forte fréquentation des forêts brûlées par le pic à dos noir a été documentée un peu partout sur son aire de répartition (ouest Américain, Hutto 1995; Alaska, Murphy et Lehnhausen 1998; Alberta, Hoyt et Hannon 2002; Québec, Nappi 2000). Dans son analyse de plus de 200 études dans l'ouest Américain, Hutto (1995) a trouvé que le pic à dos noir était plus abondant dans les forêts brûlées que dans d'autres types d'habitats, et en particulier dans les forêts récemment brûlées. Bien que cette espèce fréquente également les forêts non brûlées naturelles ou aménagées où les arbres morts abondent (Weinhagen 1998, Setterington *et al.* 2000), les densités de pics observées dans les forêts brûlées sont de loin supérieures à celles observées dans les forêts non brûlées (Hutto 1995, Nappi 2000, Hoyt et Hannon 2002). Ceci a conduit Hutto (1995) à suggérer que les forêts brûlées pouvaient constituer des habitats « sources » (i.e. habitat dont la natalité est supérieure à la mortalité; Pulliam 1988) alors que les forêts non brûlées représenteraient des habitats « puits » (natalité inférieure à la mortalité) dont les populations seraient maintenues par les oiseaux qui émigreraient des forêts brûlées lorsque les conditions deviennent moins favorables quelques années après feu.

Tout comme pour les autres espèces généralement associées aux forêts brûlées, les études menées jusqu'à présent n'ont permis que de dresser un portrait général de la réponse du pic à dos noir au feu (Hutto 1995, Hannon et Drapeau 2005, Saab et Powell 2005). En contrepartie, peu d'études nous permettent de comprendre les facteurs qui peuvent influencer l'occupation et la qualité de cet habitat pour le pic à dos noir ainsi que le rôle de cet habitat dans la dynamique des populations de cette espèce.

Tout d'abord, bien que les feux génèrent des conditions d'habitat très différentes des forêts non brûlées, il existe néanmoins une grande variabilité dans les conditions présentes après feu. Cette variabilité est susceptible d'affecter la qualité de l'habitat et la réponse de cette espèce au feu. Les conditions d'habitat peuvent varier en fonction de facteurs tels la sévérité du feu ou le type de peuplement brûlé (âge avant feu, composition, structure). Des études récentes ont montré que la sévérité du feu a un effet important sur l'abondance des espèces d'oiseaux après feu (Smucker *et al.* 2005, Kotliar *et al.* 2007). Pour le pic à dos noir, ces facteurs influencent directement la quantité et les caractéristiques du bois mort après feu. Afin d'identifier ce qui peut constituer une forêt brûlée de bonne qualité pour le pic à dos noir, il faut au préalable connaître les exigences écologiques de cette espèce en matière d'alimentation et de nidification. Bien que quelques études aient porté sur la caractérisation et les patrons de sélection des substrats d'alimentation dans les forêts brûlées (Murphy et Lehnhausen 1998, Nappi *et al.* 2003), la plupart des descriptions des sites de nidification sont, en contrepartie, anecdotiques (Saab et Dudley 1998, Dixon et Saab 2000) et aucune n'a porté sur les patrons de sélection.

Les facteurs qui influencent l'occupation temporelle de ces habitats par le pic à dos noir ont également été peu étudiés. Les études menées jusqu'à présent montrent que cette espèce est principalement abondante dans les premières années après feu. Cependant, il existe une certaine variabilité quant à la durée d'occupation des forêts brûlées par le pic à dos noir. Cette durée varie de 2 ans à plus d'une dizaine d'années après feu (Hutto 1995, Murphy et Lehnhausen 1998, Hoyt et Hannon 2002, Saab *et al.* 2007). Parce que l'occupation des forêts brûlées est principalement liée à l'abondance des insectes xylophages, la proie principale de cette espèce de pic, il est important de comprendre comment la variabilité des conditions post-feu et la dynamique de populations de ces insectes peuvent affecter l'occupation de ces forêts par les pics.

Pour la plupart des espèces associées au feu, il est difficile de déterminer le rôle de cette perturbation dans leur dynamique en forêt boréale. Cela tient au fait qu'il existe actuellement très peu d'information sur les paramètres démographiques (natalité, mortalité, émigration, immigration) de ces populations après feu, la plupart des études ayant porté essentiellement sur la réponse numérique (i.e. abondance, densité; Hutto 1995, Hannon et Drapeau 2005, Saab et Powell 2005, Schieck et Song 2006). Considérant que la présence d'une espèce ne peut garantir à elle seule que l'habitat est de bonne qualité, les données sur le succès reproducteur des espèces qui fréquentent ces habitats sont essentielles pour en évaluer la qualité (Van Horne 1983). Chez les pics, la quantification des paramètres démographiques tel que le succès reproducteur repose généralement sur très peu d'études et sur de faibles effectifs (Pasinelli 2006). Dans le cas du pic à dos noir, les quelques études ayant quantifié le succès reproducteur reposent sur des effectifs annuels relativement faibles (Goggans *et al.* 1989, Saab *et al.* 2005, Saab *et al.* 2007). Des données démographiques plus nombreuses sur la productivité des populations sont nécessaires afin d'identifier les facteurs qui influencent la qualité de l'habitat, ou encore pour mesurer et tester les hypothèses liées à certains modèles de dynamique de populations (ex. dynamique source-puit; Hutto 1995).

Effets de l'aménagement forestier sur les pics en forêt boréale

Étant donné leurs exigences écologiques et leurs associations à des attributs d'habitat qui sont typiques des forêts sous dynamique naturelle (i.e. arbres de gros diamètre, bois mort), les pics constituent un groupe d'oiseaux qui est particulièrement sensible aux effets de l'aménagement forestier (Angelstam et Mikusiński 1994, Mikusiński et Angelstam 1998, Imbeau *et al.* 2001). En Suède par exemple, six des neuf espèces présentes historiquement dans ce pays présentent divers statuts de vulnérabilité (Angelstam et Mikusiński 1994). En forêt boréale canadienne, plusieurs espèces possèdent des traits écologiques semblables aux espèces européennes, ce qui suggère une sensibilité similaire aux effets de l'aménagement forestier (Imbeau *et al.* 2001). Dans une comparaison avec la Fennoscandinavie, Imbeau *et al.* (2001) concluaient que les espèces qui montraient le plus haut niveau de sensibilité aux effets de l'aménagement forestier en forêt résineuse boréale étaient les oiseaux résidents nicheurs de cavités, avec en tête de liste les pics.

Le bois mort est l'un des attributs d'habitat les plus affectés par l'aménagement forestier traditionnel (Raphael et White 1984, Harmon *et al.* 1986, Angelstam et Mikusiński 1994, Siitonen 2001). De manière générale, les modèles de foresterie visent typiquement la récolte des arbres avant qu'ils ne commencent à se dégrader ou à mourir. En forêt boréale canadienne, ceci se traduit principalement par l'application d'un régime de futaie régulière (ex. CPRS) qui vise essentiellement une révolution de l'ordre de 70 à 100 ans (Bergeron *et al.* 1999). En comparaison, le cycle de feu de la forêt boréale québécoise varie entre 100 et plus de 500 ans, ce qui fait qu'une portion importante du territoire forestier est composée de forêts mûres et surannées (Lefort *et al.* 2004, Bergeron *et al.* 2006). Par conséquent, cette normalisation de la forêt entraîne inévitablement une diminution considérable de la proportion de forêts mûres ou anciennes (Drapeau *et al.* 2000, Bergeron *et al.* 2007) qui constituent une source importante de bois mort, en particulier de gros diamètre, et qui constitue un habitat important pour plusieurs espèces de pics.

La récolte des forêts brûlées constitue un facteur supplémentaire qui contribue à la diminution de la quantité de bois mort dans les paysages forestiers aménagés. Au Québec, les forêts affectées par les perturbations naturelles telles le feu, les épidémies d'insectes ou le chablis peuvent faire l'objet d'un « plan spécial d'aménagement en vue d'assurer la récupération des bois », plus communément appelé un « plan de récupération » (Gouvernement du Québec 2008). La récupération du bois brûlé est une pratique forestière de plus en plus répandue en forêt boréale canadienne et dans plusieurs régions forestières du monde (Lindenmayer *et al.* 2004, Schmiegelow *et al.* 2006). Bien que l'importance des forêts brûlées pour la faune et la flore soit de plus en plus documentée, il existe en revanche peu d'encadrement visant à maintenir la biodiversité associée à ce type d'habitat. Pour le pic à dos noir ainsi et pour plusieurs espèces qui utilisent le bois mort, la récupération des forêts brûlées peut avoir un impact sur la quantité et la qualité des substrats d'alimentation et de nidification disponibles.

Afin d'assurer le maintien des populations de pics dans les forêts boréales aménagées, il est nécessaire de bien comprendre le rôle du bois mort et des forêts brûlées dans la dynamique des populations de ces espèces. Tout d'abord, une meilleure connaissance de leur écologie alimentaire peut nous aider à identifier les espèces les plus sensibles à la perte de cet attribut d'habitat dans les forêts aménagées. Ceci permettra également de développer des stratégies de maintien de bois mort qui soient adéquates pour maintenir ces espèces dans les forêts aménagées. En ce qui a trait aux forêts brûlées, une meilleure compréhension des facteurs qui influencent la qualité de cet habitat pour le pic à dos noir pourrait permettre de développer des stratégies d'aménagement qui assurent le maintien d'habitats de bonne qualité pour cette espèce et pour d'autres espèces associées au bois mort ou aux forêts brûlées.

Objectifs et structure de la thèse

Cette thèse vise à approfondir nos connaissances sur l'utilisation du bois mort et des forêts brûlées par les pics en forêt boréale. Plus spécifiquement, l'objectif de cette thèse est de mieux comprendre les processus écologiques à la base de l'utilisation des forêts brûlées par le pic à dos noir et d'évaluer la contribution de ces habitats dans la dynamique des populations de cette espèce en forêt boréale. La thèse est divisée en deux parties réparties sur quatre chapitres.

La première partie de la thèse, constituée du chapitre 1, vise à déterminer l'importance du bois mort pour l'alimentation de six espèces de pics en forêt boréale et à comparer les patrons d'utilisation de cette ressource entre celles-ci. En outre, ce chapitre examine l'utilisation du bois mort par le pic à dos noir à la fois dans les forêts non brûlées et brûlées, ce qui donne une perspective élargie à notre compréhension de l'écologie alimentaire de cette espèce. Dans ce chapitre, je décris et compare les patrons de sélection des arbres et les comportements alimentaires des pics en portant une attention particulière à l'utilisation qu'ils font du bois mort. De plus, des données sur les insectes saproxyliques, recueillis par la dissection d'arbres d'alimentation des pics, servent à corroborer les résultats sur la sélection des arbres et le comportement alimentaire des pics. Cette étude a été menée dans la sapinière à bouleau blanc et dans la pessière à mousses de l'Abitibi, ce qui a permis de couvrir l'ensemble des habitats associés aux différentes espèces de pics étudiées. Ce chapitre permet notamment de mettre en perspective l'importance relative du bois mort pour le pic à dos noir en comparaison aux autres espèces présentes en forêt boréale, ainsi qu'à mieux comprendre les spécialisations alimentaires de chaque espèce de pic.

La deuxième partie de la thèse, constituée des chapitres 2 à 4, traite plus spécifiquement de la sélection d'habitat et de la démographie du pic à dos noir dans les forêts résineuses brûlées. Pour les chapitres 2 et 3, les études ont été menées dans une forêt brûlée en 1999 au Parc national des Grands-Jardins, dans la région de Charlevoix. Dans le chapitre 2, j'examine les facteurs qui sont impliqués dans la sélection des arbres pour l'alimentation et la nidification. Cette étude permet notamment de déterminer l'effet des caractéristiques de la matrice forestière avant feu et de la sévérité du feu sur la qualité des forêts brûlées pour le pic à dos noir.

Au chapitre 3, j'examine l'occupation et le succès reproducteur d'une population de pic à dos noir durant une période de trois ans après feu. Premièrement, ce chapitre vise à déterminer le temps d'occupation des forêts brûlées pour la nidification et à examiner comment cette occupation varie en fonction des conditions d'habitat post-feu à l'intérieur du paysage brûlé. D'autre part, ce chapitre vise à mesurer le succès reproducteur du pic à dos noir dans les forêts brûlées et à examiner comment celui-ci varie en fonction du temps après feu et des conditions d'habitat présentes dans les forêts brûlées. Ces données sur le succès reproducteur ont été examinées dans le cadre de la théorie sur la dynamique « source-puit » afin d'évaluer le potentiel des forêts brûlées à constituer un habitat source pour le pic à dos noir en forêt boréale.

Le chapitre 4 aborde l'effet de la sévérité du feu sur l'occupation à long terme des forêts brûlées par le pic à dos noir et par deux autres espèces d'oiseaux. Dans ce chapitre, j'émets l'hypothèse qu'une faible sévérité du feu favorise un plus long maintien des populations d'insectes saproxyliques, ce qui prolonge le temps d'occupation des forêts brûlées par les oiseaux qui s'alimentent sur ces derniers. Cette étude a été menée dans deux forêts brûlées au nord-ouest de Chibougamau. Ce chapitre présente des données sur l'abondance du pic à dos noir et des insectes saproxyliques dans les forêts brûlées 6 à 11 ans après feu.

La conclusion générale résume et met en lien les résultats présentés tout au long des quatre chapitres de la thèse. Ces résultats ont également été utilisés afin de générer des recommandations dans le cadre de l'aménagement forestier. Finalement, deux annexes qui ont permis d'alimenter davantage la réflexion et les recommandations présentées dans la conclusion générale sont présentées à la fin de la thèse.

CHAPITRE 1

FORAGING ECOLOGY AND USE OF DEAD WOOD BY WOODPECKERS IN EASTERN CANADIAN BOREAL FORESTS

1.1 Résumé

Afin d'évaluer l'importance du bois mort comme substrat d'alimentation pour les pics et afin de comparer les spécialisations alimentaires de ces espèces, nous avons quantifié et comparé les patrons de sélection d'arbres et le comportement alimentaire de six espèces de pics qui s'alimentent sur les arbres – pic mineur (*Picoides pubescens*), pic chevelu (*Picoides villosus*), pic à dos rayé (*Picoides dorsalis*), pic à dos noir (*Picoides arcticus*), pic maculé (*Sphyropicus varius*) et grand pic (*Dryocopus pileatus*) – dans les forêts boréales de l'est de l'Amérique du Nord. Un total de 266 suivis d'alimentation regroupant plus de 700 arbres ont été documentés à trois sites d'étude soient une forêt mixte, une forêt résineuse ainsi qu'une forêt résineuse brûlée. La dissection du bois de 47 arbres d'alimentation utilisés par les quatre espèces du genre *Picoides* a été menée afin d'identifier les proies potentielles et de corroborer les résultats de sélection d'arbres et de comportement alimentaire. Nos résultats indiquent que le bois mort représente un substrat d'alimentation important pour cinq des six espèces de pics. Les pics ont été catégorisés selon leur préférence pour certains stades de dégradation des arbres. Le pic maculé et le grand pic étant respectivement associés au premier (arbres vivants) et dernier (chicots très décomposés) stades de dégradation alors que les *Picoides* occupaient des positions intermédiaires sur ce gradient. Bien que les espèces du genre *Picoides* utilisaient abondamment le bois mort, nos résultats montrent des différences importantes dans leur utilisation des substrats d'alimentation, leurs proies et leurs comportements alimentaires. Le maintien de substrats d'alimentation pour la plupart des espèces de pics dans les forêts boréales de l'est requiert non seulement le maintien de bois mort mais également la prise en compte de la dynamique du bois mort (ex. recrutement et dégradation) dans les paysages forestiers aménagés.

Mots-clés : forêt boréale, pics, bois mort, alimentation, sélection, comportement, insectes saproxyliques.

1.2 Abstract

To assess the importance of dead wood as a foraging substrate for woodpeckers and to compare foraging specializations of these species, we quantified and compared tree selection patterns and foraging behaviour of six bark-foraging woodpeckers - downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), yellow-bellied sapsucker (*Sphyropicus varius*) and pileated woodpecker (*Dryocopus pileatus*) - in eastern boreal forests of North America. A total of 266 observation of foraging bouts made on more than 700 trees were recorded at three study sites characterized as mixedwood, conifer, and conifer-burned. Wood dissection was conducted on a subset of 47 foraging trees used by the four *Picoides* species to identify potential prey and corroborate foraging tree selection and behaviour results. Our results show that dead wood represents an important foraging substrate for five of the six woodpecker species. Woodpeckers were categorized according to their selection for specific stages of tree degradation. The yellow-bellied sapsucker and the pileated woodpecker represented opposite ends of this gradient, being respectively associated with earlier (live trees) and later (highly degraded snags) stages of tree degradation whereas *Picoides* species occupied more intermediate positions on the tree degradation gradient. Although *Picoides* species made extensive use of dead wood, our results highlight significant differences in species specialization in regards to substrate use patterns, associated prey and foraging behaviour. We emphasize that providing foraging substrates for most woodpecker species in eastern boreal forests not only requires maintaining dead wood but also paying heed to the underlying dynamics of dead wood (e.g. recruitment and degradation) in managed forest landscapes.

Keywords : boreal forest, woodpeckers, dead wood, foraging, selection, behaviour, saproxylic insects.

1.3 Introduction

Dead wood is an important habitat resource for many woodpecker species (Winkler *et al.* 1995, Raphael and White 1984, Angelstam and Mikusiński 1994). This association of woodpeckers with dead wood has been typically attributed to these birds' nesting requirements, as many species are known to use snags or dead portions of trees for their nest cavities (Mannan *et al.* 1980, Raphael and White 1984). Yet, many woodpeckers are known to use dead wood for foraging and there is growing evidence that at least some bark-foraging species may be dead wood specialists (Angelstam and Mikusiński 1994, Murphy and Lehnhausen 1998, Imbeau and Desrochers 2002, Nappi *et al.* 2003). Given the number of trees required for foraging, populations of these species may be much more limited by the availability of suitable foraging substrates than by potential nest trees, and may in turn be more sensitive to the reduction of dead wood in managed landscapes (Angelstam and Mikusiński 1994, Mikusiński and Angelstam 1998, Imbeau *et al.* 2001).

In Canadian boreal forests, even-aged management and post-disturbance (salvage) logging inevitably reduce the extent of old-growth and post-disturbance forests, the two most important sources of dead wood in natural forest landscapes (Imbeau *et al.* 1999, Drapeau *et al.* 2002, Hannon and Drapeau 2005). A better understanding of the foraging ecology of woodpeckers and their association to dead wood may help identify the species most vulnerable to the impacts of forest management and help develop adequate strategies for maintaining suitable foraging substrates in managed landscapes.

Use and partitioning of foraging resources among sympatric woodpecker species has received much attention in North America and Europe (e.g. Hogstad 1971, Austin 1976, Conner 1981, Bull *et al.* 1986, Török 1990). Although use of dead wood for foraging has often been reported, few studies have documented the selection *per se* (*sensu* Johnson 1980) of dead wood by foraging woodpeckers and their differential tree selection patterns. In the boreal forest, foraging ecology of woodpeckers has received little attention and such studies have mostly focused on single species (e.g. Imbeau and Desrochers 2002, Nappi *et al.* 2003).

We studied the foraging ecology of the six bark-foraging woodpecker species that co-occur in the eastern North American boreal forest: downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), yellow-bellied sapsucker (*Sphyropicus varius*) and pileated woodpecker (*Dryocopus pileatus*). In particular, our study addresses the following questions: 1) what is the relative importance of dead wood as a foraging substrate for woodpeckers in the boreal forest? and 2) how do these species differ in regards to foraging tree selection and foraging behaviour?

1.4 Methods

1.4.1 Study area

The two main study sites (Fig. 1.1, sites 1 and 2) are part of the northern Clay Belt of Quebec and Ontario, a large physiographic region dominated by clay deposits left by pro-glacial Lake Ojibway (Veillette 1994). Till deposits are characteristic of the low-elevation hills (400 m maximum elevation) that are interspersed within a generally uniform flat landscape. Forest composition shows a latitudinal transition from deciduous-conifer mixedwood forests in the south to conifer-dominated forests in the north. The southern mixedwood area is part of the *Abies balsamea-Betula papyrifera* bioclimatic domain whereas the northern area is part of the *Picea mariana*-moss bioclimatic domain (Saucier *et al.* 1998). Fire and insect outbreaks are the main natural disturbances in these forest landscapes (Morin *et al.* 1993, Bergeron *et al.* 2001, Bergeron *et al.* 2004).

We selected one site in the southern mixedwood and another in the northern coniferous forest. The mixedwood site was at the Lake Duparquet Research and Teaching Forest (LDRTF; 48°30' N, 79°22' W; Fig. 1.1, site 1). The LDRTF is a 8045-ha forest landscape composed of mainland, islands and peninsulas (Harvey 1999). Fire regime and fire history maps (Fig. 1.1) have been reconstructed for the area (Bergeron 1991, Dansereau and Bergeron 1993). The mainland fire regime in this study site is characterized by high-intensity fires. Thirteen fires within LDRTF over the last three centuries have created a complex natural forest mosaic. Stand composition varies according to time since fire, from early seral stands dominated by deciduous (trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*)), to mixed stands (with white spruce (*Picea glauca*)), to coniferous stands (dominated by balsam fir (*Abies balsamea*) and eastern white cedar (*Thuya occidentalis*)) (Bergeron and Dansereau 1993, Bergeron 2000). Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) occur in localised area throughout the region as well. Three spruce budworm (*Choristoneura fumiferana*) outbreaks occurred in the last century, the most recent between 1970 and 1987, an event that was especially severe in balsam fir-dominated stands (Morin *et al.* 1993, Bergeron *et al.* 1995). Our study took place in the eastern part of the LDRTF mainland, a conservation area that has been lightly affected by anthropogenic disturbances. This study site is hereafter referred to as the "mixedwood" site ("mxw").

The conifer-dominated study site, hereafter the "conifer" site ("con"), was located at the Muskuuchii Hills projected Biodiversity Reserve (50°12' N, 78°43' W; Fig. 1.1, site 2, (Gouvernement du Québec 2005). The biodiversity reserve covers 80100 ha, of which half consists of peat bogs on organic deposits that support black spruce stands of varying densities. The other half is composed of terraces and hills characterized by well-drained till, sand and fine sediment deposits (Gouvernement du Québec 2005). We selected a 1000-ha portion of the landscape dominated by mature stands (>120 years) on mesic sites. From 1998 to 2000, experimental partial cuts were conducted in a case-control manner that resulted in a mosaic of intact and partial cut stands. Black spruce and jack pine dominate forest composition. Other species include balsam fir, trembling aspen and paper birch.

We also made foraging observations of black-backed woodpeckers at a third study site located in the *Picea mariana*-moss bioclimatic domain about 200 km east of the Muskuuchii Hills site. This site consisted of a burned conifer forest landscape that originated from a 1996 fire (50°30' N, 75°43' W; Fig. 1.1, site 3). Vegetation was co-dominated by black spruce and jack pine with scattered white birch and trembling aspen. This fire was highly variable in severity and about 50% of the burned area consisted of areas of low burn severity (dominance of green trees) and unburned stands. At this site, foraging activities of black-backed woodpeckers were recorded opportunistically to provide additional information on the foraging ecology of this species in burned forest habitats. This 8-year-old coniferous burn landscape is hereafter referred to as the "burn" site ("burn").

1.4.2 Selection and characterization of sampling blocks

We studied woodpecker foraging ecology at pre-defined large (~20-50 ha) sampling blocks in the mixedwood and conifer sites (Fig. 1.1). At the mixedwood site, sampling blocks were distributed in four 60-year classes (60-120, 120-180, 180-240 and >240 years), based on fire history mapping of the Lake Duparquet area (Dansereau and Bergeron 1993, Harvey 1999). We selected three sampling blocks in forests of each age class (total of 12 blocks). Each sampling block consisted of one or two linear transects with a 100-m buffer on each side within which woodpecker foraging observations were conducted. Blocks ranged from 24 to 40 ha in size and totalled 448 ha at the mixedwood site. At the conifer site, six sampling blocks ranging from 20 to 48 ha and totalling about 268 ha were selected. Three of these were in unharvested mature stands and the other three were located in partially harvested mature stands.

At each forest block, sampling stations ≥ 200 m apart were distributed along linear transects (mxw = 112; con = 34). These were used to characterize and provide baseline information on the relative abundance of foraging substrates available to woodpeckers. At each sampling station, we sampled all trees >5 cm of diameter at breast height (dbh) within 600 m^2 rectangular plots (60-m long, 10-m wide). For each tree, we noted its species, dbh and degradation stage. Tree degradation was classified based on visual appearance in 5 categories according to a modified version of Maser et al. (1979): Deg1 (alive, >20% foliage); Deg2 (declining, <20% foliage); Deg3 (recently dead, hard wood, firm bark cover); Deg4 (moderate degradation, soft wood, no dead foliage present, no small twigs, some branches remaining, usually intact top); Deg5 (high degradation, soft decomposed wood, very few branches, often broken top).

Bird surveys were conducted within sampling blocks to determine the relative occurrence of each woodpecker species. At every sampling station, we used 1-min playbacks (territorial drumming and contact calls) of each species successively (separated by a 1-min period) for a total of 12 min at each station. All individuals detected within a 75-m radius during this period were recorded. Each station was visited twice between mid-May and mid-June 2003, the peak of the breeding season of these species in our study area. A species was considered present if it was detected at least once in either visit. Surveys were conducted during morning hours (sunrise to 09h30) of good weather (days of low wind and no rain). Vegetation and woodpecker sampling were conducted in 112 and 34 sampling stations respectively in the mixedwood and conifer study sites.

1.4.3 Foraging observations

Observations of foraging woodpeckers were made from mid-May to early July in 2003 and 2004 at the mixedwood and conifer sites and in June 2004 at the burn site. For mixedwood and conifer sites, observers walked systematically along the pre-defined linear transects. When a bird was heard or seen within 100 m of the transect line, it was followed until it flew out of sight or up to a maximum of 10 min (hereafter an "observation bout"). A bird was considered to be foraging if it remained on a given tree for at least 10 sec and was seen foraging at least once (i.e. one foraging technique used, see below). An observation bout could include a single or multiple trees. A sampling procedure was used in order to reduce the possibility of re-sampling the same individuals (birds were not banded). After data were collected on a given individual, we continued walking the transect until we found an individual of a different gender or species. Moreover, two consecutive observation bouts of the same species and gender had to be separated by at least an hour. We also distributed our sampling efforts among sampling blocks so that observations of foraging birds were made at the highest number of different locations as possible. No pre-defined sampling blocks were planned at the burn site. Instead, foraging observations were made in proximity to sampling stations (>400 m apart) that were distributed throughout the burn for another research project (Chapter 4); similar precautions were taken in sampling different areas of the burned landscape.

During each observation bout, we recorded foraging activities continuously using a tape recorder. Information was later transcribed using instantaneous sampling (i.e. fixed-interval time point; Martin and Bateson 1993). Observation sessions were divided into 5-sec periods at the end of which we noted the corresponding predefined foraging activity (see below). During observation bouts, we noted woodpecker species, sex, date and time of day and recorded the following four variables related to foraging behaviour: foraging height, tree section, substrate condition and foraging technique. Foraging height was recorded in four classes: lower, middle and upper third of the tree, and coarse woody debris (downed logs and stumps <1 m height). Tree section corresponded to the specific part of the tree used: trunk, branch, junction of trunk-branch and foliage. Substrate condition referred to wood condition where the bird was foraging (e.g. branch) and was noted as live or dead. We distinguished between six foraging techniques following an adaptation of classifications used by other authors (Jackson 1970, Hogstad 1976, Murphy and Lehnhausen 1998, Imbeau and Desrochers 2002): gleaning (picking insects from the surface and within bark fissures); pecking (striking the wood superficially); scaling (flaking off the bark); excavating (digging holes to access deep wood-dwelling arthropods); sap licking (digging sap holes and sucking sap from ringed trees); fly catching (short flight made for capturing aerial insects). Other behaviours not related to foraging were also recorded and classified as movement (vertical or perpendicular changes in position) or miscellaneous (e.g. drumming, grooming, resting, etc.). While a first observer recorded foraging activities, a second observer marked each tree used for foraging (flag tape and geo-referenced location). At the end of the observation bout, we characterized each used tree by recording tree species, dbh, tree position (standing or fallen) and tree degradation. Observation bouts were difficult to record for the pileated woodpecker so we searched for the large, deep and typically rectangular foraging excavations of the pileated woodpecker (Bull and Jackson 1995) and characterized trees with recent (<1 year) foraging excavations.

1.4.4 Wood-dwelling arthropod sampling

To investigate the link between tree selection, foraging behaviour and prey type, we collected invertebrates through wood dissection in a subset of trees that were used for foraging by the four *Picoides* species. Although wood dissection involves logistic and time constraints, it is a useful technique to examine potential woodpecker prey as it gives an instant and exact portrait of the invertebrate assemblage present in selected trees (Saint-Germain *et al.* 2007). It is also more appropriate than superficial bark sampling when one seeks to determine the presence of deep wood-dwelling arthropods. It is, however, limited by identification problems as most specimens are found at the larva stage and thus necessitate taxonomic expertise to identify. For each woodpecker species, we selected trees among those most intensively used in 2004 (based on observed foraging time). A total of 20 trees were selected for insect sampling at the mixedwood site, corresponding to foraging trees of downy (10) and hairy (10) woodpeckers. Similarly, 20 trees used by black-backed (10) and American three-toed (10) woodpeckers were selected at the conifer site. An additional seven trees used by black-backed woodpeckers were selected from the burn site. Thus a total of 47 foraging trees were cut down and dissected to collect and identify wood-dwelling arthropods.

Tree cutting and dissection were conducted during the last two weeks of June 2004 to obtain a representative portrait of the prey species present in the wood when foraging observations were made. From each tree, two 1-m bole segments were taken, the first at the base of the tree (0-1 m) and the second at 4 m (conifers) or half of the tree height (deciduous trees). For deciduous trees, we also collected two live and two dead branches per tree (about 5 cm diameter at the trunk junction). These wood samples were placed in plastic bags and taken to the laboratory for wood dissection. Bark was carefully removed and all larvae and adult invertebrates were collected. The bole segments were then cut in smaller pieces using axes and hatchets, following signs of insect presence (i.e. galleries) and all insects were collected. Specimens were preserved in 70% ethanol and later identified by M. Saint-Germain (McGill University). Specimens were identified to family, genus or species depending on available identification criteria. All specimens were classified by their length (> or <1 cm) and by the portion of the bole in which they were found (Bark-associates: within or under the bark; Wood-associates: within xylem).

1.4.5 Statistical analyses

Occurrence of each woodpecker species was compared between the mixedwood and conifer study sites using log likelihood ratio (G) tests. We also examined within-site variation in woodpecker occurrence. For the mixedwood site, we compared the relative occurrence of each woodpecker species among the four forest age classes. For the conifer site, comparisons were made between mature unharvested and partially logged forests.

Selection of trees for foraging was assessed for individual woodpecker species by comparing proportions of used (data from observation bouts) and available (data from sampling stations) trees for different tree variables. For this purpose, each observation bout was assigned to the closest sampling station. Foraging trees were used to calculate use proportions. For instance, if one out of four trees used by a male downy woodpecker during an observation bout was a trembling aspen, then aspen would represent 25% of tree species used. Use proportions were compared to corresponding available proportions derived from vegetation data at each sampling station. Comparisons involved standing trees only since these comprised the vast majority of foraging trees and could be directly compared to available standing tree data. Some observation bouts were recorded in the same locations and thus more likely to have involved the same individuals. Therefore, when more than one observation bout was conducted close to the same sampling station for the same species and gender in a given year, these observation bouts were merged and counted for only one comparison.

Use and available proportion comparisons were made using Compositional Analysis (Aebischer *et al.* 1993). Compositional analysis ranks habitat components based on log-ratio differences between use and available proportions. The use of ranking provides preference that is not influenced by the choice of components under study (Johnson 1980) and the use of log-ratios eliminates the problem of non-independence of habitat proportions in compositional data (Aitchison 1986). This approach generally uses the animal instead of each location (e.g. foraging tree) as the sampling unit which circumvents problems of pseudoreplication (Aebischer *et al.* 1993). Although woodpeckers were not banded and could not be individually identified in our study, using sampling stations as our sampling units allowed us to pool data based on site location and to reduce the level of pseudoreplication.

Moreover, this approach allowed making comparisons at a more local scale which may help detect consistent patterns in tree selection within heterogeneous landscapes such as ours. Tree selection analyses were conducted on the yellow-bellied sapsucker and the downy, hairy and pileated woodpeckers at the mixedwood site, and on the hairy, black-backed and American three-toed woodpecker at the conifer site. No comparisons were made at the burn site because we had no vegetation data for calculating available proportions. Tree selection analyses were first conducted on tree degradation using two (alive, dead) and five (deg1 to deg5) classes. A second set of analyses were conducted by combining degradation and tree species variables (live deciduous, dead deciduous, live conifer, dead conifer). Tree selection analyses were also conducted on dbh using four diameter classes: 5.0-14.9, 15.0-24.9, 25.0-34.9 and >35 cm. All analyses were performed with Compos Analysis Version 5.1 (Smith 2003).

Foraging behaviours recorded during observation bouts were compiled for each variable as a percentage of time per observation bout (Pechacek 2006). For instance, if a given bird was observed excavating a total of 6 sampling points during a 60-sec observation bout (i.e. total of 12 5-sec sampling points), the percentage of time spent excavating would have been 50% (6 of 12 sampling points).

Differences in the foraging ecology of *Picoides* woodpeckers were investigated using discriminant analysis (Legendre and Legendre 1998). Both foraging behaviour and tree use variables were included in the analysis. For this purpose, tree use variables were also compiled as percentage of time per observation bout, with the exception of dbh which corresponded to the mean dbh of all trees used during each observation bout. Some variables were excluded from the analysis because of high multicollinearity. Each observation bout was weighted so that all observation bouts of the same species and gender at the same sampling station contributed to only one degree of freedom in the analysis. Data on the black-backed woodpecker at the burn site were not included because some of the independent variables in the analysis had zero standard deviation which violates an assumption of discriminant analysis. However, discriminant scores for this data set were calculated and added to the discriminant function plot to allow comparisons. Discriminant analysis was performed using SPSS 15.0. Mean proportions of foraging time for variables presented in tables and figures are based on weighted means ± 1 SE (weighting by sampling station).

Wood-dwelling arthropods were compared among trees used by the different *Picoides* species. Invertebrates were pooled by tree (sum of two bole segments) and density was calculated as the number of individuals per square meter of bark sampled (branches were excluded from analyses). Densities for each wood-dwelling arthropod species or group (e.g. by size) for which at least 20 individuals were captured were compared between trees used by co-occurring species at each site (downy and hairy woodpeckers at the mixedwood site; black-backed and American three-toed woodpeckers at the conifer site) or for the black-backed woodpecker at the conifer and burn sites using Mann-Whitney non-parametric tests.

1.5 Results

1.5.1 Woodpecker occurrence

Four of the six woodpecker species differed in their relative occurrence between the southern mixedwood and northern conifer sites (Fig. 1.2). The downy woodpecker ($G = 29.1$, df = 1, $P < 0.001$) and the pileated woodpecker ($G = 0.2$, df = 1, $P = 0.696$) were both restricted to the mixedwood study site, although this last species responded only once to playbacks. Nevertheless, the observation of several pileated woodpecker individuals and active nests as well as many fresh typical pileated woodpecker foraging excavations were evidence of its presence in the mixedwood area. In contrast, no pileated woodpecker individuals and few foraging marks were observed at the conifer study site. The American three-toed woodpecker ($G = 8.1$, df = 1, $P < 0.01$) and the black-backed woodpecker ($G = 16.0$, df = 1, $P < 0.001$) were found almost exclusively at the conifer study site. The yellow-bellied sapsucker was present at both study sites but was much more abundant at the mixedwood than the conifer site ($G = 27.8$, df = 1, $P < 0.001$). The hairy woodpecker was the only species to be found in similar frequency at the mixedwood and conifer sites ($G = 2.0$, df = 1, $P = 0.157$). No significant difference was observed in the relative occurrence of woodpecker species in relation to stand age within the mixedwood landscape. At the conifer site however, *Picoides* woodpeckers tended to be more abundant in mature partial cuts than in mature uncut stands

(BBWO, $G = 4.2$, df = 1, $P < 0.05$; HAWO, $G = 4.8$, df = 1, $P < 0.05$; ATWO, $G = 3.3$, df = 1, $P = 0.068$; species code in Table 1.1).

1.5.2 Species-specific selection of foraging trees

Foraging activities of woodpeckers were recorded during 266 observation bouts totalling 16 h 18 min of field observations. A total of 767 foraging trees were characterized during the two-year study. Pooling foraging trees of each species by sampling station and retaining only standing trees reduced the sample size to 191 comparisons (Table 1.1). Compositional analysis revealed clear and distinct patterns of tree selection among species. All use proportions reported below are based on mean proportion per observation bout (after pooling per sampling station).

All species showed significant selection patterns for tree degradation (Fig. 1.3). Two species, the yellow-bellied sapsucker and downy woodpecker, showed a clear preference for live over dead trees (YBSA: Wilks' $\lambda = 0.385$, $P < 0.001$, df = 1; DOWO: Wilks' $\lambda = 0.476$, $P < 0.001$, df = 1). Live trees represented 92% and 88% of all trees used for foraging by, respectively, the yellow-bellied sapsucker and the downy woodpecker, whereas they represented 74 % of available trees. When comparing the five degradation classes, both species showed a preference for less degraded trees (YBSA: Wilks' $\lambda = 0.186$, $P < 0.001$, df = 4; DOWO: Wilks' $\lambda = 0.172$, $P < 0.001$, df = 4). Snag preference was observed for the other four woodpecker species (Fig. 1.3), although results varied depending on the number of degradation classes involved in comparisons. The pileated woodpecker used snags 62% of the time and showed a significant preference for dead trees (Wilks' $\lambda = 0.769$, $P = 0.020$, df = 1). Over the five degradation classes, this species showed a significant preference for the highest degradation class (Deg5), and to a lesser extent declining trees (Deg2), over other degradation classes (Wilks' $\lambda = 0.487$, $P = 0.013$, df = 4). The hairy woodpecker used snags 47% and 78% of the time at the mixedwood and conifer sites, respectively. Selection for snags was significant in the conifer landscape only (MXW: Wilks' $\lambda = 0.945$, $P < 0.224$, df = 1; CON: Wilks' $\lambda = 0.483$, $P = 0.016$, df = 1). At both sites, the hairy woodpecker used a variety of degradation stages. Although no significant pattern relating to degradation class was found for this species in either the mixedwood or conifer sites, hairy woodpeckers tended to select declining trees. It was also the only species to use moderately degraded snags (Deg4) in relatively high proportions. The American three-toed woodpecker used live (64%) and dead (36%) trees in similar proportions to their availability and thus showed no significant preference for either tree degradation class (Wilks' λ =0.074, P =0.809, df = 1). When considering all five degradation classes, however, this species showed a preference in decreasing order for recently-dead (Deg3), declining (Deg2) and live trees (Deg 1) (Wilks' λ =0.082, P =0.001, df = 4). The black-backed woodpecker used dead trees 80% of the time and showed the highest preference toward dead trees (Wilks' λ = 0.468, P = 0.005, df = 1). This species selected recently-dead trees (Deg3), and to a lesser extent declining trees (Deg2), more than any other degradation class (Wilks' λ = 0.240, P =0.012, df = 4).

All woodpecker species showed significant selection for specific combinations of tree species (deciduous vs. conifer) and degradation (live vs. dead). The principal tree species used are shown in Figure 1.4. Yellow-bellied sapsuckers selected live trees that included both deciduous and conifers trees (Wilks' λ = 0.393, $P < 0.001$, df = 3). Live paper birch and balsam fir were the most frequently used. Pileated woodpeckers selected both deciduous and conifer snags, which included mainly trembling aspen (30%) and balsam fir (21%) (Wilks' λ = 0.160, $P < 0.001$, df = 3). Live conifers were preferentially selected over live deciduous trees and consisted mainly of white cedar (17%). Downy woodpeckers mainly selected live deciduous trees (paper birch = 42%; trembling aspen = 39%) over both conifers and dead deciduous trees (Wilks' λ =0.085, $P < 0.001$, df = 3). Hairy woodpeckers showed a significant selection for deciduous trees, both in their live and dead stages, over conifers. This pattern was similar at the mixedwood and conifer sites (Mixedwood: Wilks' λ =0.095, $P < 0.001$, df = 3; Conifer: Wilks' λ = 0.119, P = 0.019, df = 3). Both American three-toed (Wilks' λ = 0.318, $P < 0.001$, df = 3) and black-backed (Wilks' λ =0.053, $P < 0.001$, df = 3) woodpeckers clearly selected conifers over deciduous trees. The American three-toed woodpecker specialized mainly on black spruce, which was used in dead (25%) and live stages (60%). In contrast, black-backed woodpeckers used mainly dead stages of both black spruce (32%) and jack pine (45%).

All species selected toward larger trees except the American three-toed woodpecker (Wilks' $\lambda = 0.262$, $P = 0.165$, df =3). At the mixedwood site, mean diameter of foraging trees varied between 23 (yellow-bellied sapsucker) and 28 cm dbh (pileated woodpecker). At the conifer site, mean dbh varied between 14 (American three-toed woodpecker) and 20 cm (hairy woodpecker).

1.5.3 Differences in foraging ecology of woodpeckers

The yellow-bellied sapsucker showed little overlap in foraging with *Picoides* species. Yellow-bellied sapsuckers concentrated foraging activities on trunk of live trees (Table 1.2, Fig. 1.5); this was the only species to use sap-licking as its main foraging technique (Fig. 1.6). Although they differed in several aspects of their foraging ecology, all four *Picoides* species used dead wood substrates (snag or dead portion of live trees) for a substantial portion of their foraging time (Fig. 1.5). At mixedwood and conifer sites, mean percentage of time spent foraging on dead wood substrates during a observation bout varied from 33% for the downy woodpecker to 89% for the black-backed woodpecker. This proportion was 100% for the black-backed woodpecker at the burn site.

Discriminant analysis showed that species partitioned food resources based on both tree use and foraging behaviour variables (Fig. 1.7, Table 1.3). The first two discriminant functions accounted for 95% of the explained variance. The first discriminant function mainly partitioned *Picoides* based on their relative use of conifers and of scaling foraging techniques. The second discriminant function was mainly associated with the relative use of dead wood substrates and excavation techniques. The downy woodpecker showed little variation in foraging activities in comparison with other *Picoides* (Fig. 1.7). This species used pecking as its main foraging technique (Fig. 1.6) and was the greatest user of branches (Table 1.3). The hairy woodpecker occupied an intermediate position on the discriminant function scatter plot but overlapped broadly with the downy woodpecker. The main differences between these two species were the broader range of foraging techniques used by the hairy woodpecker (Fig. 1.6) and its higher use of trunk and dead wood substrates (Table 1.2, Fig. 1.5). When foraging on branches of live trees, downy and hairy woodpeckers spent respectively 44% ($n =$

86 trees) and 56% (n = 25 trees) of their time on dead versus live branches. Although the hairy woodpecker used similar foraging techniques in the mixedwood and conifer sites, it foraged more often on conifers, trunks and coarse woody debris at the conifer site (Table 1.3). The American three-toed woodpecker used dead substrates 61% of the time while foraging (Fig. 1.5). It was the only woodpecker to use all bark-foraging techniques as well as the only *Picoides* species to use sap-licking for a significant portion of its foraging time (20%, Fig. 1.6). Scaling was the preferred technique used by this species, being employed 44% of the time. The black-backed woodpecker was the species most associated with dead wood (Fig. 1.5 and 1.7) and the species that used excavating most frequently (Fig. 1.6). Great overlap between the foraging activities of this species was observed at the burned and unburned sites (Fig. 1.7). The main difference was the higher use of coarse woody debris at the unburned site (Table 1.3).

1.5.4 Wood-dwelling arthropods in foraging trees

The foraging trees we used for wood dissection were representative of the species-specific tree selection patterns described above (Table 1.4). Foraging trees of hairy woodpeckers were overall more degraded than those of downy woodpeckers. Foraging trees of both American three-toed and black-backed woodpeckers consisted mainly of recently dead spruce trees, although foraging trees of the American three-toed were smaller in diameter than those of black-backed woodpeckers. Also, conifer trees used by black-backed woodpeckers at the burn site were slightly more degraded than those used at the conifer site.

We collected 773 arthropods from the trunk segments, of which 451 were wood-feeding coleoptera (Cerambycidae, Buprestidae, Scolytinae (sub-family of Curculionidae)). Additionally, 11 arthropods were collected in dead branches (none in live branches) of deciduous trees used by either downy or hairy woodpeckers. Cerambycidae and Scolytinae dominated the wood-feeder insect assemblage and occurred in foraging trees of virtually all *Picoides* species, though Scolytinae were totally absent from both unburned and burned trees used by black-backed woodpeckers.

Foraging trees used by co-occurring woodpecker species supported different arthropod assemblages (Fig. 1.8). Foraging trees of hairy woodpeckers contained significantly higher densities of total, large and non wood-borer arthropods than trees used by downy woodpeckers. Foraging trees of black-backed woodpeckers supported higher densities of wood-associated arthropods than trees used by American three-toed woodpeckers. In contrast, Scolytinae were exclusively found in trees selected by American three-toed woodpeckers. In terms of individual species, *Monochamus* sp. were more abundant in black-backed than American three-toed woodpecker trees. Two other abundant insects, *Acmaeops proteus* and *Pogonocherus* sp. were found exclusively under the bark of spruce trees, especially in those used by American three-toed woodpeckers. Foraging trees of black-backed woodpeckers at unburned and burned conifer sites supported similar densities of Cerambycidae, large and wood-associated arthropods. However, these consisted mainly of *Monochamus* sp. at the unburned conifer site whereas large deep-borer Cerambycidae consisted almost exclusively of *Arhopalus foveicollis* at the burn site. Foraging trees of black-backed woodpeckers at the unburned site contained higher total, small, bark-associated as well as non wood-borer arthropod densities.

1.6 Discussion

1.6.1 Dead wood use by woodpeckers

Our results indicate that dead wood is an important foraging substrate for five of the six bark-foraging woodpecker species present in the eastern North American boreal forest. Yet, woodpeckers differed in their association with dead wood, their preference for specific tree conditions, and their foraging behaviours, thereby significantly partitioning their foraging niches. Woodpecker species can be categorized according to their selection patterns for specific stages of tree degradation. The yellow-bellied sapsucker and pileated woodpecker represent opposite ends of a degradation gradient. The yellow-bellied sapsucker, well-known for its sap-licking foraging behaviour and the importance of sap in its summer diet (Tate 1973, Eberhardt 2000), was the species most strongly associated with live trees. Yet, sapsuckers spent about 12% of their foraging time on dead wood, typically on dead branches of deciduous trees where they pecked and gleaned to capture sub-cortical and cortical insects (Tate 1973).

At the opposite end of this degradation gradient was the pileated woodpecker, a species that selected mostly highly degraded snags. This woodpecker's diet is composed primarily of forest-dwelling ants, in particular carpenter ants (*Camponotus* spp.), but may also include bark and wood-boring beetles and other arthropods (Hoyt 1957, Otvos and Stark 1985, Bull *et al.* 1992). Given our observations were based on this species' typically large foraging excavations (Bull and Jackson 1995), our results for the pileated woodpecker are restricted to its use of carpenter ants. Large snags, logs and stumps with a certain amount of decay are known as important nesting sites for carpenter ants (Sanders 1970, Torgersen and Bull 1995). More degraded snags were indeed the preferred foraging trees of pileated woodpeckers, a pattern similar to that found in other studies (Bull 1987, Bull and Holthausen 1993). Live trees, in particular white cedar, also provided important foraging substrates for this species. White cedar is susceptible to heartwood decay (Farrar 1996) and therefore provided both soft wood and long-term suitability, two conditions that favour carpenter ants (Sanders 1970).

In comparison with the yellow-bellied sapsucker and the pileated woodpecker, *Picoides* species used trees in intermediate stages of degradation. Although *Picoides* species made in most cases extensive use of dead wood, our results highlight significant differences in each species' specialization in patterns of substrate use, associated wood-dwelling arthropods and foraging behaviour.

For downy and hairy woodpeckers, dead wood may be provided by deciduous snags but also by dead portions of live deciduous trees such as dead branches or other defects. Indeed, although only 12% of foraging trees used by downy woodpeckers were dead, this species spent about 33% of its time on dead portions of live trees. Similarly, 47% of foraging trees used by hairy woodpeckers were dead, although this species spent 61% of its time on dead substrates. These results are also consistent with the broad use of live but declining trees by these two species. This stage of tree degradation was the second most selected by downy woodpeckers and the most selected by hairy woodpeckers. In his detailed account of the feeding behaviour of downy woodpeckers on paper birch, Kilham (1970) noted trees with broken branches and other defects to be the most attractive to downy woodpeckers. The only invertebrates collected in branches with our wood dissection were found in dead branches. Saproxylic insects found during our dissection of live deciduous trees (i.e. Cerambycidae *Saperda calcarata*, Scolytinae *Trypodendron retusum* and *Xyloterinus politus*) are generally associated with early stages of tree degradation (Hanks 1999, Hammond *et al.* 2001). The predominant use of pecking by these woodpecker species was consistent with the presence of these sub-cortical prey. These findings suggest partial mortality in deciduous trees may play an important role in providing foraging substrates for these two species.

In contrast with the downy woodpecker, which used mostly live deciduous trees, hairy woodpeckers used snags extensively and in various degradation stages. Indeed, about half of hairy woodpecker foraging trees were dead, a proportion similar to what has been reported for this species throughout its range (Raphael and White 1984, Morrison and With 1987, Morrison *et al.* 1987, Weikel and Hayes 1999). The hairy woodpecker was the only species to make broad use of dead trees in intermediate stages of degradation (i.e. Deg4). Wood-feeding insects are typically more abundant in middle to late than in earlier stages of decay in aspens (Saint-Germain *et al.* 2007). In our study, the more degraded deciduous trees used by hairy woodpeckers supported higher densities of large wood-dwelling arthropods, both under the bark and within the wood, than live trees used by downy woodpeckers. Invertebrate assemblages however consisted of many different guilds including wood-feeders, fungivores and sub-cortical predators. The use of scaling and excavating as additional foraging techniques by the hairy woodpecker, in comparison with the downy woodpecker, was thus consistent with higher use of dead substrates (branches or trunks), and a feeding strategy for capturing bark and wood-associated arthropods.

American three-toed and black-backed woodpeckers were found almost exclusively in the northern coniferous landscape. Both species specialized on recently dead conifers for foraging. This selection for recently dead trees is principally linked to abundance patterns of their prey in conifers. In eastern Canadian forests, most wood-feeding Coleoptera associated to conifers are found in early stages of decay of their hosts (Vanderwel *et al.* 2006, Saint-

Germain *et al.* 2007). Yet, these two woodpecker species showed several differences in their specific patterns of tree selection and foraging behaviours.

The American three-toed woodpecker specialized on spruce and made extensive use of both declining and recently dead trees. This preference and the associated use of scaling and pecking as predominant foraging techniques is consistent with a specialization on bark beetles (Goggans *et al.* 1989, Imbeau and Desrochers 2002, Pechacek 2006). Indeed, foraging trees of American three-toed woodpeckers contained more Scolytinae beetles than black-backed woodpecker foraging trees and more saproxylic invertebrates associated with bark. Although the use of live trees by this species may be linked to bark beetle-feeding specialization (declining trees, Deg2), our results also emphasize the use of live trees by American three-toed woodpeckers for sap-licking (healthy trees, Deg1). Although this behaviour has been documented for the American and European (*Picoides tridactylus*) three-toed woodpeckers during the breeding season, such foraging behaviour has been generally reported to be marginal (Villard 1994, Imbeau and Desrochers 2002, Pechacek 2006). For instance, sap-licking represented only 1-2% of woodpecker foraging time in studies in North America (Imbeau and Desrochers 2002) and Europe (Pechacek 2006). In contrast, we found about 20% of foraging time was devoted to sap-licking (i.e. sap licking and related drilling behaviours) that occurred through a series of small sap holes drilled in black spruce (see also Imbeau and Desrochers 2002)). These results suggest that sap licking may be much more important during the breeding season than previously reported for the American three-toed woodpecker.

The black-backed woodpecker showed the strongest association with dead wood as it foraged almost exclusively on dead wood. In contrast to the American three-toed woodpecker, its selection for recently dead conifers was primarily linked to the presence of wood-associated arthropods (Murphy and Lehnhausen 1998, Saint-Germain *et al.* 2007). Indeed, preferred foraging trees for the black-backed woodpecker contained significantly higher abundances of wood-associated arthropods, in particular *Monochamus* spp, than American three-toed woodpecker foraging trees. Although similar foraging behaviour was observed at the unburned and burned conifer sites, excavation was used slightly more at the burn site reflecting the dominance of the wood-borer *Arhopalus foveicollis* in burned trees; larvae of this Cerambycidae was found exclusively within the wood. In contrast, some *Monochamus* larvae in their first instar stages (Rose 1957) and other saproxylic species were also present under the bark of unburned trees, a finding that explains the slightly higher use of scaling at the unburned conifer site.

Although our sample size was smaller for the hairy woodpecker at the conifer site, our results show that the hairy differed in its foraging tree selection from the black-backed and American three-toed woodpeckers by its higher use of deciduous trees. This differential selection resulted in higher use of branches and foraging heights, a finding consistent with previous studies (Bull *et al.* 1986, Villard 1994).

Picoides woodpeckers generally experience significant increases following recent disturbances that generate or involve insect outbreaks in conifer forests (Hutto 1995, Fayt *et al.* 2005, Covert-Bratland *et al.* 2006). The differences in the foraging ecology of the black-backed, American three-toed and hairy woodpeckers that we observed in unburned forests are consistent with the foraging specializations reported in previous studies conducted in recent burns (Villard and Beninger 1993, Murphy and Lehnhausen 1998, Nappi *et al.* 2003). In both burned and unburned coniferous forests, the presence of these species is tightly linked to the abundance of wood-dwelling arthropods and thus to the presence of dying and recently-dead conifers (Murphy and Lehnhausen 1998, Imbeau and Desrochers 2002, Covert-Bratland *et al.* 2006, this study). Moreover, foraging specializations of these woodpecker species may also explain the variable response patterns of these species following different disturbances. Foraging specialization of the black-backed woodpecker on wood-beetle borers is consistent with its propensity to occupy burned coniferous forests (Hutto 1995, Hannon and Drapeau 2005). Conversely, the more pronounced response of the American three-toed woodpecker to bark beetle outbreaks is consistent with this species' foraging specialization (Fayt *et al.* 2005).

1.6.2 Linkages between foraging behaviour and distribution of woodpeckers

Woodpecker distributions in eastern boreal forests may be explained in large part by the foraging specializations observed in this study. The high specialization of downy woodpeckers on live deciduous trees suggests that this species' northern distribution is largely limited by the availability of deciduous foraging trees (Nappi 2000, Setterington *et al.* 2000) which explains the absence of this species at our northern conifer site. In contrast, the broader foraging niche of the hairy woodpecker likely contributed to its presence at our conifer site. Although this species uses conifers for foraging (Murphy and Lehnhausen 1998, Covert-Bratland *et al.* 2006), it is generally rare in eastern conifer-dominated forests even following fire, and its presence is generally linked to the local abundance of deciduous trees (Setterington *et al.* 2000, Nappi 2000). The pileated woodpecker is well-known for requiring large trembling aspen for nest excavation (Harestad and Keisker 1989, Martin *et al.* 2004) and this species is generally limited by the availability of large aspen trees in the north-eastern portions of its range (Vaillancourt 2006, Gasse 2007). We found this species to use the largest foraging trees, thereby suggesting that limited availability of large trees for foraging may further contribute to the rarity of this species in northern boreal landscapes. Although both the yellow-bellied sapsucker and the American three-toed woodpecker used sap-licking in our study, our results suggest these species overlapped only slightly in their foraging ecology. The former species foraged on balsam fir and white birch, tree species more abundant in the southern mixedwood boreal forests. Conversely, the high specialization of the American three-toed woodpecker on both live and dead spruce restricts this species mainly to northern spruce forest landscapes.

Black-backed woodpeckers use a broader range of conifer species than the American three-toed woodpecker, which may explain its broader distribution (Bull *et al.* 1986, Villard and Beninger 1993, Setterington *et al.* 2000, Dixon and Saab 2000); yet we detected only one black-backed woodpecker at our mixedwood site during two field seasons, even though we surveyed fir-dominated forests > 200 year old. These stands supported high densities of balsam fir snags created after the most recent spruce budworm outbreak between 1970-1987 (Morin *et al.* 1993, Bergeron *et al.* 1995). Saproxylic insect colonization of dying and recently dead balsam fir following budworm defoliation has been well documented (Belyea 1952, Rose 1957). About 36% of all dead balsam fir sampled during our study (*n* = 1034 trees) revealed old foraging excavations of black-backed or hairy woodpeckers. We also found several old nests typical of the black-backed woodpecker (1-3 m height, in conifers). Therefore, the post-epidemic budworm period probably provided suitable habitats for the black-backed as well as the hairy woodpecker. However, most of these snags were highly degraded by time of our study and probably supported few saproxylic insects.

1.6.3 Conservation and management implications

Most bark-foraging woodpeckers in eastern Canadian boreal forests show strong affinities to dead wood for foraging. Among the six species we examined, the black-backed woodpecker showed the highest use of dead wood substrates and was very specific in its tree selection with regard to degradation stage. This finding suggests a high dependence of this species on dead wood and likewise a high vulnerability to the reduction of dead wood in managed boreal forests.

Providing trees of high forage value for woodpeckers in managed boreal forests may require different strategies for species associated with deciduous trees vs. conifers. For deciduous trees, suitable dead wood substrates may be provided by both the partial mortality present in live trees (e.g. branches) and the dead and more degraded trees. In contrast, the temporal window of foraging opportunities appears to be much shorter in conifers, which generally support high densities of saproxylic insects mainly in their declining and recently dead stages (i.e. <5 years after tree death). For the black-backed and the American three-toed woodpeckers, maintaining foraging habitat in managed forest landscapes therefore implies ensuring a continuous recruitment of recent conifer snags.

In the boreal ecosystem, old-growth and post-disturbance forests are the two most important sources of dead wood in natural forest landscapes (Imbeau *et al.* 1999, Setterington *et al.* 2000, Hannon and Drapeau 2005). Old-growth forests are important foraging habitats for woodpeckers (Setterington *et al.* 2000, Imbeau and Desrochers 2002). Late seral stands are shaped by small-scale mortality processes that may provide a constant recruitment of recent snags (Kneeshaw and Gauthier 2003) and may be particularly suitable for species that favour interior conditions (Gagné *et al.* 2007). Yet, at the landscape scale, natural large-scale disturbances such as fire and insect outbreaks may represent important sources of dead wood and provide high-quality foraging habitats for woodpeckers (Murphy and Lehnhausen 1998, Hannon and Drapeau 2005, Covert-Bratland *et al.* 2006). Although these foraging habitats are ephemeral (e.g. because all snags are generated simultaneously), the recurrence of these events at regional scales provide a more or less continuous source of foraging habitats for woodpeckers. Because these forest types are highly affected by forestry practices, both are of conservation concern for the persistence of woodpecker populations in eastern boreal forests.

The potential of managed forests to provide woodpecker foraging substrates depends on the abundance and quality of dead wood that is maintained and their capacity for future dead wood recruitment. Variable retention in even-aged cutover areas, lengthening of timber rotations and the use of harvesting practices such as partial cutting are forest management approaches that leave standing live and dead wood in the land base (Seymour and Hunter , Sullivan *et al.* 2001, Bergeron 2004). At our conifer site, partial cutting provided suitable foraging habitats for black-backed and American three-toed woodpeckers, as was evidenced by (i) foraging birds being found more often within partial cut stands than in proximate mature forests and (ii) several active nests of these two species occurring within partially cut areas. These partial cuts, while maintaining live trees, also resulted in high amounts of downed logs and in high mortality of standing trees. Given our study took place 3-6 years after partial cutting, downed logs and snags were still in early stages of degradation and supported high abundance of wood-dwelling insects. By creating a combination of open habitat and a high abundance of recently dead trees and downed logs, partial cutting also resembled post-disturbance forests. Indeed, many of the saproxylic insects found during wood dissection (e.g. *Monochamus* spp., *Acmaeops proteus*) are well-known for their high abundance following fire (Gardiner 1957, Saint-Germain *et al.* 2004, Boulanger and Sirois 2007).

Woodpeckers have been considered as good potential indicator, umbrella and keystone species in forest management (Martikainen *et al.* 1998, Martin and Eadie 1999, Mikusiński *et* *al.* 2001, Roberge and Angelstam 2006, Drever *et al.* 2008). In our study, woodpeckers' strong association with dead wood for foraging make them good indicators of the presence of this habitat resource in managed forest landscapes. Moreover, because of their association with specific degradation stages or snag recruitment, woodpeckers could be used as indicators of snag dynamics in managed forests. Maintaining these "process-limited" species (*sensu* Lambeck 1997) would benefit the variety of deadwood-dependent plant and animal species associated with distinct stages of wood degradation.

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1.9 Tables

Table 1.1. Number of foraging trees and observation bouts recorded for six woodpecker species in boreal forests in Quebec, Canada.

			Foraging trees [b, c]				*Foraging bouts* [d]			
Species	Code	Sex	MXW	CON	BURN	Total [d]	MXW	CON	BURN	Total
Yellow-bellied sapsucker	**YBSA**	All	**203 (50)**			**203**	**74 (50)**			**74**
(Sphyrapicus varius)		Female	96			96	32			32
		Male	107			107	42			42
Downy woodpecker	**DOWO**	All	**161 (50)**			**161**	**64 (52)**			**64**
(Picoides pubescens)		Female	92			92	37			37
		Male	69			69	27			27
Hairy woodpecker	**HAWO**	All	**98 (26)**	**25 (9)**		**123**	**33 (26)**	**12 (10)**		**45**
(Picoides villosus)		Female	56	12		68	18	4		22
		Male	42	13		55	15	8		23
American three-toed woodpecker	**ATWO**	All		**95 (20)**		**95**		**34 (22)**		**34**
(Picoides dorsalis)		Female		68		68		19		19
		Male		27		27		15		15
Black-backed woodpecker	**BBWO**	All		**110 (14)**	**34**	**144**		**37 (21)**	**12 (12)**	**49**
(Picoides arcticus)		Female		49	6	55		21	3	24
		Male		61	28	89		16	9	25
Pileated Woodpecker [a]	**PIWO**	All	**41 (22)**			**41**				
(Dryocopus pileatus)										
Total			**613**	**120**	**34**	**767**	**171**	**83**	**12**	**266**

[a] Based on recent foraging excavations.

[b] Number of trees characterized.

[c] Values in ( ) indicate number of comparisons involved in Compositional Analyses.

[d] Values in ( ) indicate weighed sample sizes used for data computations and the discriminant analysis.

Table 1.2. Mean proportion of foraging time spent for different foraging height and tree section classes for five woodpecker species in boreal mixedwood (mxw), conifer (con) and burn (burn) sites. Values represent weighed means ± 1 SE.

	YBSA	DOWO	HAWO		ATWO	BBWO	
	(mxw)	(mxw)	(mxw)	(con)	(con)	(con)	(burn)
Foraging height							
Upper third	36.9 (6.2)	57.0 (6.1)	56.6 (8.3)	24.7 (13.2)	16.1 (6.6)	6.3 (4.9)	7.4 (5.3)
Middle third	39.1 (6.3)	25.6 (4.9)	21.5 (6.4)	22.1 (13.1)	33.5 (7.7)	12.0 (5.9)	16.0 (10.5)
Lower third	24.0 (6.0)	13.6 (3.9)	17.0 (6.2)	10.0 (7.7)	21.0 (6.0)	11.0 (5.9)	45.0 (14.3)
Coarse woody debris	0 (0)	3.9 (2.7)	4.9 (3.9)	43.2 (14.7)	29.4 (8.7)	70.8 (9.8)	31.6 (13.3)
Tree section							
Trunk	80.0 (4.9)	39.8 (5.2)	56.2 (7.9)	90.0 (10.0)	95.3 (3.5)	97.4 (2.3)	99.4 (0.4)
Branches	18.1 (4.8)	52.9 (5.3)	40.6 (8.0)	10.0 (10.0)	0.6 (0.8)	2.1 (2.1)	0.5 (0.3)
Junction	1.9 (1.0)	6.8 (2.3)	3.2 (1.6)	0 (0)	4.2 (3.4)	0.5 (0.8)	0.1 (0.1)
Foliage	0.1 (0.3)	0.5 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 1.3. List of variables included in the discriminant analysis and used to compare foraging ecology of *Picoides* woodpeckers in eastern Canadian boreal forests. Values indicate correlations of these variables with discriminant functions (structure matrix).

Variable		Code	Discriminant function	
			First	Second
Tree species	*Conifer*	Con	0.76*	-0.06
Tree diameter	*Mean DBH*	DBH	-0.23	0.30
Foraging height	*Upper third*	Upp	-0.21	-0.05
	Middle third	Mid	-0.01	-0.25*
	Coarse woody debris	CWD	0.26	0.44
Tree section	*Branches*	Bra	-0.27	-0.03
Substrate condition	*Dead substrate*	Dead	0.17	0.45*
Foraging technique	*Scaling*	Sca	0.38*	-0.22
	Excavating	Exc	0.19	0.63*
	Pecking	Pec	-0.23	0.09
	Gleaning	Gle	-0.20	-0.04

Table 1.4. Characteristics of trees used by foraging woodpeckers and sampled to examine wood-dwelling arthropod composition and abundance.

	DOWO (MXW; n = 10)	HAWO (MXW; n = 10)	ATWO (CON; n = 10)	BBWO (CON; n = 10)	BBWO (BURN; n = 7)
Tree species [a]					
Black spruce			10	10	6
Jack pine					1
Trembling aspen	5	5			
Paper birch	5	5			
Diameter at breast height [b]	24.8 (13.3-31.8)	15.1 (12.5-31.3)	9.5 (6.2-14.3)	17.8 (13.2-22)	15.1 (10.7-20.7)
Degradation class [b]	1 (1-1)	3 (1-5)	3 (2-4)	3 (3-4)	4 (4-4)

[a] Number of trees for each tree species

[b] Median (Min-Max)

1.10 Figures

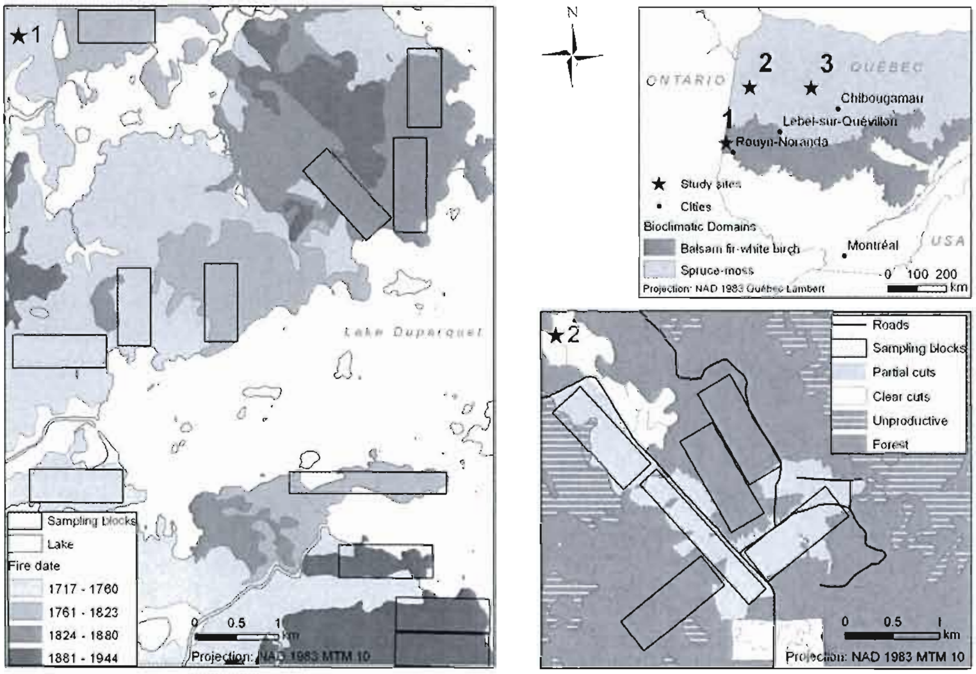

Figure 1.1. Location of study sites (1-Mixedwood site; 2-Conifer site; 3-Burn site) in the boreal forest of Quebec, Canada. Enlargements show location of forest blocks at the mixedwood and conifer study sites within which sampling stations were distributed and foraging observations were made.

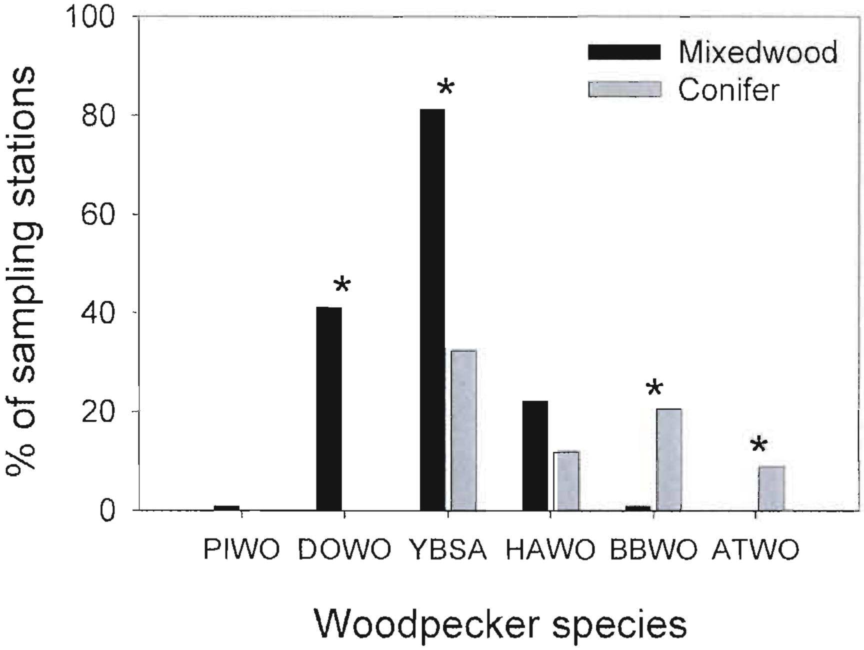

Figure 1.2. Relative occurrence (% of sampling stations) of six woodpecker species at the mixedwood (n = 112) and conifer (n = 34) study sites. Asterisks show significant differences.

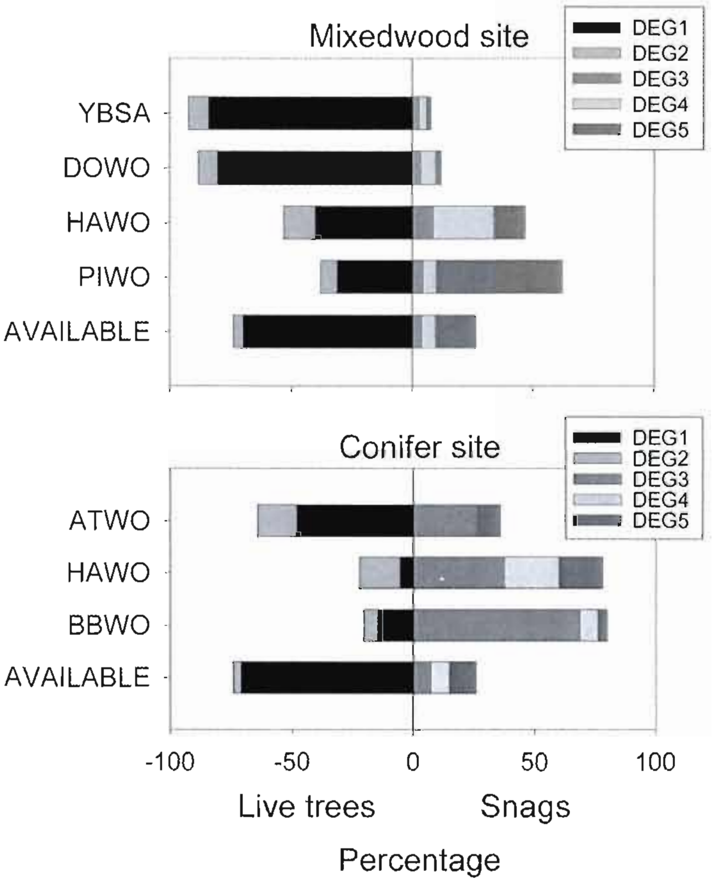

Figure 1.3. Use of foraging trees (mean proportion used) based on tree degradation classes for six woodpecker species at the mixedwood and conifer study sites. Live tree classes (Deg1 = healthy, Deg2 = declining) are identified as negative percentages whereas snag classes (Deg3 = recently dead, Deg4 = moderate degradation, Deg5 = high degradation) are identified as positive percentages. "Available" represent the mean proportion of each class at each site based on all vegetation sampling stations.

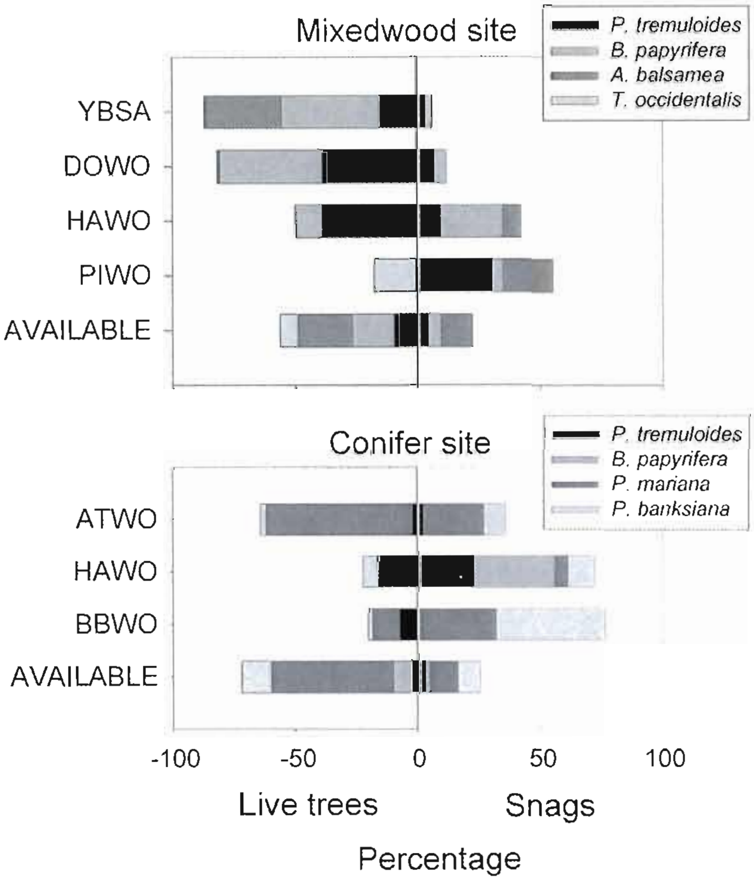

Figure 1.4. Use of foraging trees (mean proportion used) based on tree degradation classes (live vs dead) and tree species at the mixedwood and conifer study sites. Live trees are identified as negative percentages whereas snags are identified as positive percentages. Only the four main tree species at each site are shown. "Available" represent the mean proportion of each class at each site based on all vegetation sampling stations.

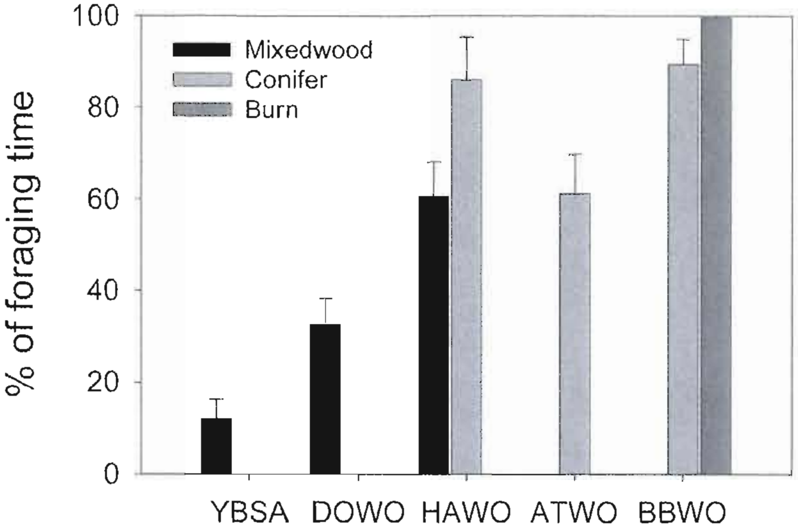

Figure 1.5. Mean proportion of foraging time spent on dead wood substrates (snags or dead portions of live trees) by five woodpecker species in boreal mixedwood, conifer and burn sites. Bars represent weighed means + 1 SE.

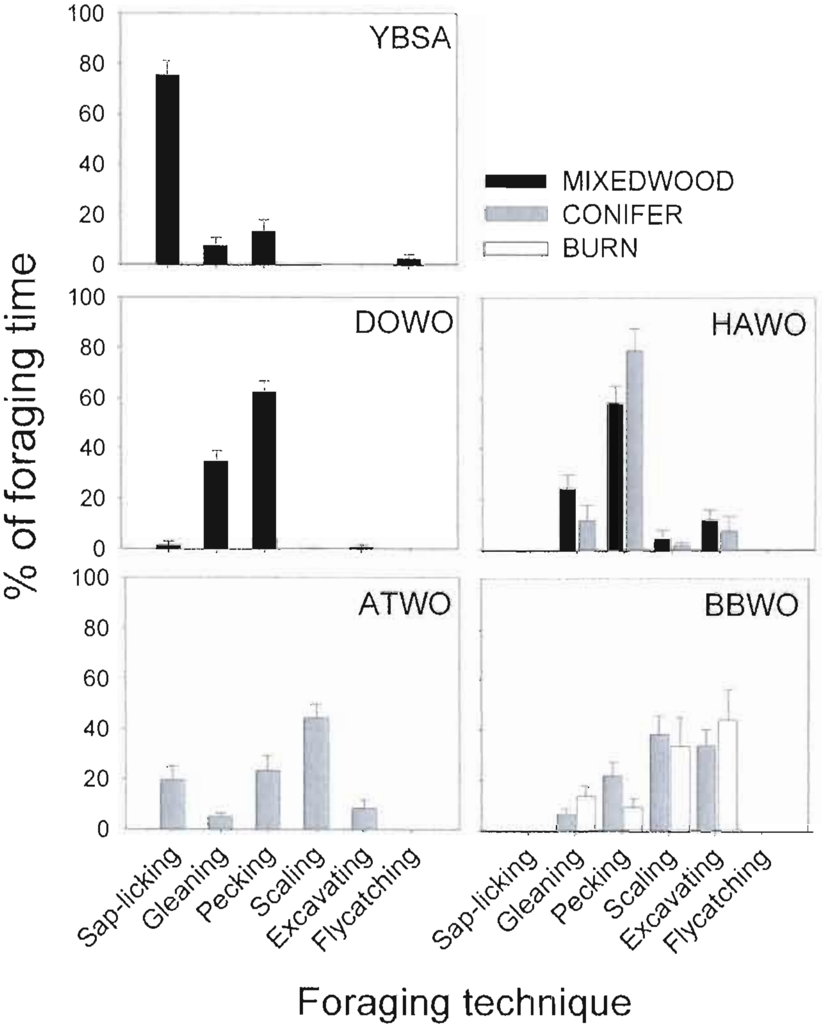

Figure 1.6. Mean proportion of foraging time spent using different foraging techniques by five woodpecker species in boreal mixedwood, conifer and burn sites. Bars represent weighed means + 1 SE.

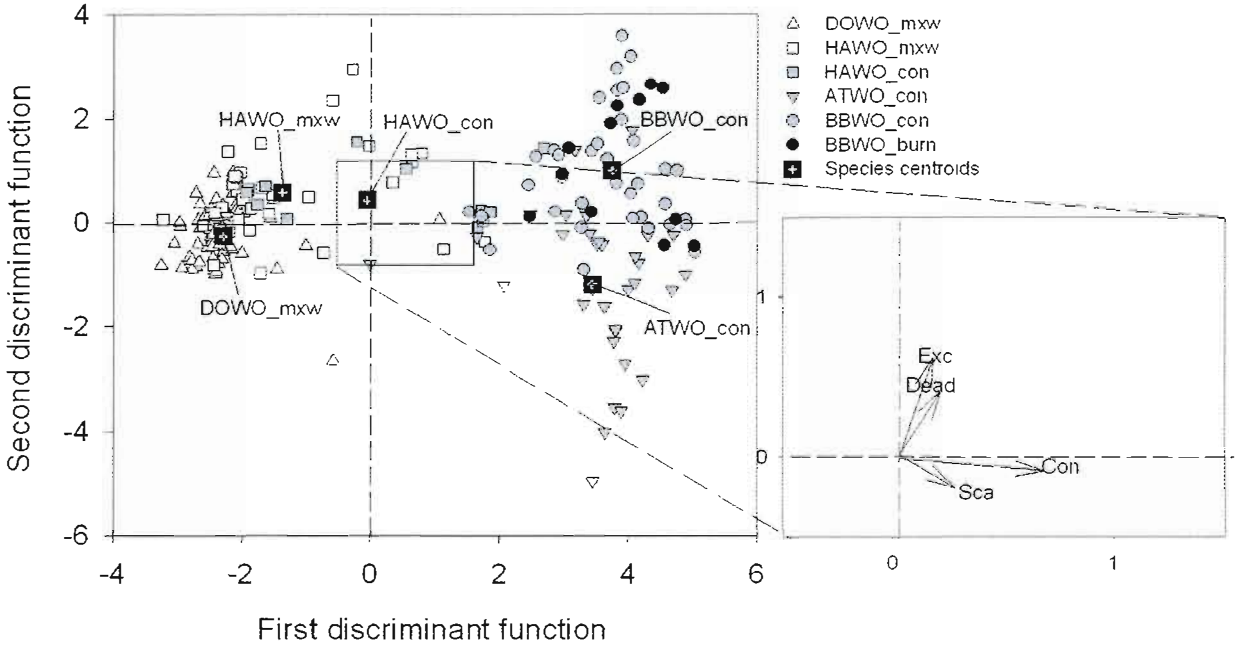

Figure 1.7. Foraging niche partitioning among Picoides woodpeckers as shown by the scores of the first two functions of the discriminant analysis. Group centroids are the mean discriminant scores for each group. Mxw = Mixedwood site; Con = Conifer site; Burn = burn conifer site. See Table 1.1 for species code and sample size and Table 1.3 for variable code.

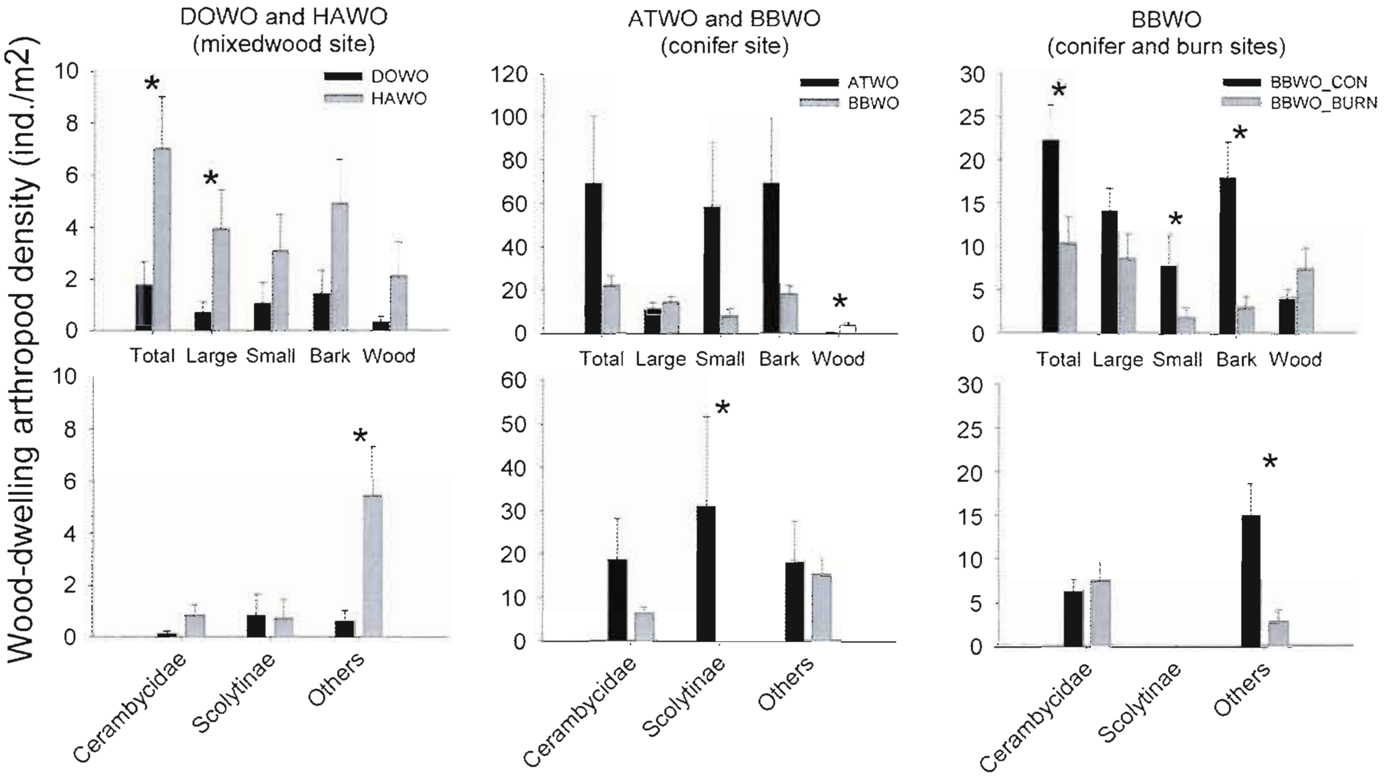

Figure 1.8. Wood-dwelling arthropod densities (ind./m^2) in trees used for foraging by co-occurring species at each site (downy and hairy woodpeckers at the mixedwood site; black-backed and American three-toed woodpeckers at the conifer site) and by the black-backed woodpecker at the conifer and burn sites. Large (>1 cm in length), Small (<1 cm in length), Bark (found in or under bark), Wood (found within xylem). Stars indicate significant differences between species or sites ($P < 0.05$).

1.11 Appendix

Appendix 1.1. Summary of wood-dwelling arthropod captures made from wood dissection of trees used by foraging woodpeckers. "no." is the number of individuals captured; "freq" is the number of trees the taxon was found; "%" is the percentage the taxon represents relative to all individuals captured; "site found" represents the percentages of individuals from each taxon that were found within the wood (wood-associated) vs. within or under the bark (bark-associated).

	All logs (*n* = 47)				HAWO (MXW; *n* = 10)		DOWO (MXW; *n* = 10)		ATWO (CON; *n* = 10)		BBWO (CON; *n* = 10)		BBWO (BURN; *n* = 7)	
Taxon	no.	freq	%	Site found (wood/bark)	no.	freq	no.	freq	no.	freq	no.	freq	no.	freq
Cerambycidae														
Acanthocinus sp.	1	(1)	0	0 / 100	0		0		1	(1)	0		0	
Acmaeops proteus	20	(9)	3	0 / 100	0		0		14	(5)	4	(2)	2	(2)
Anastrangalia sanguinea	1	(1)	0	100 / 0	0		0		0		0		1	(1)
Anthophylax attenuatus	0		0	0 / 0	0		0		0		0		0	
Arhopalus foveicollis	44	(5)	6	100 / 0	0		0		0		0		44	(5)
Cerambycinae	2	(2)	0	0 / 100	0		0		1	(1)	1	(1)	0	
Lamiinae	4	(3)	1	75 / 25	0		0		1	(1)	3	(2)	0	
Lepturinae	18	(11)	2	28 / 72	3	(3)	0		12	(5)	3	(3)	0	
Monochamus sp.	36	(9)	5	83 / 17	0		0		1	(1)	35	(8)	0	
Pogonocherus sp.	90	(2)	12	0 / 100	0		0		90	(2)	0		0	
Rhagium inquisitor	19	(4)	2	0 / 100	0		0		5	(1)	14	(3)	0	
Saperda calcarata	8	(2)	1	100 / 0	6	(1)	2	(1)	0		0		0	
Xylotrechus undulatus	1	(1)	0	100 / 0	0		0		0		1	(1)	0	
Not identified	5	(2)	1	100 / 0	0		0		0		2	(1)	3	(1)
Large (> 1 cm)	150	(25)	19	65 / 35	9	(4)	2	(1)	30	(5)	59	(9)	50	(6)
Small (< 1 cm)	99	(9)	13	0 / 100	0		0		95	(5)	4	(4)	0	
Total	249	(26)	32	39 / 61	9	(4)	2	(1)	125	(6)	63	(9)	50	(6)
Buprestidae														
Large (> 1 cm)	14	(10)	2	7 / 93	0		2	(2)	6	(4)	6	(4)	0	
Small (< 1 cm)	2	(2)	0	0 / 100	0		0		2	(2)	0		0	
Total	16	(10)	2	6 / 94	0		2	(2)	8	(4)	6	(4)	0	

	All logs (*n* = 47)				HAWO (MXW; *n* = 10)		DOWO (MXW; *n* = 10)		ATWO (CON; *n* = 10)		BBWO (CON; *n* = 10)		BBWO (BURN; *n* = 7)	
Taxon	no.	freq	%	Site found (wood/bark)	no.	freq	no.	freq	no.	freq	no.	freq	no.	freq
Curculionidae[1]														
Dryocoetes affaber	4	(1)	1	0 / 100	0		0		4	(1)	0		0	
Dryocoetes autographus	13	(1)	2	0 / 100	0		0		13	(1)	0		0	
Ips latidens	3	(1)	0	0 / 100	0		0		3	(1)	0		0	
Polygraphus rufipennis	6	(1)	1	0 / 100	0		0		6	(1)	0		0	
Trypodendron retusum	16	(2)	2	56 / 44	9	(1)	7	(1)	0		0		0	
Xyloterinus politus	3	(3)	0	67 / 33	1	(1)	2	(2)	0		0		0	
Not identified	141	(3)	18	0 / 100	0		0		141	(3)	0		0	
Total	186	(7)	24	6 / 94	10	(1)	9	(2)	167	(4)	0		0	
Others														
Large (> 1 cm)	147	(25)	19	5 / 95	27	(6)	6	(2)	29	(5)	78	(9)	7	(3)
Small (< 1 cm)	175	(24)	23	6 / 94	31	(4)	3	(1)	62	(7)	66	(9)	13	(3)
Total	322	(32)	42	6 / 94	58	(7)	9	(3)	91	(8)	144	(10)	20	(4)
Total	773	(40)	100	16 / 84	77	(9)	22	(5)	391	(9)	213	(10)	70	(7)

[1] All individuals were <1 cm.

CHAPITRE 2

PRE-FIRE FOREST CONDITIONS AND FIRE SEVERITY AS DETERMINANTS OF THE QUALITY OF BURNED FORESTS FOR DEADWOOD-DEPENDENT SPECIES: THE CASE OF THE BLACK-BACKED WOODPECKER

2.1 Résumé

Les forêts brûlées représentent typiquement des habitats de haute qualité pour plusieurs espèces dépendantes du bois mort. Cependant, les conditions d'habitat présentes après feu peuvent varier grandement, et par conséquent, peuvent affecter la qualité d'habitat pour ces espèces. Afin d'identifier les conditions d'habitat favorables à la nidification du pic à dos noir (*Picoides arcticus*) dans les pessières brûlées boréales, nous avons étudié la sélection d'habitat suite à un feu de forte sévérité (~4500 ha) qui a eu lieu en 1999 dans le Parc national des Grands-Jardins, au centre du Québec, Canada. Nos objectifs étaient: (i) d'identifier les facteurs impliqués dans la sélection d'arbres brûlés pour la nidification et l'alimentation; et (ii) de déterminer l'importance de l'âge des forêts avant feu dans la sélection des sites de nidification et d'alimentation par le pic à dos noir. Un total de 92 sites de nidification et des suivis focaux sur un sous-ensemble de 10 individus nicheurs ont été utilisés pour étudier la sélection des arbres morts. Nos résultats montrent que les conditions forestières avant feu et la sévérité du feu constituent deux éléments importants qui peuvent affecter la qualité d'habitat pour le pic à dos noir dans les forêts brûlées. Les pics à dos noir sélectionnaient les arbres de gros diamètre, plus dégradés (morts avant le feu) ainsi que des feuillus pour la nidification. En revanche, ils s'alimentaient essentiellement sur des épinettes noires mortes suite au feu et montraient une sélection pour les chicots de plus gros diamètres et modérément brûlés. Les perturbations passées (feu et coupe) ont considérablement affecté la structure d'âge des forêts avant feu, créant une mosaïque de peuplements matures (>80 ans) et jeunes (~40 ans) brûlés. Au sein de cette mosaïque, les pics se concentraient principalement dans les peuplements matures brûlés tant pour la nidification que pour l'alimentation. Nos résultats suggèrent que les forêts résineuses matures et surannées brûlées représentent des habitats de haute qualité pour le pic à dos noir en forêt boréale canadienne, ce qui signifie qu'une partie de ces peuplements devraient être maintenus pour cette espèce lors de la récupération des bois brûlés après feu. Étant donné l'influence de l'âge des forêts sur la qualité des forêts brûlées pour le pic à dos noir, le rajeunissement de la matrice forestière en forêt boréale aménagée soulève des inquiétudes quant à la disponibilité à long terme des forêts brûlées de haute qualité pour cette espèce.

Mots-clés : feu, bois mort, Picidae, nidification, alimentation.

2.2 Abstract

Burned forests typically represent high-quality habitats for many deadwood-dependent species. Yet, post-fire conditions may vary greatly within and among burns and, thereby, may affect habitat suitability for these species. To identify habitat conditions suitable for nesting black-backed woodpeckers (*Picoides arcticus*) in burned spruce-dominated boreal forests, we studied habitat selection after a high-severity wildfire (~4500 ha) that occurred in 1999 within the Parc national des Grands-Jardins, in central Quebec, Canada. Our objectives were to: (i) identify factors involved in the selection of snags for both nesting and foraging; and (ii) determine the importance of pre-fire forest age in the selection of nesting and foraging sites by the black-blacked woodpecker. A total of 92 nest sites in addition to focal surveys on a subset of 10 nesting individuals were used to investigate snag selection. Our results show that both pre-fire forest conditions and fire severity are important in determining the quality of post-fire habitats for black-backed woodpeckers. Black-backed woodpeckers selected large, degraded "pre-fire" and deciduous snags for nesting. In contrast, they foraged mainly on large and moderately burned spruce snags created by fire. Past disturbances (fire and logging) markedly affected the age structure of these forests prior to the fire and created a mosaic of burned mature (>80 years old) and young (~40 years old) stands. Within the burn, woodpeckers concentrated their nesting and foraging activities in burned mature stands. Our results suggest that burned mature and overmature conifer forests represent high-quality habitats for the black-backed woodpecker in the Canadian boreal forest, meaning some of these stands should be retained during salvage logging. Because of the influence of forest age on the quality of burned forests for the black-backed woodpecker, the decrease in the amount of late seral stands to the benefit of younger stands in managed boreal forest landscapes raises concern about the long-term availability of high-quality post-fire habitats for this species.

Keywords : fire, dead wood, Picidae, nesting, foraging.

2.3 Introduction

Burned forests typically represent high-quality habitats for many plant and animal species (Saab and Powell 2005, Hutto 2006, Lindenmayer *et al.* 2008). In the boreal as in many other forest ecosystems worldwide, many species have been identified as fire-associated, fire-specialized, fire-favoured or fire-dependent (Jonsell *et al.* 1998, Wikars and Schimmel 2001, Wikars 2002, Saab and Powell 2005, Hannon and Drapeau 2005). Indeed, fire generates short-term habitat conditions that are often scarce or patchily distributed in unburned or managed forests (Lindenmayer *et al.* 2008). In particular, fires generate high densities of snags and are thus an important source of dead wood at the regional scale (Angelstam and Mikusiński 1994, Pedlar *et al.* 2002, Lehmkuhl *et al.* 2003). In fire-mediated landscapes, fire may thus contribute to the persistence of populations of deadwood-dependent species such as many saproxylic insects (Wikars 2002, Saint-Germain *et al.* 2004a, b) and cavity-nesting birds (Hutto 1995, Saab and Powell 2005, Nappi and Drapeau In press).

Although post-fire forest conditions are markedly different than those present in unburned forest types, they can also vary greatly within and among burns. Part of this heterogeneity is caused by variability in fire severity. In the boreal forest, where fires have been historically described as severe stand-replacing disturbances, recent studies have shown that wildfires may leave an important portion of stands unburned or partially burned (Kafka *et al.* 2001, Bergeron *et al.* 2002, Schmiegelow *et al.* 2006). In addition, forest conditions present at the time of fire (such as tree species composition, stand age and stand structure) may vary as well and, consequently, greatly influence post-fire conditions (Kafka *et al.* 2001, Vierling *et al.* 2008). The resulting variability in post-fire conditions may affect habitat resources for fire-associated species (Wikars and Schimmel 2001, Purdon *et al.* 2004, Smucker *et al.* 2005). For deadwood-dependent species, this variability in post-fire conditions may be particularly important as it will determine the quantity and the characteristics of snags present in burned forests, and thus the suitability of these habitats for feeding and breeding activities (Saint-Germain *et al.* 2004b, Koivula and Schmiegelow 2007, Vierling *et al.* 2008).

Forest management may influence both the abundance and the suitability of habitats created by wildfire. In North American boreal forests for instance, harvesting of post-fire forests ("salvage logging") has become an important management activity in recent years which reduces the availability of post-fire habitats (Nappi *et al.* 2004, Schmiegelow *et al.* 2006, Lindenmayer *et al.* 2008). Because salvage logging operations may target specific tree characteristics (i.e. specific tree size, species or fire damage class), remaining burned stands may not be representative of natural post-fire conditions and may not be suitable for deadwood-associates (Kotliar *et al.* 2002). Fine-scale investigation of habitat selection by deadwood-dependent species in burns is therefore necessary in order to determine their habitat requirements and to generate appropriate snag-management guidelines that will maintain their habitats in managed burned forests (Hutto 2006).

We investigate snag and habitat selection by black-backed woodpeckers (*Picoides arcticus*) in burned boreal black spruce forests. More specifically, our first objective was to identify factors involved in the selection of snags for both nesting and foraging. Our second objective was to determine the importance of pre-fire forest age in the selection of nest and foraging sites. We used the black-backed woodpecker as our focal species because it is a deadwood-specialist (Dixon and Saab 2000, Chapter 1) and a well-known fire-associated species that responds strongly and positively to the high abundance of snags in recently burned forests throughout its range (Hutto 1995, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). As with other woodpecker species (Martikainen *et al.* 1998, Conner *et al.* 2001, Virkkala 2006), the black-backed woodpecker could play numerous roles in the ecological functioning, conservation and management of forested ecosystems. For instance, it may serve as an umbrella species given that other fire-associates such as many saproxylic insects depend on the same resource, namely burned wood. Also, the black-backed woodpecker may represent an important keystone species in post-fire forests by providing cavities for other cavity-nesters during the first years after fire (Saab *et al.* 2004).

2.4 Methods

2.4.1 Study Area

This study was conducted in the Parc national des Grands-Jardins (310 km^2), a provincial park located approximately 120 km northeast of Quebec City, Canada (47°44'N, 70°46'W; Fig. 2.1). The park is located on the Laurentian Highlands (mean altitude of 800 m a.s.l.). Vegetation typically reflects the southern boreal forest zone (Saucier *et al.* 1998) and includes the southernmost lichen woodlands in eastern Canada (Payette *et al.* 2000a). Mean annual temperature is 0°C and total annual precipitation averages 1405 mm, with 407 mm falling as snow (Boisclair 1990). Wildfires have profoundly shaped the land, with 13 fires burning about 40% of the park during the 20th century (Payette and Delwaide 2003). In addition, 39% of the area was logged between 1940 and the creation of the park in 1981 (Payette and Delwaide 2003). No logging has occurred since the park was created.

In 1999, between May 30 and June 25, a fire burned 4546 ha of conifer-dominated forest mostly within the park boundaries (Société de protection des forêts contre le feu 2000, Ministère des Ressources naturelles et de la Faune 2006, Fig. 2.1). The burned landscape was dominated by black spruce (*Picea mariana*), with scattered balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). This fire was generally severe with most of the stands being totally burned. Burn severity was evaluated by the Quebec Ministry of Natural Resources and Wildlife based on the percentage of the crown cover that had been burned (based on a Landsat imagery at a 30 m × 30 m pixel resolution). Based on this evaluation, 96% of the area affected by the fire was composed of high-severity burned stands (stands with >90% of the crown cover burned) whereas 4% consisted of low-severity burned stands (dominance of unburned crown cover). We obtained a similar burn severity estimate with field measures taken at random burned sites (3.14-ha plots, n = 32); mean percentage of burned crown cover at these sites was 98.3 ± 4.0%.

Because of the history of natural and anthropogenic disturbances, the fire burned a mosaic of stand ages (Fig. 2.1). We used tree height as a surrogate for stand age to classify stands as mature (canopy height >7 m) or young (canopy height <7 m) based on digital pre-fire forest inventory maps (Ministère des Ressources naturelles et de la Faune 2006). Young stands mostly originated from previous logging in the late 1950s and early 1960s, therefore averaging 40 years of age (Payette *et al.* 2000b). Mature stands originated from a fire in 1922 or from stands undisturbed by either fire or harvesting in the last century; therefore mature stands were >80 years old. About half of the burned landscape was composed of mature stands (47%) with the rest composed of young stands (53%). No salvage logging occurred within the burned landscape.

2.4.2 Snag selection for nesting

We searched for active nests during the first three post-fire breeding seasons (2000 to 2002) in accessible and delineated areas of the burn. Nest searching methods were similar to the ones described in Dudley and Saab (2003). Within these delineated portions of the burn, nests were searched along transects separated by 200 m and which spanned the entire delineated areas. All transects were walked three times (from early May to early July) and nest searching effort was standardized among these delineated areas. Nests were located by following adults to their cavity, by searching for cavities or by listening for nest excavation or begging nestlings. To increase our chance of locating nests and to confirm the presence-absence of potential nesting pairs in a given area, birds were attracted using 5-min playbacks (woodpecker drumming and calls) at sampling stations 200 m apart along the linear transects. Each occupied station (where a bird responded to playback or where a pair was seen) was visited until the nest was located. Unoccupied stations were visited at least three times using playbacks during morning hours (05h00 to 12h00) to confirm the absence of nesting pairs. Approximately 1200 ha of burned forest were covered by systematic nest searches (about 25% of the total burned landscape). Some nests were also found outside these surveyed areas and were included in nest tree selection analyses. We considered nests to be active when egg laying was completed and incubation initiated.

At each nest site, we measured characteristics of the nest tree as well as all trees larger than 15 cm in diameter at breast height (dbh) within a 225-m^2 plot centred on the nest. We used this diameter threshold because it corresponded to the smallest dbh value used by a black-backed woodpecker for nesting during the course of our study. All nest sites were located in severely burned stands; therefore, all nest and surrounding unused trees were snags. For each snag, we noted dbh, species, fire severity and degradation stage. Fire severity, at the tree level, was based on percentage of the trunk surface burned: light = up to 35% of the trunk; moderate = 36-99% of bark burned; severe = trunk completely burned. Degradation stage was assessed with an index used to differentiate trees that died after the fire ("fire-created snags"; Deg1) from those that were dead prior to the fire ("pre-fire snags"; Deg2 and Deg3). Decisions were based on several criteria, including visual appearance, quantity of bark and branches and tree top condition. This latter criterion was used to separate pre-fire snags with an intact top (Deg2) from snags with broken tops (Deg3).

Using the set of nest and unused trees, we first conducted simple logistic regressions to determine if each of the above characteristics (i.e. dbh, species, fire severity and degradation) was a significant predictor of nest tree selection by woodpeckers ($P < 0.05$). We then used Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002) to assess the relative strength of candidate models based on different combinations of the variables that were significant (all possible combinations). This approach uses the model log-likelihood (which reflects the overall fit of the model) while penalizing for the addition of parameters. Each model was ranked according to its AIC$_c$ weight so that models with highest values were the most parsimonious. Because trees are clustered within each plot, our observations were not independent. To adjust for this possible autocorrelation, models were estimated using generalized estimating equations (GEE) available through the GENMOD procedure in SAS and by invoking the REPEATED statement (Allison 1999). This method takes into account the clustered structure of data and produces standard errors and test statistics that are adjusted for autocorrelation. In addition, we statistically weighted the number of trees per plot so that each plot contributed one degree of freedom in the model (Desrochers 1992). Degradation and fire severity were treated as class variables, using the highest value as the omitted category. For tree species, black spruce was the omitted category; therefore, coefficients of other tree species are comparisons between each of these values and the black spruce value (Allison 1999). All regressions were performed using SAS (SAS Institute Inc. 2004).

2.4.3 Snag selection for foraging

To investigate foraging tree selection, we monitored a sub-sample of 10 individuals (six males, four females) from seven nesting pairs during the second breeding season. Our data are based on focal surveys of foraging birds that were conducted during the nestling stage, a period where males and females make frequent visits to the nest to feed nestlings. Each "observation bout" started at the nest and the bird was followed until it was lost or until it returned to its cavity (typically a direct unidirectional flight from the last foraging tree to their nest tree). During each observation bout, we recorded locations with a Global Positioning System (precision 5-10 m) and marked trees on which woodpeckers foraged for at least 10 sec or where they were seen extracting prey. Because observations are correlated within each observation bout, we focused on maximizing the number of observation bouts per individual rather than the number of foraging locations. Foraging observations were made during morning hours (05h00-12h00) between June 11 and July 6, 2001.

Our goal was to compare trees used for foraging with trees potentially available to nesting birds, therefore within their home range (i.e. third-order selection *sensu* Johnson 1980). We thus used woodpecker foraging locations to delineate foraging areas (hereafter "core foraging areas") and then compared characteristics of used and available trees within these core foraging areas. These were estimated and delineated using the minimum convex polygon method using all foraging locations. We choose this method because we were interested in delimitating the outer boundaries of the core foraging areas (Harris *et al.* 1990). Incremental plots (based on one random location per observation bout) were used to assess whether the number of observation bouts was high enough to reach an asymptote in area estimation (Kenward 2001). Asymptotes were generally obtained by 40-50 observation bouts. Although we obtained stable estimates for all birds, our method, as compared to standard radio-tracking, may underestimate the total home range of a bird given that more peripheral locations could be left unrecorded. Hence, we consider these core foraging areas as areas where nesting woodpeckers concentrate most of their foraging effort during the nestling period.

"Available" trees were sampled in four 225-m^2 plots randomly selected within each core foraging area (samples were then merged for each core foraging area). Foraging and available trees were characterized by dbh, tree species, fire severity and degradation stage. However, tree species and degradation stage variables were not retained for the analysis: black spruce fire-created snags represented 93.7% of the total available trees and were selected in almost the same proportion (93.3%) as their availability. Our analysis therefore compares use and availability based on the combination of dbh and fire severity classes. Comparisons of use and availability data were made using the Compositional Analysis method (Aebischer *et al.* 1993). In essence, this approach ranks habitat components based on log-ratio differences between use and available proportions, thereby eliminating the problem of non-independence of habitat proportions (Johnson 1980, Aitchison 1986). This approach also uses the animal instead of each observation as the sample unit to avoid problems of pseudoreplication (Hurlbert 1984, Aebischer *et al.* 1993). Analyses were performed with Compos Analysis Version 5.1 (Smith 2003).

2.4.4 Nest and foraging site selection based on pre-fire forest age

We assessed site selection based on stand type prior to fire (burned mature versus burned young stands) at two spatial scales. First, we investigated whether woodpecker nests were located in areas with higher proportions of burned mature forests as compared to their availability in the landscape. For this purpose, proportions of burned mature forests surrounding nests were compared to proportions calculated from random locations (Potvin *et al.* 2000). Because some portions of the landscape were composed of burned mature forests only, we restricted our analysis to a 700-ha portion of the landscape that consisted of a mosaic of burned young and mature stands. For all nests (n = 41) and an equivalent number of random locations, we measured the proportion of burned mature forest within a 250-m radius from nest using digital pre-fire forest inventory maps. This radius was chosen because the area covered (19.6 ha) was close to mean core foraging areas of nesting pairs in this study. Proportions of mature burned forest were compared between nest and random locations using a non-parametric Mann-Whitney U test.

Second, we examined whether woodpeckers were selecting mature stands in higher proportions than their availability within core foraging areas. This analysis was conducted on the same individuals that were monitored for foraging tree selection. Eight of the 10 individuals had core foraging areas containing both mature and young stands and were thus used for this analysis. Available and use proportions of forest types were compared using Compositional Analysis (Aebischer *et al.* 1993). Availability corresponded to the proportion of core foraging areas occupied by mature versus young stands. Usage was based on the proportion of foraging locations (one random location per observation bout) within each stand type.

Differences in snag density between stands classified as either mature or young by digital pre-fire forest cover maps were assessed using 225-m^2 random plots ($n = 49$) at least 300 m apart sampled during a simultaneous study on bird communities (P. Drapeau, unpublished data). Comparisons were conducted separately for three diameter levels (>10, >15 and >20 cm dbh) using non-parametric Mann-Whitney U tests. We also compared snag density among nest sites, core foraging sites and random sites using 225-m^2 plots. Nest site plots ($n = 92$) were centred on the nest and corresponded to the same plots used for nest tree selection analysis. Core foraging site plots ($n = 66$) consisted of plots sampled in proximity to nests (50 m from nest, random azimuths) and were therefore considered as part of each bird's potential home range based on previous investigation of core foraging areas. Random site plots corresponded to the ones described above. Comparisons among random site, core foraging site and nest site plots were conducted separately for three diameter levels (>10, >15 and >20 cm dbh) using non-parametric Kruskal-Wallis tests.

2.5 Results

2.5.1 Nest trees

Ninety-two nest trees were located during the 3-year study and used to assess nest tree selection. Although some nests were re-used in a subsequent year, we considered these re-used nests as single nest trees. Tree dbh, species and degradation were significant predictors of nest tree selection based on simple logistic regressions. Of the set of candidate logistic regression models, two had ΔAIC_c values <2 (a threshold suggesting substantial evidence for the model, Burnham and Anderson 2002). The best model included the main effects of these three variables (Table 2.1, Fig. 2.2).

Despite considering only trees greater than 15 cm in dbh, diameter was still an important criterion in nest tree selection (Table 2.1, Fig. 2.2a). Mean dbh was 22.2 cm, with roughly 70% of nest trees being larger than 20 cm dbh (although these only represented 30% of the available trees within nest plots). Black-backed woodpeckers tended to select trembling aspen and paper birch over black spruce (which represented most coniferous trees) for nest excavation (Table 2.1, Fig. 2.2b). About half of the nests were excavated in deciduous trees (36% for trembling aspen; 15% for paper birch), a proportion much higher than the relative availability of these tree species in the nest plots (12% for trembling aspen and 4% for paper birch). Conversely, black-backed woodpeckers under-utilized black spruce in relation to its availability (37% of nest trees versus 72% of available trees). Nests were occasionally excavated in other coniferous trees (8% balsam fir; 3% jack pine; 1% tamarack) in about the same proportions as their relative availabilities in nest plots (8% balsam fir, 2% jack pine, 2% tamarack). Although most nests were in fire-created snags (Deg1), black-backed woodpeckers typically selected pre-fire snags (Deg2 and Deg3) in higher proportion than their availability (Table 2.1, Fig. 2.2c).

2.5.2 Foraging trees

Black-backed woodpecker foraging was recorded on 1723 trees during 570 observation bouts (Table 2.2). Foraging occurred within core foraging areas that surrounded nests and which covered 6.9-16.7 ha (based on 10 individuals, Table 2.2). Selection of foraging trees by these 10 individuals was assessed for fire-created black spruce snags based on the combination of two variables (dbh and fire severity) and using a total of 1608 foraging trees and 1265 available stems. Black-backed woodpeckers showed consistent patterns in their selection of foraging trees based on dbh and fire severity (Wilk's $\lambda = 0.013$, $P = 0.028$, df = 8; Table 2.3; Fig. 2.3). They consistently selected larger trees over smaller ones for foraging. Within each dbh class, moderately burned trees were preferred over severely or lightly burned trees. Fire severity also affected the overall ranking based on dbh by causing moderately burned trees of 10.0-14.9 cm dbh to be preferred over lightly burned trees ≥15 cm dbh (Table 2.3).

2.5.3 Nest and foraging sites

Woodpecker nest sites were surrounded by higher proportions of burned mature forest than random sites, although this result was only marginally significant ($Z = -1.809$, $P = 0.071$; Fig. 2.4). Within their core foraging areas, black-backed woodpeckers concentrated most of their foraging in burned mature stands as compared to their availability (Wilk's $\lambda = 0.659$, $P = 0.012$, df = 1; Fig. 2.5). Snag density comparisons between burned young and mature stands showed that burned mature stands typically supported higher densities of snags. This pattern was significant ($Z = -2.092$, $P = 0.036$) and marginally significant ($Z = -1.887$, $P = 0.059$) for comparisons implying, respectively, 10 cm and 15 cm dbh levels. No significant difference was observed between stand types for snags >20 cm dbh ($Z = -1.107$, $P = 0.268$). Snag densities were highest in nest plots, lowest in random plots and intermediate in core-foraging area plots, a result consistent across all dbh levels (all Kruskal-Wallis tests, $P < 0.05$; Fig. 2.6). For instance, density of snags > 15 cm dbh was about two times higher in nest (~400 snags/ha) than in random plots (~200 snags/ha).

2.6 Discussion

Although recently burned forests typically represent high-quality habitats for many plant and animal species, the quality of such habitat is greatly influenced by heterogeneity in post-fire forest conditions (Purdon *et al.* 2004, Saint-Germain *et al.* 2004b, Smucker *et al.* 2005, Koivula and Schmiegelow 2007, Kotliar *et al.* 2007, Vierling *et al.* 2008). Our results for the black-backed woodpecker show that post-fire habitat quality is influenced by the combined effect of pre-fire forest conditions – i.e. tree species, diameter and degradation stage – and fire severity (at the tree scale). Yet, our study also indicates that conditions preferred by this species may differ markedly between nesting and foraging, therefore emphasizing the importance of considering both nesting and foraging requirements when determining post-fire habitat suitability.

2.6.1 Importance of pre-fire tree characteristics

Forest conditions present at the time of fire directly influence characteristics of trees available thereafter for deadwood-dependent species. Our results show that diameter, species and degradation stage of trees are characteristics that are of crucial importance in determining the quality of nesting and foraging substrates for the black-backed woodpecker. Tree diameter is particularly important for nest tree selection as it directly influences potential cavity size and thickness of the insulating and protective wood wall (Schepps *et al.* 1999). In post-fire forests, as in other forest types, use or selection of large trees for nest excavation by primary cavity-nesting birds is well documented (e.g. Raphael and White 1984, Saab and Dudley 1998). Although previous observations reported the use of relatively small-diameter trees by nesting black-backed woodpeckers as compared to other species (Saab and Dudley 1998, Vierling *et al.* 2008, Saab *et al.* 2009), our results underscore the importance of tree size for the black-backed woodpecker, especially in the boreal forest where trees are of relatively small diameter. Minimum and mean diameters of selected trees in our study represented the smallest values recorded for this species throughout its range (Raphael and White 1984, Goggans *et al.* 1989, Weinhagen 1998, Saab and Dudley 1998). Given the internal diameter of black-backed woodpecker nest cavities averages 11 cm (Raphael and White 1984, Martin *et al.* 2004), many of the nest trees in this study are close to the minimum diameter threshold required for nest excavation. This suggests large trees may have been limited in our burned landscape.

As for nesting, tree diameter was an important factor in foraging tree selection. Larger trees, which typically contain higher densities of wood-boring larvae (Nappi *et al.* 2003, Saint-Germain *et al.* 2004b,c), were higher quality foraging substrates in our study area. The cerambycid *Monochamus scutellatus* was among the most abundant saproxylic species in these burned spruce trees (Saint-Germain *et al.* 2004b) and represented the main prey of the black-backed woodpecker (Nappi and Drapeau In press). Preference for large snags by such deep wood-boring insects can be attributed to the requirements of late-instar larvae, which excavate deep galleries into sapwood and heartwood (Gardiner 1957, Cerezke 1977). Tree diameter is also correlated with bark and phloem thickness, two attributes that enhance micro-habitat conditions for these insects: thicker bark increases protection of sub-cortical tissues from excessive desiccation (Gardiner 1957, Furniss 1965) and phloem is of higher nutritional quality for larvae that feed extensively on cambium and phloem tissues during first-instar stages (Rose 1957, Saint-Germain *et al.* 2004b).

Black-backed woodpeckers showed clear preferences for some tree species and degradation stages, but these differed markedly between nest and foraging substrates. Our results show that deciduous trees were clearly preferred over coniferous trees by black-backed woodpeckers for nesting. This finding emphasizes the importance of deciduous trees, in particular aspen, as key nesting substrates for cavity nesters (Li and Martin 1991, Hutto 1995, Kotliar *et al.* 2002, Koivula and Schmiegelow 2007). In our study, aspen may have been preferred in part because of its relatively high diameter compared to conifers. High aspen use may also be related to its susceptibility to heartwood decay, which provides a soft substrate for excavation while providing a sound sapwood shell (Basham 1991, Jackson and Jackson 2004, Losin *et al.* 2006).

Based on broad classes of tree degradation, our results show woodpeckers tend to select trees for nesting that were already dead or in an advanced stage of decay at the time of fire.

Interaction effects between tree species and degradation classes were not assessed in our models because of small sample sizes, but woodpecker preference for pre-fire snags was principally for white birch and black spruce. When alive, white birch is much less affected by heartwood rot than trembling aspen, although birches decay rapidly after death (Basham 1991). Among eastern boreal conifers, black spruce is less affected by trunk decay, irrespective of tree age, and is mainly affected by root rot and butt decay (Basham 1991). Trees not previously invaded by heart-rot fungi provide little immediate opportunity for woodpecker excavation at the time of tree death (Jackson and Jackson 2004). For these two tree species, pre-fire snags already affected by trunk decay (such as broken top snags) provide easily excavated nesting substrates in the first years after fire, a period when most snags are still relatively intact. Selection of softer trees by cavity excavators is known to vary among species (Schepps *et al.* 1999). Selection of softer substrates by black-backed woodpeckers is of particular interest given this species has one of the strongest excavator morphologies among American woodpeckers (Spring 1965, Kirby 1980) and has been shown to nest in relatively hard snags as compared to other species (Saab and Dudley 1998). Our results therefore emphasize the importance of pre-fire snags (especially with broken tops) as nest trees even for strong excavators such as the black-backed woodpecker (Hutto 1995, Haggard and Gaines 2001, Lehmkuhl *et al.* 2003).

Preferences for tree species and degradation stage for foraging contrasted sharply with preferences for nesting. Foraging of black-backed woodpeckers occurred almost exclusively on fire-killed spruce snags that dominated the burned landscape. Burned conifers represent high-quality substrates for wood-feeding beetles (Cerambycidae, Buprestidae and the sub-family Scolytinae (family Curculionidae)) in the first years after fire (Saint-Germain *et al.* 2004b, Boulanger and Sirois 2007). Therefore, these recent conifer snags represented an abundant foraging resource for black-backed woodpeckers (Murphy and Lehnhausen 1998, Nappi *et al.* 2003). Trees that were already dead or weakened before fire (pre-fire snags) were rarely used by woodpeckers as foraging substrates. These more degraded snags had probably little or no recent phloem, a critical nutritional condition for wood-boring insects (Saint-Germain *et al.* 2004b).

2.6.2 Importance of pre-fire forest age

Because of its direct effect on tree diameter, forest age at the time of fire is a critical determinant of habitat quality for the black-backed woodpecker, especially in conifer-dominated northern boreal forests where trees can take a long time to reach adequate sizes for woodpeckers. In our study, within-burn variation in stand age caused important variability in large snag availability. When the 1999 fire occurred, a large part of the landscape that originated from an 80-year-old fire was almost exclusively mature. This portion of the burn supported high densities of large burned coniferous trees as well as a scattered presence of large aspens that originated from the 1922 fire. In addition, legacies that escaped the 1922 fire may have persisted to create the decayed pre-fire snags present in the 1999 fire. This portion of the burned landscape clearly provided high-quality post-fire habitat conditions for black-backed woodpeckers. In contrast, other portions of the burned landscape were dominated by young stands (app. 40 years at time of fire) with scattered patches of mature forest. In these portions of the burn, our results on nest site selection at the landscape scale showed that woodpeckers selected nest sites with higher proportions of mature forest. At the scale of their core foraging areas, woodpeckers also concentrated their foraging activities in mature forest stands. Together, these results suggest the 40-year-old burned forest patches were less adequate habitats for woodpeckers and that birds were maintained in these portions of the burn by nearby patches of mature forest.

2.6.3 Importance of fire severity

Deadwood-dependent species may be affected by fire severity at two different scales. First, variability in fire severity may occur at the stand scale as reflected by the variable percentage of trees killed or damaged by fire, which influence the availability of snags for deadwood users. Second, fire severity may vary at the tree scale (e.g. percentage of burned bark) and, thereby, influence the micro-habitat conditions suitable for foraging or breeding activities. These two scales of variation in fire severity have been shown to influence the response of invertebrate and vertebrate species to fire (Saint-Germain *et al.* 2004b, Smucker *et al.* 2005, Koivula and Schmiegelow 2007, Vierling *et al.* 2008). Because the black-backed woodpecker relies on recently dead trees for foraging, it typically responds positively to burn severity at the stand scale (percentage of burned trees; Koivula and Schmiegelow 2007). In our study, most burned stands showed high levels of tree mortality (often close to 100%) and the transition at burned-unburned forest edges was generally sharp. Yet, our results clearly show that variation in fire severity was present at the tree level within these severely burned stands and that this variability likely influenced habitat suitability for woodpeckers.

At the tree level, fire severity was an important factor in foraging tree selection, as woodpeckers tended to select moderately burned trees over more severely or lightly burned trees. This selection pattern was likely linked to the abundance of wood-boring beetles. Higher fire severity has been shown to negatively affect wood-borer densities in our study sites (Saint-Germain *et al.* 2004b, c). It has been hypothesized that this effect of fire severity is more pronounced for spruce than pine species because the former are less protected from desiccation by their thinner bark (Gardiner 1957, Ross 1960). The lower use of lightly burned trees shortly after fire is more difficult to interpret. Some of these lightly burned trees may have died the year after the fire, meaning tree mortality may not have been synchronized with flight and oviposition periods of *M. scutellatus* (Gardiner 1957, Ross 1960, Dixon *et al.* 1982). Alternatively, woodpeckers may have avoided these trees because the bark was more tightly attached to the tree and would have involved higher energy costs to capture insects. The moderately burned trees preferred by foraging woodpeckers were concentrated at burned-unburned forest edges: this further supports the idea that burned forest edges may represent high quality sites for many saproxylic insects and woodpeckers (Murphy and Lehnhausen 1998, Werner 2002, Saint-Germain *et al.* 2004c).

2.6.4 Management implications

Pre-fire forest conditions and fire severity are factors that should be considered when planning the conservation of burned forests for the black-backed woodpecker in managed post-fire landscapes. Because foraging requirements differ in several aspects from nesting requirements, both should be considered in post-fire management guidelines (Hutto 2006).

Although only a few scattered potential nest trees per hectare are necessary for nesting purposes, foraging activities require a much higher concentration of suitable trees, to the order of several hundred per hectare as suggested by our study. Based on our size estimates of core foraging areas, large unsalvaged forest patches of about 20 ha composed mainly of mature and overmature forests should be maintained in eastern boreal spruce forests. These forests are likely to contain the large snags required for foraging (i.e. >10 cm dbh) and for nesting (i.e. >20 cm dbh), and they are also more likely to contain the more decayed pre-fire snags preferred as nest trees. Although black-backed woodpeckers use severely burned stands (high percentage of tree mortality), their preference for moderately burned trees suggests burned-unburned forest edges should receive particular conservation attention when planning post-fire salvage logging.

Maintaining high-quality habitat conditions for black-backed woodpeckers may also provide suitable conditions for other deadwood-dependent species that have similar habitat requirements, including many saproxylic insects. In our study, more than 15 species of Coleoptera emerged from burned spruce trees (Saint-Germain *et al.* 2004b), some of which were potential prey for woodpeckers. Moreover, suitability of tree substrates for these insects is affected similarly by tree diameter and fire severity variables (Saint-Germain *et al.* 2004b, c).We therefore believe the black-backed woodpecker could be considered an umbrella species for deadwood-dependent species in burned North American boreal forests. In addition, several other species rely on the cavities excavated by this woodpecker in post-fire habitats, meaning the maintenance of adequate habitat resources for this keystone species (*sensu* Simberloff 1998) would thus also favour other cavity-nesters (Saab *et al.* 2004). In the boreal forest, the black-backed woodpecker is often the most abundant woodpecker species in the first years following fire (Nappi 2000, Hoyt and Hannon 2002, Koivula and Schmiegelow 2007). Secondary cavity nesters commonly observed in cavities excavated by black-backed woodpeckers in our study area include the eastern bluebird (*Sialia sialis*), the tree swallow (*Tachycineta bicolor*) and the red squirrel (*Tamiasciurus hudsonicus*).

Given pre-fire forest inventory and fire severity maps are generally available to forest managers, these two sources of information could be used to delineate conservation areas in salvaged burns for deadwood-dependent species as well as for other fire-associates. Recent studies carried on both plant and animal communities have shown that species are typically influenced by both pre-fire conditions and fire severity (e.g. Purdon *et al.* 2004, Saint-Germain *et al.* 2004b, Smucker *et al.* 2005, Koivula and Schmiegelow 2007, Kotliar *et al.* 2007, Vierling *et al.* 2008). However, given other fire-associated species and taxa can have different habitat requirements (Purdon *et al.* 2004, Smucker *et al.* 2005, Koivula and Spence 2006), we recommend that conservation of black-backed woodpecker habitats be part of a coarse-filter approach in efforts to maintain the full range of variation in post-fire conditions.

While much of the recent conservation literature has been devoted to the impacts of salvage logging in burns, our study illustrates that conditions created by extensive even-aged forest management prior to fire are at least equally important for the determination of post-fire conditions relevant for black-backed woodpeckers. No salvage logging occurred in the Parc national des Grands-Jardins. However, about half of our burned stands were harvested 40 years ago and were thus too young to provide adequate foraging and nesting habitats for the black-backed woodpecker. Although fires and other natural disturbances generate young stands, timber harvesting is now adding to and, in many regions, surpassing fire in its extent (Delong and Tanner 1996, Perera and Baldwin 2000, Perron 2003). Prior to forest management, a large portion of the eastern boreal region was dominated by forests older than 100 years under natural disturbance dynamics (Bergeron *et al.* 2001, Bouchard *et al.* 2008, Cyr *et al.* In press). Under regulated forest rotations of less than 100 years, the forest landscape will be largely dominated by young forests in decades to come (Bergeron 2004, Cyr *et al.* In press). Because fire suppression in this biome has had only limited effects until now (Hannon and Drapeau 2005), it is likely that a pattern of successive disturbances (fire after forest harvesting) will add to or partly replace the one created by successive natural disturbances (Payette *et al.* 2000a, Payette and Delwaide 2003). As the abundance and extent of mature and old-growth forests will continue to decrease in North American eastern boreal forest landscapes submitted to even-aged management, fire will burn increasingly younger forests. If not enough mature and overmature forests are maintained in managed landscapes, this indirect effect of forest management, in addition to salvage logging and fire suppression, will likely reduce the extent and quality of post-fire habitat for the black-backed woodpecker and many other deadwood-dependent species.

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2.9 Tables

Table 2.1. Parameter estimates and their significance levels for the model best supported by the data (based on AICc weight) describing nest tree selection by black-backed woodpeckers.

			95% CI			
Parameter	Estimate [b]	S.E.	Lower	Upper	Z	*P*
Diameter at breast height	7.11	1.74	3.70	10.52	4.09	<0.001
Species						
Populus tremuloides	1.79	0.30	1.20	2.38	5.96	<0.001
Betula papyrifera	1.15	0.59	0.00	2.30	1.96	0.050
Abies balsamea	-0.13	0.39	-0.90	0.64	-0.33	0.741
Pinus banksiana	0.63	0.62	-0.60	1.85	1.00	0.316
Larix laricina	-2.56	0.71	-3.96	-1.16	-3.58	<0.001
Picea mariana	0.00	-	-	-	-	-
Degradation [a]						
DEG1	-1.84	0.53	-2.87	-0.81	0.00	<0.001
DEG2	0.50	0.79	-1.04	2.05	0.64	0.523
DEG3	0.00	-	-	-	-	-

[a] Deg1 = fire-created snag; Deg2 = pre-fire snag with intact top; Deg3 = pre-fire snag with broken top.

[b] One level of the "species" and "degradation" variables is zero because estimates are based on comparisons with this level.

Table 2.2. Sample sizes of foraging observations (number of sampling days, observation bouts and foraging trees) and core foraging area estimates for 10 nesting black-backed woodpeckers 2 years after fire.

Nest	Sex	Days	Bouts	Trees	Area[a] (ha)
1	F	4	54	180	8.0
2	M	5	56	162	14.9
3	M	4	50	221	6.9
4	M	4	83	105	10.6
5	F	4	45	127	10.2
5	M	4	60	283	13.1
6	F	5	61	236	16.7
6	M	4	30	71	10.3
7	F	6	64	186	11.6
7	M	6	67	152	13.8
Mean per individual		5	57	172	11.6

[a] Estimations are based on minimum convex polygons, including 100% locations.

Table 2.3. Ranking matrix showing preferences for combinations of diameter (dbh) and fire severity classes of foraging black-backed woodpeckers in recently burned forests. Signs indicate preference (+) or avoidance (-) of a given class in the left-hand column over the other classes of the first row (+++ or --- indicates significant selection). Rank in the right-hand column is based on the sum of the positive elements of each row; a highest rank indicates highest preference.

		DBH 5.0-9.9			DBH 10.0-14.9			DBH ≥ 15.0			
DBH class (cm)	Severity	Light	Moderate	Severe	Light	Moderate	Severe	Light	Moderate	Severe	Rank
DBH 5.0-9.9	Light		-	+	-	---	-	-	---	---	1
	Moderate	+		+	---	---	---	-	---	---	2
	Severe	-	-		---	---	---	-	---	---	0
DBH 10.0-14.9	Light	+	+++	+++		-	-	-	---	-	3
	Moderate	+++	+++	+++	+		+++	+	---	-	6
	Severe	+	+++	+++	+	---		-	---	---	4
DBH ≥ 15.0	Light	+	+	+	+	-	+		-	-	5
	Moderate	+++	+++	+++	+++	+++	+++	+		+++	8
	Severe	+++	+++	+++	+	+	+++	+	---		7

2.10 Figures

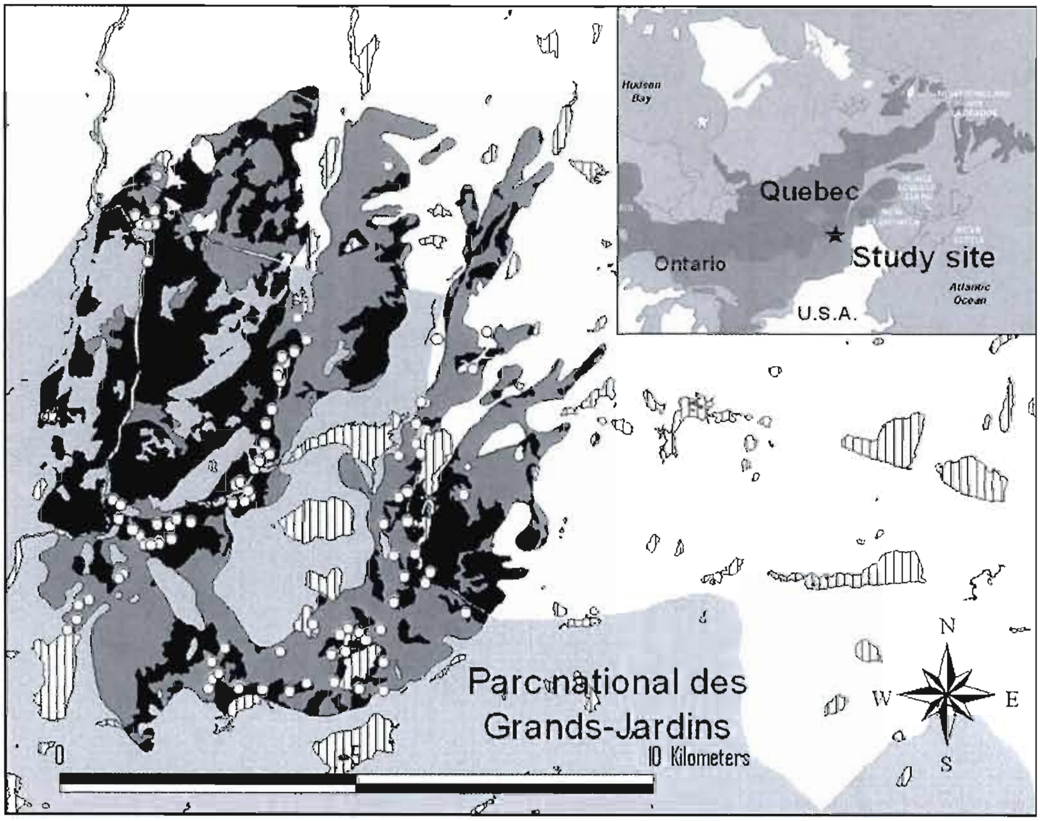

Figure 2.1. Location of the Parc national des Grands-Jardins (Quebec, Canada) and the 1999 fire. Forest stands within the burned landscape were classified according to their development stages prior to fire : black = burned mature stands, dark grey = burned young stands (park is in light grey; water bodies are hatched). Nests located during the 3-year study are indicated by white dots.

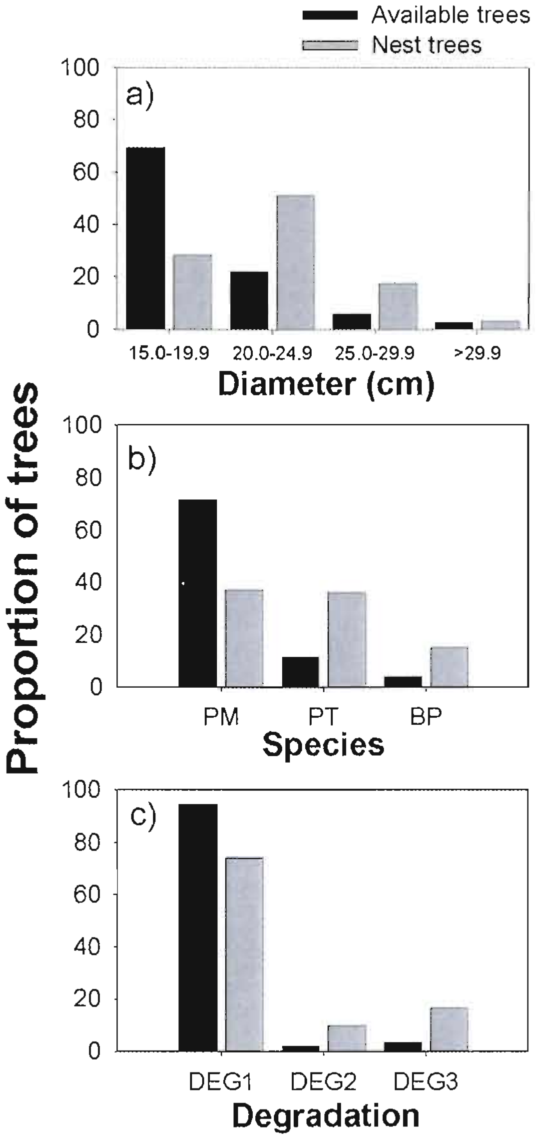

Figure 2.2. Relative proportion of available trees ($n = 988$) and nest trees ($n = 92$) for the three variables involved in nest tree selection (based on logistic regression, Table 2.1) : a) diameter at breast height (dbh), b) tree species and c) degradation. Dbh is presented in three classes for illustration. Tree species includes only the three most frequently used species: PM = *Picea mariana*; PT = *Populus tremuloides*; BP = *Betula papyrifera*. Degradation classes include: Deg1 = fire-created snag; Deg2 = pre-fire snag with intact top; Deg3 = pre-fire snag with broken top. Available trees were summed from the nest vegetation plots.

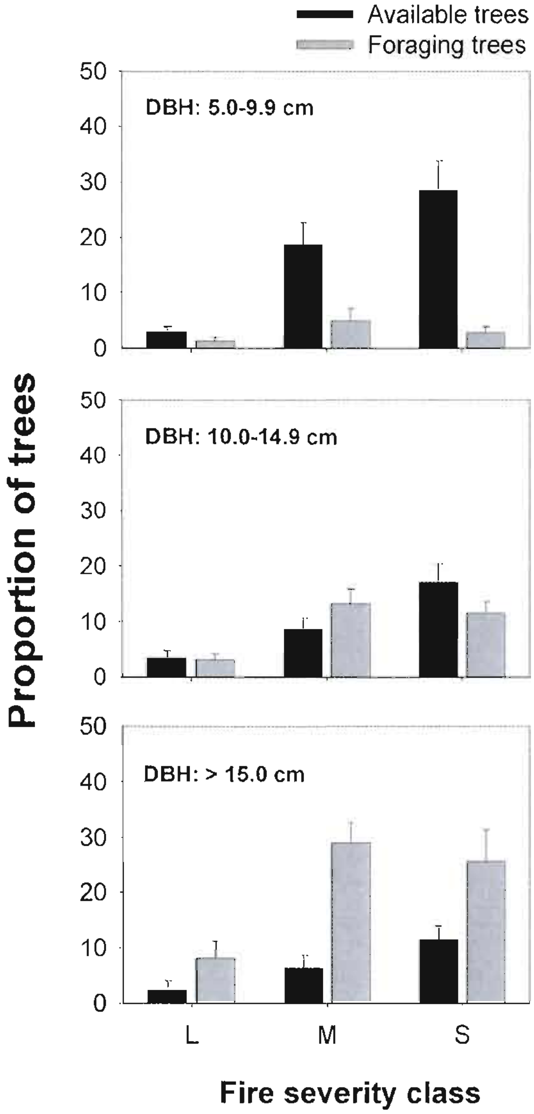

Figure 2.3. Relative proportion of available trees (*n* = 1265) and foraging trees (*n* = 1608) for different diameter (dbh) and fire severity classes. Bars represent mean relative proportions (+ 1 S.E.) of each class (based on the 10 individuals).

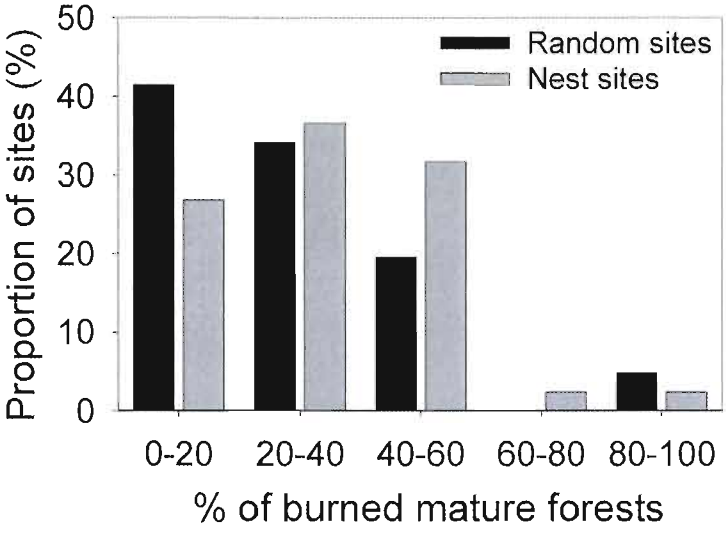

Figure 2.4. Proportion of nest sites (*n* = 41) and random sites (*n* = 41) as a function of the percentage of burned mature forest within a 250m-radius (20% classes). Comparisons were made for a 700 ha continuous portion of the burned landscape that contained mixed proportions of burned young and burned mature stands.

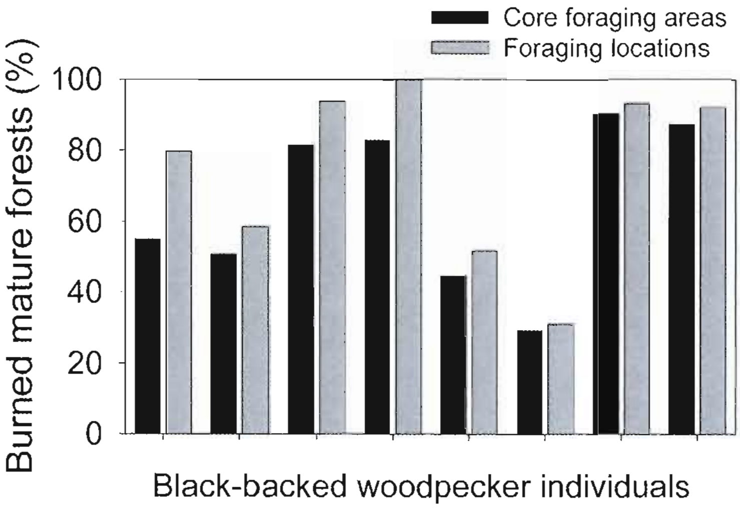

Figure 2.5. Comparison of the proportion of burned mature forest within core foraging areas and the proportion of foraging locations that occurred in burned mature forests for eight nesting black-backed woodpeckers.

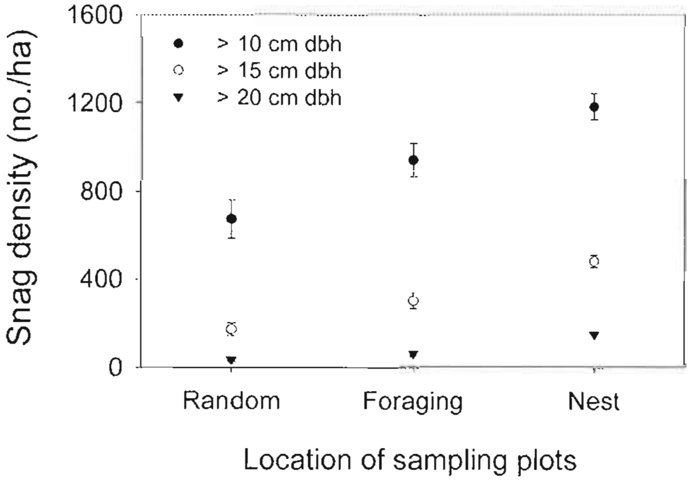

Figure 2.6. Mean density of snags (± 1 S.E.) in random site plots (*n* = 49), core foraging site plots (*n* = 66) and nest site plots (*n* = 92).

CHAPITRE 3

REPRODUCTIVE SUCCESS OF THE BLACK-BACKED WOODPECKER (*PICOIDES ARCTICUS*) IN BURNED BOREAL FORESTS: ARE BURNS SOURCE HABITATS ?

3.1 Résumé

Le pic à dos noir (*Picoides arcticus*) est considéré comme une espèce spécialiste des feux partout dans son aire de répartition. Étant donné sa forte abondance dans les forêts récemment brûlées, il a été suggéré que les forêts brûlées constituaient des habitats sources pour l'espèce. Nous avons mené une étude de trois ans après feu pour évaluer l'occupation temporelle et le succès reproducteur du pic à dos noir dans des pessières noires récemment et sévèrement brûlées du centre du Québec, Canada. Nous avons examiné comment le succès reproducteur variait temporellement et spatialement à l'intérieur d'un paysage brûlé et nous avons évalué le statut source-puit de la population au fil des ans. La densité de nids était élevée dans l'année suivant le feu mais a décliné significativement au cours de la période de trois ans. Basé sur 106 nids, le succès de nidification a diminué de 84% la première année suivant le feu à, respectivement, 73% et 25% pour la deuxième et troisième année après feu. La densité de nids et le succès reproducteur étaient plus élevés dans les secteurs à forte proportion de forêts matures brûlées que dans ceux dominés par des forêts jeunes brûlées. Le succès reproducteur était également plus élevé à proximité des forêts non brûlées. La comparaison de la productivité annuelle de la population avec plusieurs estimés de taux de survie suggère que ces forêts brûlées consituaient un habitat source pour les deux premières années suivant le feu, bien que ce statut variait selon les conditions forestières présentes avant le feu. Nos résultats suggèrent que les forêts brûlées peuvent contribuer significativement à la taille des populations dans les écosystèmes dynamisés par le feu. Les pratiques d'aménagement forestier telles que la suppression des feux, la coupe de récupération et le rajeunissement de la structure d'âge des forêts dans les paysages forestiers aménagés peuvent réduire la quantité et la qualité des forêts brûlées qui constituent des habitats importants pour le pic à dos noir et d'autres espèces associées au feu.

Mots-clés : feu, bois mort, oiseaux, Picidae, succès de nidification, source-puit.

3.2 Abstract

The black-backed woodpecker (*Picoides arcticus*) is considered a fire specialist throughout its breeding range. Given its high abundance in recent burns, it has been hypothesized that post-fire forests are source habitats for this species. We conducted a 3-year post-fire study to evaluate the temporal occupancy and reproductive success of black-backed woodpeckers in high-severity burned black spruce forests of central Quebec, Canada. We examined how reproductive success varied temporally and spatially within a burned landscape and investigated the potential source or sink status of this woodpecker population over time. Woodpecker nest density was high in the year after fire but declined significantly over the 3-year period. Based on 106 nests, nest success declined from 84% the first year after fire to 73% and 25%, respectively, for the second and third years after fire. Nest density and reproductive success were higher in areas with high proportions of burned mature forests than in areas dominated by burned young forests. Reproductive success was also higher in proximity to unburned forests. Comparison of annual productivity with a range of survival estimates indicated that these burned forests likely functioned as source habitats for the first two years following fire, although this status varied as a function of pre-fire forest age. Our results suggest that post-fire forests may contribute significantly to population levels in fire-prone ecosystems. Forest management practices that reduce the amount of mature and over-mature forests can affect the quality of post-fire habitats important to the black-backed woodpecker and other fire-associated species.

Keywords : fire, dead wood, birds, Picidae, nest success, source-sink.

3.3 Introduction

Wildfire is a major natural disturbance of many North American forest ecosystems, and is increasingly recognized as an important determinant of forest biodiversity (Saab and Powell, 2005; Noss and Lindenmayer, 2006). Beyond its role in forest dynamics (Bergeron, 2000; Brown and Smith, 2000; Kuuluvainen, 2002), fire also creates short-term habitat conditions that are suitable and sometimes critical to many plant and animal species. In the boreal forest for instance, many plants, invertebrates and vertebrates are found either exclusively or at higher abundances in post-fire habitats than in other natural or managed forest types (Nguyen-Xuan et al., 2000; Saint-Germain et al., 2004a; Hannon and Drapeau, 2005; Buddle et al., 2006; Schieck and Song, 2006). Burned forests are particularly important as they provide abundant high-quality snags for many deadwood-dependent species such as saproxylic insects (Jonsell et al., 1998; Wikars, 2002; Saint-Germain et al., 2004b,c) and cavity-nesting vertebrates (Drapeau et al., 2002; Hannon and Drapeau, 2005; Saab and Powell, 2005).

Because fire-associated species (i.e. species found in higher abundance in post-fire habitats) evolved in a context where wildfires have long been the primary process driving forest dynamics, it is hypothesized that fires play an important role in the abundance and the long-term maintenance of regional populations (Berg et al., 1994; Hutto, 1995; Murphy and Lehnhausen, 1998). This hypothesis has important implications for conservation because alteration of fire regimes and post-fire logging may pose a serious threat to the persistence of post-fire forest habitats and their associated biodiversity (Lindenmayer et al., 2004; Noss and Lindenmayer, 2006). Although many studies have provided valuable information on the response (e.g. presence and abundance) of forest species to fire, much less information is available on the demography (e.g. birth and mortality) of fire-associated species in post-fire habitats (Saab and Powell, 2005). Because abundance is not necessarily an adequate indicator of habitat quality (Van Horne, 1983; Vickery et al., 1992; Saab et al., 2007; but see Bock and Jones, 2004), it is essential to measure critical demographic parameters such as reproductive success to assess the ecological role of burned forests in the population dynamics of fire-associated species, and ultimately to the persistence of their regional populations. Moreover, recent studies have shown that species responses to fire are sensitive to heterogeneity (i.e. fire severity, pre-fire forest composition and structure) and temporal changes in post-fire conditions (Smucker et al., 2005; Kotliar et al., 2007; Saab et al., 2007; Vierling et al., 2008). Understanding how these factors influence reproductive success may help determine when and which portions of a burn are most suitable for fire associates and, thus, should be maintained during post-fire forest logging (Lindenmayer et al., 2008).

The black-backed woodpecker (*Picoides arcticus*) has a breeding distribution that coincides closely with the range of boreal and mountainous conifer forests in North America and is considered a fire-specialist throughout its breeding range (Dixon and Saab, 2000; Hannon and Drapeau, 2005; Saab and Powell, 2005). This species responds positively to beetle concentrations (in particular Cerambycidae beetles) following large-scale disturbances, especially in high-severity burned forests where woodpecker densities are typically higher than in other forest types (Hutto, 1995, 2008; Murphy and Lehnhausen, 1998; Nappi, 2000; Hoyt and Hannon, 2002; Koivula and Schmiegelow, 2007). Higher abundance of black-backed woodpeckers in burns led Hutto (1995) to suggest that populations of this species are maintained by a patchwork of recently burned forests across the landscape. In other words, burned forests would act as source habitats from which birds emigrate once post-fire conditions become unsuitable, thereby helping maintain sink populations in unburned forests (Hutto, 1995; Murphy and Lehnhausen, 1998). Although large numbers of black-backed woodpeckers in recently burned forests suggests these forests are high-quality habitats, little information exists on the species reproductive success (e.g. often based on small numbers of nests) and on the factors that influence this reproductive success in burns (but see Saab et al., 2007; Vierling et al., 2008).

In 1999, a fire burned ~4500 ha of coniferous forest in the Parc national des Grands-Jardins in central Quebec, Canada. Because logging was not allowed within the park and because accessible burned forests are promptly salvage logged in Quebec (Nappi et al., 2004), this fire provided a unique opportunity to study black-backed woodpecker population dynamics in unsalvaged post-fire forests. In this paper, we examine the occupancy and reproductive success of a black-backed woodpecker population over 3 years following a stand-replacing wildfire in black spruce forests of eastern Canada. Specifically, we sought to answer the following: (1) how long are these burned forests used for nesting, (2) what is the reproductive success of this species in this habitat and how does it change in relation to time since fire and to within-burn variability in forest conditions, and (3) are these burned forests likely to be source or sink habitats for this species and how does this status change over time and with post-fire forest conditions?

3.4 Methods

3.4.1 Study area

This study took place in the Parc national des Grands-Jardins (310 km^2), a provincial park located in the Charlevoix Highlands approximately 120 km north-east of Quebec City in Quebec, Canada (47°44' N; 70°46' W; Fig. 3.1). Elevation at our study sites ranges from 600 m to 900 m. Mean annual temperature is 0°C and total annual precipitation averages 1405 mm, with 407 mm falling as snow (Boisclair, 1990). While vegetation is typical of the spruce-moss bioclimatic domain, the park also contains the southernmost lichen woodland stands in eastern Canada (Payette et al., 2000a). Black spruce (*Picea mariana*) is the dominant tree species, with lesser abundances of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Fire has been the main natural disturbance with 13 fires burning about 40% of the total park area during the 20th century (Payette and Delwaide, 2003). In addition, 39% of the area was logged between 1940 and the creation of the park in 1981 (Payette and Delwaide, 2003).

Between 30 May and 25 June 1999, a fire burned 4546 ha of conifer-dominated forest mostly within the park limits (Société de protection des forêts contre le feu, 2000; Fig. 3.1). This fire was generally severe with most of the stands being totally burned. Burn severity was evaluated by the Quebec Ministry of Natural Resources and Wildlife based on the percentage of the crown cover that had been burned (based on a Landsat imagery at a 30 m × 30 m pixel resolution). Based on this evaluation, 96% of the area affected by the fire was composed of high-severity burned stands (stands with >90% of the crown cover burned) whereas 4%

consisted of low-severity burned stands (dominance of unburned crown cover). We obtained a similar burn severity estimate with field measures taken at random burned sites (3.14-ha plots, $n = 32$); mean percentage of burned crown cover at these sites was 98.3 ± 4.0%.

Although forests were relatively homogeneous in their pre-fire composition (black spruce dominance), the history of natural and anthropogenic disturbances had created a mosaic of stand ages. Stand age largely determines tree diameter, one of the most important factors for foraging and nest snag selection by black-backed woodpeckers (Nappi et al., 2003). As we expected this to influence the quality of post-fire habitat for black-backed woodpeckers, we used tree height as a surrogate for tree diameter to classify stands as mature (canopy height >7 m) or young (canopy height <7 m) based on pre-fire digital forest inventory maps. Given the overall high severity of the burn, no difference in burn severity was observed between burned mature and young stands. Based on field measures of burn severity, mean percentage of burned crown cover at burned mature stands was 99.0 ± 1.7% whereas it was 97.8 ± 4.7% at burned young stands (Mann-Whitney test, $Z = -0.128$, $P = 0.899$).

The north-western portion of the burned landscape originated from a 1922 fire (Payette et al., 2000b) and was dominated by mature stands (approximately 80-year old stands); this area is hereafter referred to as the "burned mature landscape" (Fig. 3.1). The remaining burned matrix was dominated by young stands that originated from previous logging that occurred in the late 1950s and early 1960s, therefore averaging 40 years of age (Payette et al., 2000b), and was interspersed with mature stands left undisturbed at the time of previous logging; this area is hereafter referred to as the "burned young landscape".

3.4.2 Nest search and nest density estimation

We searched for black-backed woodpecker nests during the first three breeding seasons following fire (2000-2002). Active nests were located by systematic searching in delineated portions of the burn that were accessible (e.g. road access). Overall, 1185 ha of burned forest was surveyed (26% of the total burned forest landscape): 305 ha in the burned mature landscape and 880 ha in the burned young landscape. Nest searching methods were similar to the ones described in Dudley and Saab (2003). Within these delineated portions of the burn, nests were searched along transects separated by 200 m and which spanned the entire delineated areas. All transects were walked three times and nest searching effort was standardized among these delineated areas. Transects were walked during morning hours (05h00 to 12h00) and nests were located by searching for cavities, by listening for nest excavation or begging nestlings or by following adults to their cavity. To increase our chance of locating nests and to confirm the presence or absence of potential nesting pairs in a given area, birds were attracted using 5-min playbacks at sampling stations 200 m apart along these transects. These surveys were distributed from early May to early July in order to cover the peak of the breeding season in our area (median day for start of incubation = 30 May, $n = 111$ nests) and to increase our chance of detecting nests when birds are more likely to respond to playback (outside the incubation stage). Additional visits in potentially occupied areas (e.g. where a pair was observed) were made until nests were located. We considered nests to be active when egg-laying was completed and incubation initiated. The same delineated areas were sampled each year with an equivalent sampling effort. Nest density was estimated each year based on the number of active nests within the surveyed areas. These estimates were made separately for the burned mature and young landscapes. Some additional nests were found opportunistically outside these surveyed areas and were included in reproductive success analyses (see below).

3.4.3 Reproductive success

We monitored each nest every 3-6 days until fledging or nest failure. Nest cavities excavated by black-backed woodpeckers were particularly low (Table 3.1). All cavities but two were easily accessible. We were therefore able to make direct observations of nest content (number of eggs or nestlings) using a small mirror and a flashlight (Fayt, 2003). A nest was considered to fail if evidence of predation or abandonment was observed during the nesting period or if it was no longer occupied by at least one young before the potential fledge interval (<80% of the average nesting cycle; Saab and Vierling, 2001). Predation included cases with signs of predation (e.g. nest destroyed), loss of eggs, and loss of nestlings or usurpation by another species prior to potential fledge interval. Abandonment included cases where eggs or nestlings were left unattended for more than two visits. We estimated length of the nesting period based on our own data set using nests with known nesting chronologies (incubation period = 11 days (n = 38), nestling period = 24 days (n = 11), total nesting period = 35 days (n = 29)). We assumed egg-laying to be asynchronous and incubation to start with the last egg, based on our own observations and on information reported for the closely-related species *Picoides tridactylus* (Leonard, 2001). Using a 35-day nesting period, the start of the potential fledge interval corresponded at 28 days after the onset of incubation.

Nest success was calculated using Johnson's (1979) method which takes into account unequal periods of nest observation (Mayfield, 1961, 1975) and produces standard errors of estimates. For each year, we computed daily nest mortality rate as the total number of nest failures divided by the total number of observation days (for all nests pooled within a year) and then derived the daily nest survival rate (1-daily mortality rate). Nest success was then calculated as daily survival rate raised to the exponent corresponding to the length of the total nesting cycle (35 days). Nest success estimates give the probability of a nest surviving its whole nesting cycle and successfully fledging at least one young. The first day of observation corresponded to the first day the nest containing eggs or nestlings was found or the first day of incubation when the nest was discovered prior to incubation. For the last day of observation, we used midpoint between last active day (a visit with at least one young at nest) and last check for nests that failed, whereas we used the last active day for successful nests or nests with uncertain fate ("Last Active-A" approach of Manolis et al., 2000). Productivity of successful nests was based on the number of young observed near the time of fledging (>80% of nesting cycle or higher count of last two active visits).

3.4.4 Data analyses

Differences in nest densities among years were assessed for the burned mature and young landscapes using Goodness-of-fit tests. We investigated the effect of temporal, nest tree and nest site variables on reproductive success by selecting variables considered to have a potential effect on the breeding performance of woodpeckers based on a literature review and our own experience of the area and species under study. We first tested the effect of these explanatory variables on daily nest mortality rate using Mayfield logistic regression (Aebischer, 1999; Hazler, 2004). With this modeling approach, each nest represents multiple binomial trials (failure/success) and number of trials corresponds to the number of days the nest was under observation (exposure days). This method reduces the bias associated with unequal periods of observation (Mayfield, 1961, 1975) while allowing the inclusion of individual explanatory variables into the analysis (Hazler, 2004). Three different categories of "failure" were considered as the dependent variable: (1) all failures (including both predated and abandoned nests), (2) predation only (abandoned nests were excluded from the data set) and (3) abandonment only (predated nests were excluded). We also examined the effect of these same explanatory variables on individual nest productivity by analyzing clutch size and fledgling number using cumulative logit models (Allison, 1999). Modeling of clutch size included all nests for which incubation had been initiated. When modeling fledgling number, we excluded nests that had been predated and we considered abandoned nests as zeros in terms of productivity; therefore we assumed the same factors were involved in abandonment and in the productivity of successful nests and that these factors were different than the ones involved in predation.

Explanatory variables were divided into three groups (Table 3.1). We first tested the effect of time since fire given that we expected habitat quality (i.e. abundance of Cerambycidae beetles) to decline with years elapsed since fire (Murphy and Lehnhausen, 1998; Covert-Bratland et al., 2006). A second group included variables at the nest tree level that likely influence reproductive success of cavity nesters: nest height, tree diameter at nest height, diameter of cavity entrance, cavity depth and cavity orientation (Conner, 1975; Nilsson, 1984; Rendell and Robertson, 1989; Wiebe, 2001). The last group included site variables indicative of habitat quality for woodpeckers. Snag density was measured using 225 m^2 plots centred on each nest and estimates were produced for different diameters at breast height (dbh; >10, >15 and >20 cm). Proportion of burned mature forest surrounding nests was estimated for different radii (100, 250 and 500 m) from the combination of digital pre- and post-fire forest inventory maps. Each nest was also assigned to one of the two landscape classes described in the study area section (burned mature vs. burned young landscapes). We also tested the effect of nest proximity to burn edges on reproductive success as we expected nest predation to be highest close to unburned forest (Saab and Vierling, 2001). Conversely, we hypothesized that productivity per nest would be higher for nests closer to unburned forest as these portions of the burn may represent higher-quality foraging habitats for woodpeckers (Murphy and Lehnhausen, 1998; Saint-Germain et al., 2004b). Proximity to unburned forest was measured with two variables based on digital post-fire forest inventory maps : (1) proportion of unburned forest surrounding nests (within 100, 250 and 500 m radii) and (2) shortest distance to unburned forest (>1 ha) using different distances (more or less than 100, 200, 300, 400 or 500 m). Because elevation may also affect the density of wood-boring beetles (Saint-Germain et al., 2004b), this was also included as an explanatory variable and was measured using a global positioning system and topographic maps.

Mayfield logistic and cumulative logit regression models were performed in two steps. We first conducted regressions on each group of variables separately using stepwise selection to select significant variables in each set ($p < 0.05$). Variables that came out as significant in each set were then entered concurrently using stepwise selection in a final regression model. Daily nest mortality and nest productivity models predict opposite responses in terms of reproductive success. A positive relationship of a given variable with daily nest mortality (e.g. predation) indicates a negative influence on reproductive success. Conversely, a positive relationship with productivity (e.g. no. of fledglings) indicates a positive influence on reproductive success. Models were evaluated for overdispersion by estimating the variance inflation factor $\hat{c}$ (Deviance/DF) and standard errors were adjusted when $\hat{c}$ was >1 using the deviance statistic (Allison, 1999; Hazler, 2004). All regressions were performed using proc Logistic in SAS (SAS Institute Inc., 2004).

We assessed whether burned forests represented potential source habitats for the black-backed woodpecker during the three post-fire breeding seasons. This assessment was made separately for the burned mature and young landscapes. Three demographic parameters are necessary to estimate the source-sink status of a population: productivity, juvenile survivorship and adult survivorship (Pulliam, 1988). The source-sink status was calculated each year by comparing annual productivity to a source-sink threshold that corresponds to the minimal annual productivity necessary to maintain a viable population. This source-sink threshold was calculated according to the following equation (Trine, 1998; Bourque and Villard, 2001):

Source-sink threshold = 2 × adult mortality / (1- juvenile mortality)

We calculated annual productivity from our data and used estimates of adult and juvenile survival rates from the literature. Annual productivity was calculated for each year and each landscape as the product of the mean number of fledglings per successful nest and nest success (Donovan et al., 1995). Secondary nesting and brooding were not incorporated in the calculations since less than 2% of all nesting events were second nesting attempts in our study and black-backed woodpeckers raise only one brood per year (Dixon and Saab, 2000). The population was considered a source in a given year if annual productivity was high enough to compensate for adult and juvenile mortality (source-sink threshold). Conversely, a population was considered a sink if annual productivity was insufficient to compensate for adult and juvenile mortality.

Estimates of survival rates are often limited for woodpeckers (Pasinelli, 2006; Wiebe, 2006), and no estimate is available for the black-backed woodpecker. We used survival rate estimates for other woodpecker species in other study areas and derived a range of survival estimates that could be used to assess the potential source or sink status of our population (Saab and Vierling, 2001). Wiebe (2006) reviewed the literature for survival rates of adult North American and European woodpecker species and reported an average survival rate for all species combined of 0.58. Mean survival rates for individual *Picoides* species varied between 0.48 and 0.82 for stable populations. Therefore, we assumed that adult survival rate of black-backed woodpeckers was within these values and used three rates representative of this range (low: 0.50; medium: 0.65; high: 0.80). Rates of juvenile survival are even less documented and many authors have used a range of 30-50% of adult survival rates in models of population dynamics of migratory bird species (Donovan et al., 1995; Trine, 1998). Given that the black-backed woodpecker is a resident species, we used 50% of adult survival rate as a reference to determine a range of juvenile survival rates (low: 0.25; medium: 0.33; high: 0.40). We computed the source-sink thresholds under these nine different scenarios. According to the intermediate scenario, productivity higher than 2.1 offspring per nest per year would indicate the population is a source. Productivity thresholds for the lowest and highest survivorship scenarios were, respectively, 4.0 and 1.0 offspring per nest per year.

3.4.5 Prey identification

In order to identify black-backed woodpecker's main prey, we collected stomach contents of two adults nesting in different sites in June 2001. Birds were forced to regurgitate by orally administrating a 1.5% solution of antimony potassium tartrate (according to the methods described by Poulin et al. (1994)). We also collected a fecal sample from one of these birds. The samples were conserved in a 70% ethanol solution and items were later identified by M. Saint-Germain (Université du Québec à Montréal).

3.5 Results

3.5.1 Woodpecker nest density

We observed a significant decline in nest density of black-backed woodpeckers for both the burned mature ($\chi^2 = 30.0$, df = 2, $p < 0.001$) and young landscapes ($\chi^2 = 38.1$, df = 2, $p < 0.001$). The decline of nest density was constant and densities observed by the second year were about half the densities observed the first year post-fire (Fig. 3.2). Nesting activity in year 3 was marginal compared to the first 2 years post-fire. Nest density in the burned mature landscape area was more than twice the density observed in the burned young landscape, a difference that was maintained through time.

3.5.2 Reproductive success and source-sink status

We found 111 active nests over the 3-year study from which 106 could be used to estimate nest success (i.e. > 1 observation day; Table 3.2). Nest success declined from 84% the first year post-fire to 73% and 25% the second and third year following fire (Table 3.2). A total of

19 nest failures occurred over the 3-year study of which 47% (9) were attributed to predation and 53% (10) to abandonment. Both predation and abandonment rates were low but increased with time since fire. The relative importance of each cause of failures (predation and abandonment) remained similar each year. Observed predation cases during the study included one nest destruction by a black bear (*Ursus americanus*) and one nest usurpation by an eastern bluebird (*Sialia sialis*). Other potential nest predators in our study area included the red squirrel (*Tamiasciurus hudsonicus*), the american marten (*Martes americana*) and weasels (*Mustela* spp.). Mean number of young produced by a successful nest averaged three young per nest, a value that remained constant over the 3-year period.

Both years since fire and nest site variables significantly influenced reproductive success of black-backed woodpeckers. Years since fire had a positive effect on daily nest mortality, although this result was significant only for the regression that included all failures regardless of cause (Table 3.3). Conversely, time since fire influenced clutch size negatively. Nest site conditions had a similar influence on clutch size and number of fledglings although different variables were involved in the models (Table 3.3). Nesting pairs located in the burned mature landscape had larger clutch sizes than those nesting in the burned young landscape. Similarly, nests that were surrounded by a higher proportion of burned mature forest within a 100 m radius tend to fledge more young (Table 3.3, Fig. 3.3). In addition, nests in proximity to unburned forest were more productive than nests located further inside the burn (Table 3.3, Fig. 3.3).

In both the burned mature and young landscapes, annual productivity of black-backed woodpeckers in the first year post-fire was sufficient to compensate for adult and juvenile mortality in six of the nine source-sink threshold scenarios, including the intermediate scenario (Fig. 3.4). This status remained similar for the burned mature landscape in the second year post-fire (six of nine scenarios). For the burned young landscape however, annual productivity in year 2 was below the intermediate source-sink threshold scenario and was likely to offset mortality for only four of the nine scenarios examined. Active nests were rare by year 3, which precluded precise estimation of annual productivity. However, these few active nests had low nest success and, consequently, mean productivity of nests fell below all scenarios.

3.5.3 Woodpecker prey

Diet of the two examined nesting birds consisted mainly of Cerambycidae larvae. Stomach contents of one bird consisted of six head capsules of *Monochamus scutellatus* and three complete *M. scutellatus* larvae. Stomach content of the other bird was two *Acmaeops proteus* larvae, three other Cerambycidae larvae (probably *M. Scutellatus*) and Lepidoptera cocoon remnants. The fecal sample of the latter contained seven head capsules of *Monochamus* sp. and one large Lycosidae spider.

3.6 Discussion

Burned forests are considered important habitat for the black-backed woodpecker, a status largely based on the higher abundance of this species in burns as compared to other habitat types (Hutto, 1995, 2008; Hannon and Drapeau, 2005; Saab et al., 2005). The high nest density and reproductive success of black-backed woodpeckers observed in this study suggest that severely burned spruce forests may indeed represent a high-quality nesting habitat for this species. Nest density was as high as 0.11 nests/ha in our study area, among the highest densities of nesting pairs reported for this species across its range (Dixon and Saab, 2000; Saab et al., 2007; Vierling et al., 2008). Our comparison of woodpeckers' annual productivity with a range of survival estimates suggests that these burned forests likely functioned as a source habitat for this species (Hutto, 1995; Murphy and Lehnhausen, 1998). Yet, results on nest density and reproductive success also indicated that habitat quality of these post-fire forests was temporally limited and varied within our burned landscape.

3.6.1 Effect of time since fire

Temporal occupancy patterns of cavity-nesting birds after fire differ depending on species-specific habitat requirements. Whereas aerial and ground foragers may occupy burns for more than a decade after fire, bark-foraging *Picoides* woodpeckers (black-backed, American three-toed *Picoides dorsalis* and hairy *Picoides villosus* woodpeckers) are typically restricted to the first few years following fire (Murphy and Lehnhausen, 1998; Covert-Bratland et al., 2006; Saab et al., 2007). In our study, nesting activity of black-backed woodpeckers declined sharply with time since fire, with woodpeckers being nearly absent by the third year following fire. This short occupancy pattern is mainly linked to the ephemeral availability of bark and wood-boring beetles, *Picoides* woodpeckers' main prey, that typically colonize these snag forests soon after disturbance (Murphy and Lehnhausen, 1998; Saint-Germain et al., 2004c; Boulanger and Sirois, 2007). Wood-feeding insects that colonize spruce snags are typically limited to the early stages of degradation since most of these species reproduce only in heavily stressed or recently dead trees (Saint-Germain et al., 2007). Because severe stand-replacing fires create a pulse of snags in more or less the same initial post-fire stage, foraging opportunities for *Picoides* woodpeckers are temporally constrained by the life cycles of these saproxylic insects in snags.

In spruce forests of Alaska, Murphy and Lehnhausen (1998) observed a similar 3-year decline in black-backed woodpecker abundance which they attributed to the decrease of *M. scutellatus,* the woodpecker's main prey in their study. This deep-boring cerambycid is well-known for colonizing stands soon after disturbance and larvae of this species remain in the wood for 1-3 years before emerging as adults (Rose, 1957). *M. scutellatus* was the most common cerambycid species in burned spruce trees of our study area (Saint-Germain et al., 2004c) and stomach contents of two nesting birds suggests that larvae of this wood-borer were the woodpecker's main prey as well. Rearing experiments at our sites indicate that *M. scutellatus* adults of the 1999 cohort emerged primarily 2 years after fire (11 % in 2000; 89% in 2001; 0% in 2002; C. Hébert, unpublished data). Few wood-borers were still found in our burned landscape after the first 2 years (C. Hébert, personal communication). The observed decline in woodpecker nest density is thus likely to have reflected changes in prey availability over the course of our study.

Annual productivity of black-backed woodpeckers also decreased significantly over the 3-year period. Given that the number of young produced per successful nest remained relatively constant over the 3-year period, the decrease in the annual productivity was mainly linked to the decrease in nest success. Part of this decrease in nest success was caused by an increased level of predation. Although few nests were predated, predation rate was two times higher the second than the first year post-fire. This increase in predation rate might have been caused by partial recolonization of these burned areas by mammalian predators (e.g. red squirrels), although this effect seems to be limited in the first years following fire (Saab and Vierling, 2001; Fisher and Wilkinson, 2005; Vierling et al., 2008). The other cause of this decrease in nest success was the increase in nest abandonment. As food availability is a crucial determinant of breeding performance in birds (Martin, 1987), the observed pattern in nest abandonment may have been caused by a decrease in the availability of food resources (wood-boring beetles). Lower food availability would also explain the observed decrease in mean clutch size with time since fire, although no significant effect was detected for the number of young produced per nest. The similarities in occupancy patterns found in this and in another study conducted in Alaska (Murphy and Lehnhausen, 1998), together with our results on reproductive success, suggest burned forests represent important breeding habitats for the black-backed woodpecker in the first 2 years following fire in northern spruce forests.

3.6.2 Effect of within-burn variability in forest conditions

Spatial variability of post-fire conditions within burns can greatly influence occupancy patterns of fire-associated species (Kashian and Barnes, 2000; Saint-Germain et al., 2004b; Smucker et al., 2005; Kotliar et al., 2007). For species that depend on dead wood, pre-fire forest conditions directly determine species, diameter and degradation stage of burned snags and thereby influence the quality of burned forests for these species. Tree diameter is of particular importance for woodpeckers as large trees are required for nesting and provide high concentrations of saproxylic insects (Nappi et al., 2003; Saint-Germain et al., 2004c). Because of its effect on tree size, forest age may influence post-fire habitat quality, especially in northern conifer boreal forests where trees may take a long time to reach adequate sizes for woodpeckers. Although the burned landscape we studied was dominated by pure black spruce stands, previous natural and anthropogenic disturbances have generated stands of varying age.

Our results show that pre-fire differences in forest age influenced both nest density and productivity of black-backed woodpeckers. Nest density in the burned mature landscape was more than two times the density observed in the burned young landscape, a difference that likely reflected the concentration of food resources. We also found that the proportion of burned mature forests surrounding nests had a positive influence on productivity (no. of fledged young). These results indicate that forest conditions (density of large trees) at the moment of fire have an important influence on the quality of post-fire habitats for black-backed woodpeckers. In our study area, burned mature forests that were at least 80 years old likely represented higher quality habitats for the black-backed woodpecker than 40-year-old stands.

The distance of a nest to unburned forest edges also influenced black-backed woodpecker reproductive success. Murphy and Lehnhausen (1998) noted woodpeckers concentrate at the burn periphery where spruce trees were less heavily scorched. Although woodpecker nests in our study were found up to 1 km inside the burn, the proximity of nests to unburned forest edges had a positive effect on woodpecker productivity. These forest-burn ecotones may provide better foraging opportunities, as snags close to unburned edges are generally less severely burned and thus more likely to support high densities of wood-boring beetles (Saint-Germain et al., 2004c). Saint-Germain et al. (2004b) showed proximity of burned forests to unburned areas, after controlling for fire severity, had a positive effect on *M. scutellatus* densities, a pattern that is probably linked to the feeding requirements of wood-borer adults. Contrary to our expectations, nests close to unburned forests were not more likely to be predated, a pattern that is partly explained by the overall low predation pressure in these burned forests. Because of its influence on nest density and reproductive success, within-burn heterogeneity caused by pre-fire forest conditions (e.g. forest age) and fire severity patterns (e.g. distance to unburned forest) may together be an important determinant of the quality of burned forest habitat for the black-backed woodpecker.

3.6.3 Burned forests as source habitats

Hutto (1995) proposed that burned forests could function as source habitats for the black-backed woodpecker and that populations in unburned forests could represent sink populations maintained through emigration from burns after conditions become less suitable (see also

Murphy and Lehnhausen 1998). Our productivity data show that the burned forests we studied likely functioned as source habitats for the black-backed woodpecker. However, our results also emphasize that this source status varied both temporally and spatially within the burn. Our comparison of annual productivity with survival estimates suggests burned forests were more likely to represent source habitats in the first two years after fire. Only a few nests were active by year three and productivity, although based on a small sample, was much lower than in the first 2 years. In addition, we observed that pre-fire forest conditions had an important effect on reproductive success and, thus, on the source-sink status. Burned mature forests were more likely to represent source habitats than burned young forests in the second year post-fire.

Several other factors including pre-fire forest composition, fire characteristics (e.g. severity, size, season), saproxylic insect assemblage (e.g. species, abundance) and woodpecker population density at a regional scale may influence temporal occupancy pattern, density and reproductive success of the black-backed woodpecker in burns. Indeed, other studies have reported longer temporal use of burns by black-backed woodpeckers (>2 years, Hoyt and Hannon, 2002; Saab et al., 2007) or high nest success many years following fire (Saab et al., 2007). Also, both woodpecker abundance and reproductive success have been shown to be influenced positively by fire severity (Koivula and Schmiegelow, 2007; Vierling et al., 2008). The burned forests we studied were relatively homogeneous in their pre-fire forest composition and burn severity, being dominated by severely burned black spruce stands. Although this study does not cover all post-fire conditions, the results we obtained for these severely burned spruce forests are probably representative of many burned forests used by the black-backed woodpecker. Indeed, spruce forests of the Boreal Shield ecozone represent an important portion of the black-backed woodpecker's distribution and these forests are largely shaped by severe stand-replacing fires, those with which black-backed woodpeckers are generally associated.

Despite the inherent variability in post-fire forest conditions, burned forests likely represent high-quality habitats for the black-backed woodpecker. Indeed, the high reproductive success observed in our study in the first 2 years following fire (73-84%) is consistent with previous results reported in other burned forests (87%: Saab and Dudley, 1998; 100%: Dixon and

Saab, 2000). Vierling et al. (2008) also found nest success of black-backed woodpeckers to increase with higher fire severity and reported a 80% nest success in high-severity *Pinus ponderosa* burned stands. Although black-backed woodpeckers occupy unburned forests as well (Bent, 1939; Weinhagen, 1998; Setterington et al., 2000), few estimates of reproductive success are available to compare with post-fire habitats. Yet, results of studies conducted following pine beetle outbreaks suggest that nest success of the black-backed woodpecker in beetle-affected forests is generally less than what is observed in burned forests (63%: Goggans et al. 1989; 44-78%: Bonnot et al. 2008). This higher nest success in burned than unburned forests is consistent with what has been reported for other cavity nesting birds. For instance, Saab et al. (2005) reviewed available data on reproductive success of six cavity-nesting bird species (including the black-backed woodpecker) between burned and unburned forests of the Rocky Mountains and found nest success was typically higher in burned than unburned habitats. The relative higher nest success in burns does not mean that other forest types are unsuitable for breeding black-backed woodpeckers (see also Bonnot et al. 2008). Rather, these results emphasize that burned forests provide highly favourable conditions that are less likely to be found at similar levels in unburned forests.

Two factors are likely responsible for this relatively higher reproductive success in burns. First, nests in burns may be less susceptible to predation, which is often the major cause of nesting failure in birds (Nilsson, 1984; Martin, 1992). For instance, Saab and Vierling (2001) found higher nest success of Lewis woodpecker (*Melanerpes lewis*) in burned than in unburned forests, a result mainly caused by higher predation levels in unburned forests. Given that recolonization of burned forests by nest predators associated with unburned forests may take several years (Saab and Vierling, 2001; Gentry and Vierling, 2007), predation may thus have a limited effect on black-backed woodpecker nest success considering the short-term occupancy of this species in burns. Second, recent burns provide high concentrations of high-quality foraging substrates that are otherwise scarce or patchily distributed in other forest types (Imbeau and Desrochers, 2002; Pedlar et al., 2002; Saint-Germain et al. 2004c). Because nest predation by mammalian predators is likely to decrease with increasing fire severity (i.e. less protection cover and forage for mammal species) whereas foraging opportunities (i.e. snag density) typically increase, nest success is likely to be highest in high-severity burned forests such as the ones we studied (see also Vierling et al., 2008).

We observed considerable variation in the reproductive success of woodpeckers within our burned landscape, even though our stands were relatively similar in pre-fire forest composition and burn severity. This underscores the importance of estimating reproductive success in a wide variety of burn conditions and with a large number of nests. Also, this suggests that estimating reproductive success in unburned forests would be even more problematic as forest conditions may be much more variable than what is observed in burned forests. For instance, dead wood quality and availability in unburned forests may be highly variable due to factors operating at different scales (from individual snag recruitment to larger-scale disturbances). Given that differences in habitat conditions affected the reproductive success of woodpeckers within our burned landscape, a similar effect may occur in unburned forests (e.g. higher reproductive success where density of foraging snags is higher) and it is likely that reproductive success would vary much more than in post-fire habitats.

The high reproductive success observed in this and previous studies suggests that burned forests may contribute significantly to population levels of the black-backed woodpecker, especially in regions where the fire cycle is short. Although fire is recognized as the main natural stand-replacing disturbance in the Canadian boreal forest, fire cycle (the time required to burn an area equal in size to the reference area) has been shown to vary widely among regions (e.g. 50 to over 500 years; Van Wagner, 1978; Foster, 1983; Bergeron et al., 2004, 2006). This variability inevitably affects the availability of post-fire habitats for the black-backed woodpecker. In regions where the fire cycle is short, recent burns may cover an important proportion of the area. Because fire cycle also influences forest age structure, the proportion of mature and old-growth forests – which can represent alternative habitat for black-backed woodpeckers (Weinhagen, 1998; Setterington et al., 2000) – will tend to decrease with a shorter fire cycle. Given that burned forests generally support much higher densities of woodpeckers (Hutto, 1995; Hoyt and Hannon, 2002), an important proportion of black-backed woodpeckers may be recruited in burns on an annual basis in regions with short fire cycle.

The source-sink dynamic proposed by Hutto (1995) for the black-backed woodpecker entails that the net surplus of individuals produced in source (burned) habitats would compensate for the net loss of individuals in sink (unburned) habitats (Pulliam, 1988). This equilibrium in a closed population (no emigration, no immigration) depends both on population growth in each habitat ($\lambda>1$ in sources, $\lambda<1$ in sinks) and on the relative proportion of the population in these habitats (Pulliam, 1988). In regions with a short fire cycle, this source-sink dynamic is plausible given that recent burns would support an important proportion of the population and thus compensate for potential deficits in unburned habitats. However, in regions where the fire cycle is longer, potential habitats for black-backed woodpecker consist mainly of mature and old-growth forests. The net surplus generated by burned forests in these regions is unlikely to compensate for deficits generated in unburned habitats (given the high proportion of these areas) if indeed the mean productivity in these habitats is less than population replacement levels. It is thus likely that bird productivity in at least some of these unburned habitats (e.g. some old-growth forests) is high enough to allow population persistence. A non-mutually exclusive alternative would be that regions with short fire cycles serve as regional sources from which surplus individuals disperse into forest regions with long fire cycles (regional sinks).

3.6.4 Conservation implications

Alteration of fire regimes and forest management practices in North American boreal forests may have important impacts on the availability of wildfire-created habitats. Fire suppression may considerably reduce the availability of this habitat in historically fire-mediated forest ecosystems. In Fennoscandian boreal forests for instance, fire suppression has efficiently controlled the extent of wildfires, which is thought to have contributed to the decline of many fire-associated species (Ahnlund and Lindhe, 1992; Angelstam and Mikusiński, 1994; Berg et al., 1994; Jonsell et al., 1998). In Canadian boreal forests, wildfires are still relatively common although comparisons of historical and current burn rates indicate a decrease in the extent of fires in most regions (Bergeron et al., 2004). Yet, post-fire logging ("salvage logging") in boreal burned forests is becoming an important economic activity that may reduce both the quantity and quality of burned habitats for fire-associated species (Nappi et al., 2004; Schmiegelow et al., 2006). A major impact of this management practice is the removal of burned trees of commercial size that are also the most valuable to deadwood-dependent species such as saproxylic insects and bark-foraging woodpeckers. Our results clearly indicate that burned conifer forests represent important nesting habitats for the black-backed woodpecker, as for other cavity-nesting birds (Saab et al., 2005). Conservation of post-fire habitats may thus play a key role in the persistence of black-backed woodpecker populations and many other fire-specialists in managed forest landscapes. Large continuous tracks of unsalvaged stands of commercial value (i.e. large diameter snags) and located close to unburned forests should therefore be maintained as black-backed woodpecker nesting habitat.

Even-aged management in the boreal forest is likely to induce large-scale changes in the age structure of forest stands, a change that may also affect populations of the black-backed woodpecker (Imbeau et al., 2001). Indeed, this management approach will inevitably reduce the availability of mature and old-growth forests (Bergeron et al., 2007; Drapeau et al., 2009), an important alternative habitat for the black-backed woodpecker (Setterington et al., 2000). This practice may also indirectly affect the quality of post-fire forest habitats. As the abundance and extent of over-mature forests decrease, fire is more likely to burn younger stands, which, in turn, are less likely to support the required densities of larger trees suitable for foraging and nesting. Indeed, our data show that burned forests that were younger at the time of fire supported lower densities of nesting pairs and lower levels of productivity than older forests. Therefore, current management practices in the boreal forest that produce younger forest mosaics may interfere with stand-replacing fires and create post-fire habitats that are less suitable for the black-backed woodpecker and other fire-associated species.

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3.9 Tables

Table 3.1. Summary of explanatory variables used in regression models to predict daily nest mortality or nest productivity of black-backed woodpeckers (based on all 111 nests monitored).

Variables	Mean (SD)	Min	Max
Temporal			
Years since fire	Class : second year is compared with year one; third year is compared with year one		
Nest tree level			
Nest height (m)	2.23 (1.10)	0.55	5.39
Tree diameter at nest height (cm)	20.9 (3.9)	13.5	33.5
Diameter of cavity entrance (cm)	4.8 (0.4)	4.2	6.8
Cavity depth (cm)	30 (4)	20	41
Cavity orientation	Dummy : four orientations (N, E, S, W)		
Nest site level			
Snag density (no./ha)			
> 10 cm dbh	1182 (587)	89	2844
> 15 cm dbh	485 (255)	44	1200
> 20 cm dbh	151 (132)	1	622
Burned mature forest (%)			
Radius 100 m	51.0 (38.0)	0	100
Radius 250 m	45.0 (29.5)	0	96.6
Radius 500 m	38.5 (21.3)	0	79.5
Landscape context	Dummy: "burned mature" (1) vs "burned young" (0) landscape		
Unburned forests (%)			
Radius 100 m	6.9 (18.1)	0	100
Radius 250 m	9.6 (15.2)	0	76.6
Radius 500 m	14.9 (15.2)	0	61.8
Distance to unburned forest (m)	Dummy: less (1) or more (0) than a given distance to unburned forest (100, 200, 300, 400, 500 m)		
Elevation (m)	750 (41)	655	900

Table 3.2. Reproductive success of black-backed woodpeckers in the first three years following the 1999 fire in the Parc national des Grands-Jardins, Quebec, Canada.

Time since fire	*n*[1]	Observation days	Daily survival rate	Nest success	No. of young per successful nest	Productivity per nest[2]
1 year	61	1564	0.995 ± 0.002	0.84 ± 0.05	3.09 ± 0.10	2.59 ± 0.25
2 year	41	1024	0.991 ± 0.003	0.73 ± 0.08	3.00 ± 0.12	2.20 ± 0.31
3 year	4	52	0.962 ± 0.027	0.25 ± 0.25	3.00[3]	0.76 ± 0.74

[1] Number of nests with more than 1 observation day

[2] Nest success * mean number of young per successful nest

[3] Based on one nest only

Table 3.3. Variables that influence daily nest mortality (Mayfield logistic regressions) and nest productivity (cumulative logit regressions) of black-backed woodpeckers.

		Explanatory variables								
		Temporal			Nest tree			Nest Site		
Model	*n*[1]	Variable[2]	Relation[3]	*P*[4]	Variable[2]	Relation[3]	*P*[4]	Variable[2]	Relation[3]	*P*[4]
Daily nest mortality										
All Failures	*106*	**Year**	+	**0.0369**				D200	-	
								UB500	+	
Predation	*106*	n.s.			n.s			n.s		
Abandonment	*106*	n.s.			n.s			n.s		
Nest productivity										
Clutch size	*85*	**Year**	-	**0.0008**	N	-		**Land_M**	+	**0.0113**
								D100	+	**0.0377**
Number of fledglings	*97*	n.s.			n.s			**BM100**	+	**0.0309**
								D200	+	**0.0102**

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[1] Sample sizes differed among models according to data availability.

[2] Significant predictors for each individual group of variables are listed (with relation signs). Variables that came out as significant in the final model are indicated in bold with their significance levels: Year = years since fire; N = north-oriented cavity; UB500 = % of unburned forests within 500-m radius; Land_M = burned mature landscape; BM100 = % of burned mature forest within 100-m radius; D100 = less than 100 m from unburned forest edges; D200 = less than 200 m from unburned forest edges.

[3] Daily nest mortality models: a positive relationship indicates lower reproductive success; Nest productivity models: a positive relationship indicates higher reproductive success.

[4] Significance at last step.

3.10 Figures

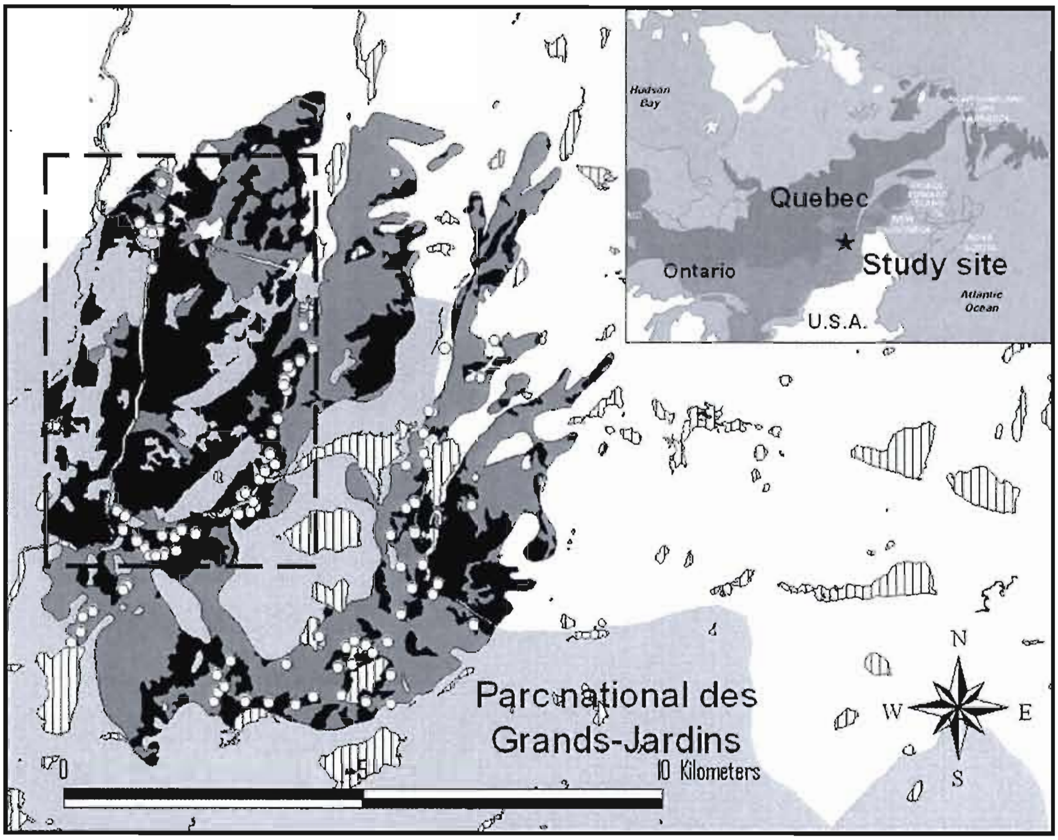

Figure 3.1. Location of the Parc national des Grands-Jardins (Quebec, Canada) and the 1999 fire. Forest stands within the burned landscape were classified according to their development stages prior to fire : black = burned mature stands, dark grey = burned young stands (park is in light grey; water bodies are hatched). The north-western portion of the burn (rectangle) was dominated by burned mature stands: this area is referred to as the "burned mature landscape". Other portions of the burn were dominated by young burned stands and referred to as the "burned young landscape". Nests monitored over the three-year study are indicated by white dots.

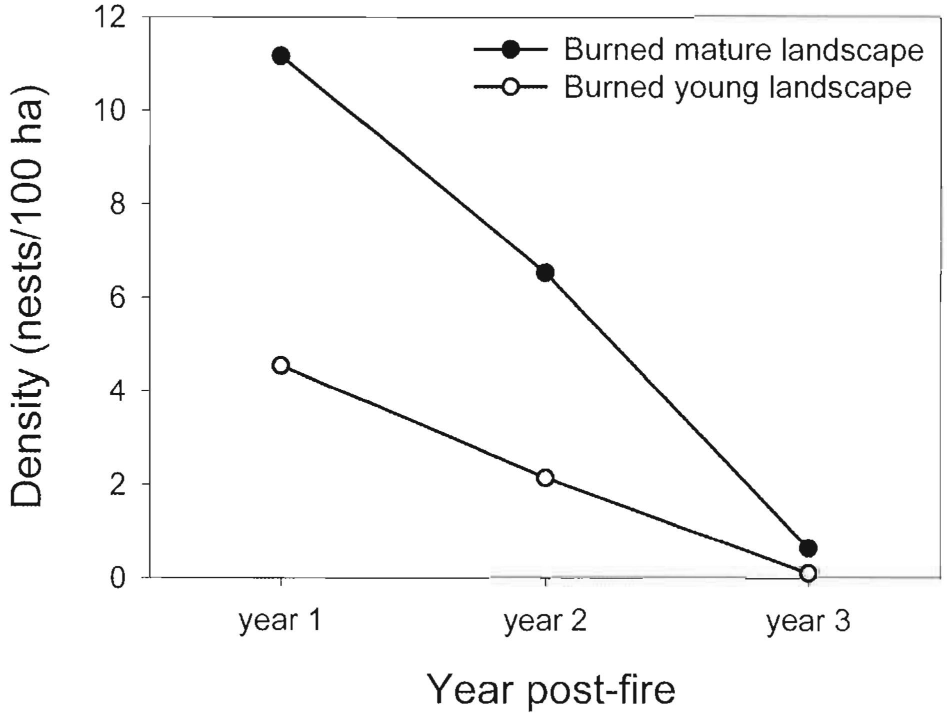

Figure 3.2. Nest density of black-backed woodpeckers in the first 3 years following the 1999 fire in the Parc national des Grands-Jardins, Quebec, Canada. Nest densities were estimated separately for two portions of the burned landscape: burned mature and burned young landscapes (see methods for details).

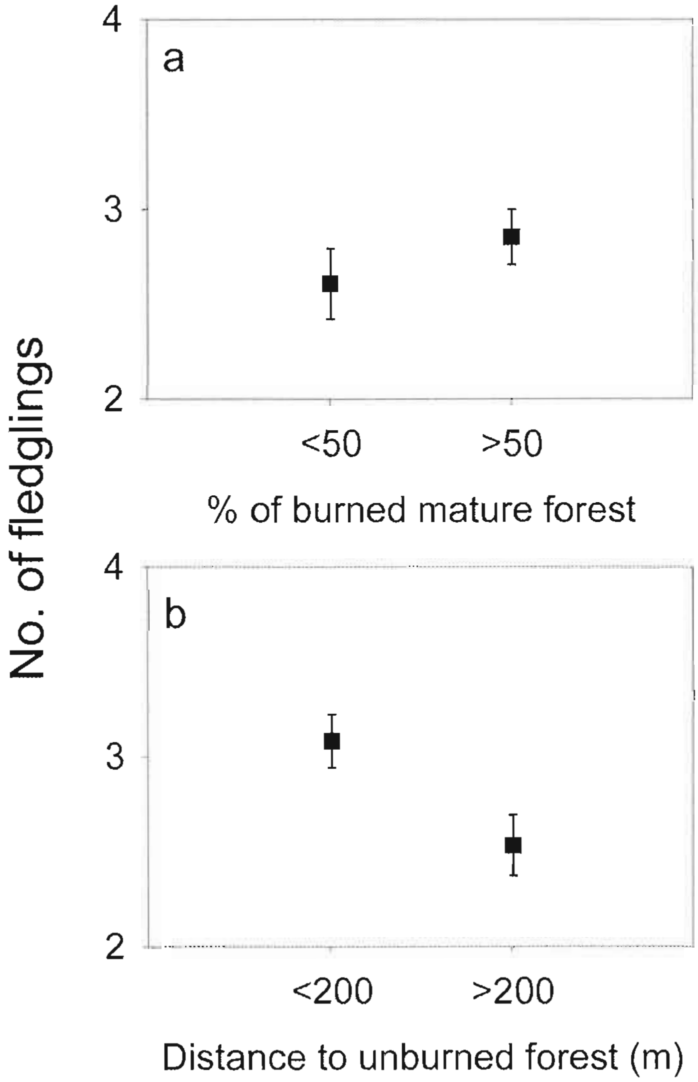

Figure 3.3. Relationship between nest productivity (mean no. of fledglings ± SE) and a) percentage of burned mature forest surrounding nests (within 100m radius) and b) distance to unburned forest (< or > 200 m).

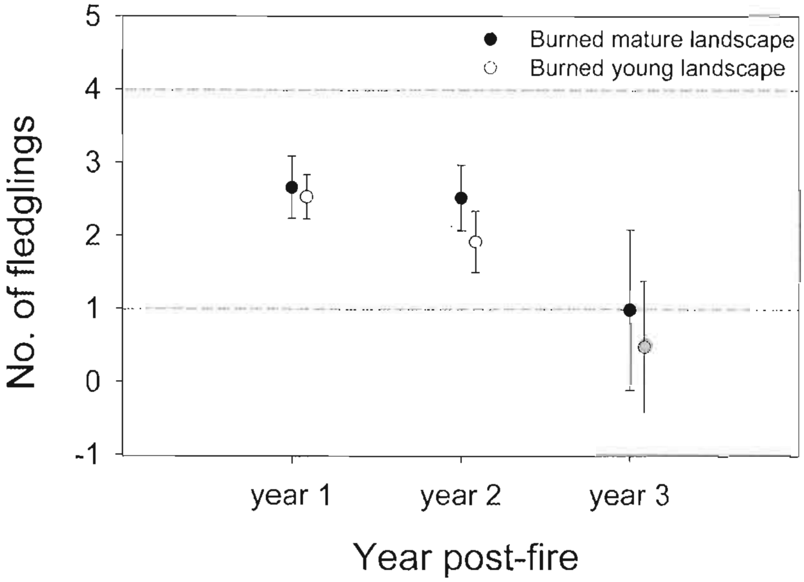

Figure 3.4. Comparison of nest productivity (mean no. of fledglings ± SE) with source-sink thresholds. Dotted lines represent the number of young per nest necessary to compensate for mortality rates based on the highest threshold scenario (lowest adult and juvenile survival rate values), the intermediate threshold scenario (intermediate adult and juvenile survival rate values) and the lowest threshold scenario (highest adult and juvenile survival rate values). Productivity above a given line indicates that the population likely functions as a source.

CHAPITRE 4

EFFECT OF FIRE SEVERITY ON LONG-TERM OCCUPANCY OF BURNED BOREAL CONIFER FORESTS BY BARK-FORAGING BIRDS AND SAPROXYLIC INSECTS

4.1 Résumé

Les feux peuvent varier grandement dans leur sévérité, et ce même en forêt boréale canadienne où les régimes de feu sont caractérisés essentiellement par des feux sévères. Nous avons examiné les effets de la sévérité du feu sur l'occupation à long terme des forêts brûlées par (i) trois espèces d'oiseaux qui s'alimentent sur l'écorce des arbres et (ii) les insectes associés au bois mort. L'étude a été menée de 6 à 11 ans après feu, dans des forêts résineuses brûlées de sévérité variable au Québec, Canada. Nos résultats suggèrent que la faible sévérité du feu a créé des conditions d'arbres morts propices à la présence, à long terme, d'oiseaux et d'insectes associés au bois mort. Le pic à dos noir, une espèce spécialiste des forêts récemment brûlées, était encore abondant 6 et 8 ans après feu. Ceci s'explique par la présence, plusieurs années après feu, de plusieurs espèces d'insectes associées aux arbres récemment morts ainsi que par l'effet positif de la faible sévérité du feu sur l'abondance de *Arhopalus foveicollis*, un Cerambycidae caractérisé par un long cycle vital dans le bois mort. Le pic à dos rayé et le grimpereau brun, ainsi que leurs proies (scolytes), étaient plus abondants dans les peuplements brûlés de plus faible sévérité. Nous concluons que les arbres et les peuplements brûlés de plus faible sévérité présents au sein des brûlis présentant une sévérité variable peuvent favoriser la présence à long terme de réseaux trophiques impliquant les insectes saproxyliques et les oiseaux qui s'en nourrissent dans les forêts brûlées de la forêt boréale.

Mots-clés : épinette noire, pic à dos noir, *Picoides arcticus*, pic à dos rayé, *Picoides dorsalis*, grimpereau brun, *Certhia americana*, Cerambycidae, Scolytinae, *Arhopalus foveicollis*.

4.2 Abstract

Fire severity can vary greatly within and among burns, even in the Canadian boreal forest where fire regimes consist mostly of stand-replacing fires. We investigated the effects of fire severity on the long-term occupancy of burns by (i) three bark-foraging birds and (ii) insects associated with dead wood. Based on observations made 6 to 11 years after fire in mixed-severity burned conifer forests of Quebec, Canada, our results indicate that low fire severity likely provided snag conditions suitable for the long-term presence of deadwood-associated birds and insects. The black-backed woodpecker, a post-fire forest specialist, was still abundant 6 and 8 years after fire. This pattern was likely explained by the persistence of several saproxylic insect species that are associated with recently dead trees and by the positive effect of lower fire severity on the abundance of the cerambycid *Arhopalus foveicollis*, a species with a long life cycle in dead wood. The American three-toed woodpecker and the brown creeper, and their associated prey (Scolytinae beetles), were found in higher abundance in burned stands of lower versus higher severity. We conclude that less severely burned snags and stands within mixed-severity burns may favour the long-term presence of trophic webs that involve saproxylic insects and bark-foraging birds in burned boreal forests.

Keywords : black spruce, black-backed woodpecker, *Picoides arcticus*, American three-toed woodpecker, *Picoides dorsalis*, brown creeper, *Certhia americana*, Cerambycidae, Scolytinae, *Arhopalus foveicollis*.

4.3 Introduction

Fires in the boreal forest are typically characterized as severe stand-replacing disturbances that cause widespread tree mortality (Brown and Smith 2000; Bergeron *et al.* 2002). However, recent studies indicate these fires may vary spatially in their severity, leaving varying proportions of stands unburned or partially burned (Kafka *et al.* 2001; Bergeron *et al.* 2002; Schmiegelow *et al.* 2006). In eastern Canadian boreal forests, for example, zones of low burn severity where unburned trees dominate can comprise over 50% of the area affected by fire (Bergeron *et al.* 2002). Such variation in fire severity can have a profound influence on forest dynamics and on the post-fire response of vegetation (Purdon *et al.* 2004; Jayen *et al.* 2006; Macdonald 2007) and wildlife (Smucker *et al.* 2005; Schmiegelow *et al.* 2006; Koivula and Spence 2006).

Burned forests represent high-quality habitats for many deadwood-dependent species (Hutto 1995; Wikars 2002; Hannon and Drapeau 2005; Saab *et al.* 2005; Nappi and Drapeau In press). Wildfires, especially when severe, can generate sudden and massive increases in the availability of dead wood. High abundance and nutritional quality of fire-killed trees often lead to increased concentrations of wood-boring and bark beetle populations (Saint-Germain *et al.* 2004a, 2004b), which in turn attract bark-foraging birds such as several woodpecker species (Murphy and Lehnhausen 1998; Hoyt and Hannon 2002; Nappi *et al.* 2003; Koivula and Schmiegelow 2007).

Fire severity can affect both quantity and quality of fire-created snags and thus the response of deadwood-associated species to fire. For example, many deadwood-specialists respond positively to the increased availability of snags brought on by high-severity fire (Koivula and Schmiegelow 2007; Hutto 2008). At the same time, fire severity at the individual tree scale (e.g. trunk charring) can affect the quality of snags for saproxylic insects and thus for foraging woodpeckers. For example, severely scorched black spruce (*Picea mariana*) trees may support lower densities of saproxylic insects than more lightly affected trees (Nappi *et al.* 2003; Saint-Germain *et al.* 2004b). Therefore, the availability of suitable dead wood substrates may decrease beyond a certain threshold of fire severity.

Although several studies have documented the short-term effects of fire severity on saproxylic insects (Gardiner 1957; Ross 1960; Saint-Germain *et al.* 2004b) and bark-foraging birds (Murphy and Lehnhausen 1998; Koivula and Schmiegelow 2007), few have investigated the effect of fire severity on the long-term occupancy of burned forests by these species. Saint-Germain *et al.* (2007b) found that colonization of black spruce snags by wood-feeding insects is generally limited to the early stages of snag degradation. As most trees die rapidly after severe fire, the presence of such insects is generally limited to the first few years after fire (Werner 2002; Saint-Germain *et al.* 2004b; Boulanger and Sirois 2007); this is also the case for bark-foraging birds (Murphy and Lehnhausen 1998; Nappi and Drapeau In press). However, occupancy by these species may be quite different following fires of lower severity (i.e. fires which leave significant portions of partially burned stands; Brown and Smith 2000). For example, tree mortality in less severely burned stands can be significantly delayed (Gardiner 1957; Dixon *et al.* 1984), thereby extending the availability of recently dead trees for saproxylic insects.

This study investigates the influence of fire severity on long-term occupancy of burned forests by deadwood-associated species based on observations made 6 to 11 years after fire in two burns that showed high variability in burn severity (i.e. mixed-severity burns). Our main objectives were to 1) determine the presence and abundance of bark-foraging birds and saproxylic insects in these old burned forests and 2) assess the influence of within-burn variability in fire severity on the occupancy patterns of these deadwood-associated species. We hypothesized that bark-foraging birds and saproxylic insects, typically associated with initial post-fire conditions in high-severity burns, would be found many years after fire in the low-severity portions of these mixed-severity burned landscapes.

4.4 Methods

4.4.1 Study area

This study was conducted in the black spruce-moss bioclimatic domain of north-western Quebec, Canada (Saucier *et al.* 1998; Fig. 4.1). Fire is the main natural disturbance in the region, which has and continues to experience the shortest fire cycle of Quebec's spruce-moss boreal forest (Lefort *et al.* 2004; Bergeron *et al.* 2006). The current fire cycle (1945-1998) for the region is estimated at 136 years (Lefort *et al.* 2004). Forest cover of the study sites was co-dominated by black spruce and jack pine (*Pinus banksiana*). Other tree species included white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*) and tamarack (*Larix laricina*).

We selected burn sites according to several criteria. Burns had to be more than five years old, dominated by mature conifer stands, heterogeneous in burn severity, not or only lightly salvage-logged and accessible. Only two burns in the region met all these criteria. These represent two of several major fires that started in June 1996 and were located approximately 100 km north-west of the city of Chibougamau (Fig. 4.1). The largest of the two fires (Fire 392) started on June 11 and covered 24995 ha between 50°15' and 50°32'N and between 75°40' and 75°50'W. The second fire (Fire 481) occurred approximately 5 km south-east of the first; it started on June 12 and burned 4641 ha. The area affected by the fires was composed mostly of mature stands of commercial value (>70 years). The two burned sites were considered together as they originated more or less simultaneously, were close to each other, and were similar in their pre-fire composition and fire severity patterns (Table 4.1).

Fire severity was evaluated by the Quebec Ministry of Natural Resources and Wildlife (MNRW) in the first weeks following fire via aerial surveys. This evaluation was based on tree damage (green trees with intact crowns, trees with reddish crowns, charred trees with burned crowns, blowdown trees) and stands were classified into six fire impact classes based on the relative percentage of each tree damage category (based on percentage of crown cover; Table 4.1). The fire impact maps showed that the two study burns were highly variable in fire severity and contained important proportions of low-severity burned stands (Fig. 4.1, Table 4.1). In both cases, about half of the burned landscape consisted of burned stands with a dominance of green trees (i.e. light impact class). Because of this high variability in fire severity, these burns are hereafter referred to as "mixed-severity" burns (Brown and Smith 2000).

4.4.2 Vegetation sampling

A total of 80 sampling stations (60 in Fire 392 and 20 in Fire 481) were distributed at least 500 m apart within the burns. Fire impact maps were used to distribute these sampling stations and thereby ensure adequate representation across the full range of variation in fire severity. The evaluation of fire severity based on the MNRW fire impact maps only focuses on short-term effects of fire at a coarse resolution (>1 ha). To evaluate fire severity many years after fire (i.e. considering the subsequent mortality of trees) and at finer scales (stand and individual tree scales), we measured fire severity at these sampling stations in 2002 (6 years post-fire).

At each sampling station, vegetation measurements were taken within five 25-m-radius circular plots. The first plot was centred on the sampling station whereas the other plots were placed at 50 m from the centre of the station in each of the four cardinal directions. For each variable, the mean over the five plots was used in further analyses. Fire severity was estimated as the percentage of dead crown cover. Based on this percentage, each of the 80 sampling stations was then attributed to one of the following fire severity classes: unburned (0% dead), low (1-50%), moderate (51-99%) and high (100%). Because we were interested in the characteristics of burned trees in relation to fire severity, we also measured the following four variables:

- Tree condition – proportion of trees in each of three classes of degradation: live trees, declining trees (alive but <20% of foliage intact or broken top or other signs of severe damage), dead trees;
- Trunk charring – proportion of trees in each of four classes based on the percentage of trunk charred: uncharred, lightly charred (1-40% of the trunk charred), moderately charred (41-95% of the trunk charred) and severely charred (96-100% of the trunk charred);
- Bark loss – proportion of trees in each of four classes based on the percentage of bark lost (25% classes);
- Tree species – proportion of trees that were black spruce or jack pine.

4.4.3 Tree death estimates

To examine tree mortality delay in relation to fire severity, three 10 x 20 m plots were established in 2004 (8 years post-fire) in jack pine-dominated stands. Two plots were located in stands of moderate severity (Plots 1 and 2, 61% and 69% tree mortality respectively, percent mortality based on basal area in 2004) whereas the other plot was located in a stand with high burn severity (Plot 3, 100% tree mortality). Every snag (tree without green foliage at least 1.3 m tall and with diameter at breast height (dbh) $\geq$ 5 cm) and every fallen dead tree with its stump in the plot was sampled ($n = 96$).

Cross sections were taken from all dead trees that were sound enough to allow dendrochronology analyses. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to minimize fragmentation. To maximize chances of successful cross-dating, three cross sections were taken from each bole when possible: at the stump, at breast height and in the upper part (approximately 3 m from the top for intact trees and near the breakage point for broken trees). This allowed us to 1) validate year of death with multiple cross-dated sections and 2) increase the chances of obtaining the last ring produced in stressed trees (Mast and Veblen 1994; Cherubini *et al.* 2002). In boles with advanced decay, the height at which cross sections were taken varied depending on bole conditions to maximize cross-dating success. A total of 212 cross sections were dried and sanded to make xylem cells clearly visible. Ring width was measured for each cross section along two radii using a Velmex micrometer (precision of 0.01 mm) under 40x magnification (Velmex Inc.).

To determine year of death, each individual series was cross-dated against master chronologies built for black spruce and jack pine from nearby living trees using marker years and the COFECHA program (Holmes 1983). When discrepancies for year of death were observed for cross sections belonging to the same tree, the more recent year was retained. We assumed the last growth ring corresponded to the year of death. However, trees showing a last ring in 1995 were considered to have died in 1996, the year the fire occurred. Indeed, most snags showed a last growth ring in 1995 that we attributed to the fire having occurred early in the 1996 growth season, probably before onset of the growing season. All trees that died the year of fire or in subsequent years were successfully cross-dated.

4.4.4 Bird sampling

We examined the effect of fire severity on three bird species: the black-backed woodpecker (*Picoides arcticus*), the American three-toed woodpecker (*Picoides dorsalis*) and the brown creeper (*Certhia americana*). These species were chosen because they colonize recent burns (Hutto 1995, Hannon and Drapeau 2005), are bark-foragers and show differences in their foraging ecology and prey preferences (Murphy and Lehnhausen 1998; Hejl *et al.* 2002) that we expected would influence their response to fire severity.

Bird censuses were conducted during the summer of 2002 (6 years post-fire) using point counts (Blondel *et al.* 1970; Drapeau *et al.* 1999) and playbacks (territorial drumming and contact calls). At 80 sampling stations, all individuals of the three species were recorded during 5-min intervals for a total of 15 min. Each point count was then followed by a 1-min playback of each species successively (separated by a 1-min silent period) for an additional period of 6 min at each station. Only contacts made within the 75-m radius were considered. Each sampling station was visited twice during the breeding season. A sampling station was considered occupied by a focal species if it was seen in at least one visit. An additional survey was conducted during the summer of 2004 (8 years post-fire) to confirm the presence or absence of black-backed woodpeckers and American three-toed woodpeckers in the burned areas. This was done by visiting once a subset of 55 sampling stations. For this survey, we used 1-min playbacks (separated by 1-min silent periods) that we played twice for each species (total of 8 min per station). Surveys were conducted from sunrise to 10h00 am during days of low wind and no rain. All surveys were conducted between early June and early July, the period of peak breeding activity for these species in the region (Nappi and Drapeau In press).

4.4.5 Insect sampling

To identify the saproxylic insect species present in these burned areas and to investigate the effect of fire severity on their abundance at the stand scale, we captured insects using Lindgren funnel traps (Phero Tech Inc.) baited with semiochemical lures (α-pinene, ethanol and ipsenol). Semiochemicals were used to maximize catch rates of wood-feeding taxa that are often under-represented in datasets collected through passive sampling (Chénier and Philogène 1989; Allison *et al.* 2001; Saint-Germain *et al.* 2006; 2007a). A total of 11 traps were placed in 2004 (8 years post-fire) at a subset of sampling stations selected to cover both low- and high-severity fire classes. Traps were set on June 10 using propylene-glycol as preservative fluid and were emptied twice during the summer (July 15 and August 13).

Although indirect sampling techniques such as funnel traps are useful to document insect assemblages at the stand level, they may not provide an accurate portrait of the saproxylic insects present in the wood and can not be used to investigate adequately the effect of tree level variables (Saint-Germain *et al.* 2007b). Therefore, we used snag dissection to more precisely identify insect species present in burned snags and measure the influence of tree species and fire severity on insect abundance at the tree scale.

Two series of logs were dissected to investigate occurrence patterns of saproxylic insects. The first dissection series was conducted in 2004 (8 years post-fire) to identify and compare the abundance of saproxylic insects between black spruce and jack pine. We selected 10 trees of each of the two species in close proximity to funnel traps for wood dissection. Seven of these trees were observed being used by foraging black-backed woodpeckers and all sampled trees were located in known foraging areas. Fire severity was controlled by selecting only lightly charred trees (burned at their base only, <40% charred, bark fully intact) of similar diameter (range 10.7-20.7 cm of diameter at breast height, dbh). With the second series of dissection, we evaluated the effect of fire severity on abundance of saproxylic insects. This was done in the summer of 2007 (11 years post-fire) in the same sector previously sampled. We selected 24 black spruce trees (range 15.9-30.9 cm dbh) showing contrasting levels of fire severity (12 lightly and 12 severely charred trees). In contrast to lightly charred trees, severely charred trees had lost most of their bark (>75%) with any remaining bark being completely charred. Overall, a total of 44 trees were used for wood dissection. Snags of the 2004 series were also analyzed to determine year of death following the dendrochronological method described above.

Tree felling and dissection took place between mid-June and mid-July. Each tree was felled and a 1-m bole segment was taken from the base (0-1 m above ground). These bole segments were put in plastic bags and taken to the laboratory for dissection. Bark was carefully removed and all larvae and adult invertebrates were collected. Segments were then cut into smaller pieces with hatchets, following insect galleries, and all insects found were collected. Specimens were conserved in 70% ethanol for preservation and later identified to family, genus or species.

4.4.6 Statistical analyses

Comparisons of tree characteristics (tree condition, trunk charring, bark loss, tree species) among fire severity classes were assessed using Kruskal-Wallis tests. For each bird species, differences between frequencies of occurrence among the fire severity classes were assessed using log-likelihood ratio (G) tests. For saproxylic insects, we combined stands into two classes of fire severity (because of the low number of funnel traps) and compared insect captures using Mann-Whitney tests. The low severity class included sampling stations with green tree dominance (range in dead crown cover: 14-47%) whereas the high severity class included stations dominated by dead trees (range in dead crown cover: 75-100%). Analyses were conducted for saproxylic taxa with >20 captures. Densities of saproxylic insects in bole segments were compared between tree species or fire severity classes using Mann-Whitney tests. Insect density was calculated as the total number of individuals per cubic meter of wood.

4.5 Results

4.5.1 Fire severity and tree characteristics

Field measures of fire severity (% dead crown cover) 6 years after fire indicated that the heterogeneity reported by fire impact maps was still present many years after fire. Indeed, many forest stands were still characterized by mixed proportions of live trees and snags

(Table 4.2). Yet, tree mortality was generally higher than what was reported by fire impact maps, especially for sampling stations originally classified within the light impact class.

Fire severity, as estimated by the percentage of dead crown cover, adequately reflected the effect of fire at the tree scale (all Kruskal-Wallis tests $P < 0.001$; Table 4.2). Proportion of live and declining trees tended to decrease with increasing fire severity whereas the opposite was observed for dead trees. Trunk charring was also clearly related to fire severity at the stand scale: trees that were moderately or severely charred increased in proportion from unburned to high-severity burned stands. The proportion of lightly charred trees showed a roughly modal distribution and peaked in moderate-severity burned stands. Bark loss was also well reflected by stand-level fire severity as the proportion of trees that retained their bark tended to decrease with increased fire severity. The two main tree species, black spruce and jack pine, were found in stands of all severity classes and stands were often mixed in their composition. However, there was a tendency for black spruce to increase in proportion in lower-severity burned stands. Despite these relationships between fire severity at the stand scale and characteristics of trees, heterogeneity in tree characteristics was high within stands even in areas that were severely burned (i.e. total mortality). For example, even stands in moderate- and high-severity fire classes were characterized by an important proportion of trees that were lightly affected by fire (e.g. based on trunk charring or bark loss; Table 4.2).

Results based on dendrochronological analyses revealed a distinct pattern of tree mortality delay in the lower-severity stands. Whereas the high-severity stand exhibited total mortality in 1996, the two moderate-severity stands experienced a delayed mortality for some trees with a 1 to 5 year time lag (Fig. 4.2).

4.5.2 Bark-foraging birds

Six years after fire, the black-backed woodpecker was detected at 74% of the sampling stations. This species was the most abundant of the three bark-foraging species studied in the burned landscapes, representing 77 % of all individuals detected. Although the black-backed woodpecker was more abundant in burned than unburned stands 6 years after fire ($G = 5.9$, df

= 1, $P < 0.05$), no significant difference in occurrence was observed among burned stands of different fire severity classes ($G = 2.0$, df = 2, $P = 0.377$, Fig. 4.3). Despite lower sampling effort in 2004 (8 years post-fire), this species was nevertheless detected at 27% of sampling stations. No difference in occurrence was observed among burned and unburned stands ($G = 2.6$, df = 1, $P = 0.108$) or among burned stands of different fire severity classes 8 years after fire ($G = 4.2$, df = 2, $P = 0.123$).

The American three-toed woodpecker was rarely observed in our burned landscape. We observed only five American three-toed woodpeckers in 2002 (6 years after) and none in 2004 (8 years after fire). Although no significant difference in occurrence was found among the four classes of fire severity in 2002 ($G = 2.1$, df = 3, $P = 0.553$; Fig. 4.3), the few observations of these birds were made in burned stands of low and moderate severity. The brown creeper was detected at 23 % of the sampling stations 6 years after fire. Occurrence of this species decreased with increasing fire severity ($G = 11.6$, df = 3, $P < 0.01$; Fig. 4.3).

4.5.3 Saproxylic insects

Thirty-three wood-feeding insect species belonging to the families Cerambycidae and Buprestidae, and the subfamily Scolytinae (family Curculionidae) were captured with funnel traps in the burned areas 8 years after fire (Table 4.3). Cerambycidae alone accounted for 71% of all captures of these three taxa and included mainly *Rhagium inquisitor* (L.), *Monochamus scutellatus* (Say), *Acmaeops proteus* (Kirby) and *Arhopalus foveicollis* (Haldeman). Together, these four species represented 88% of all Cerambycidae. The most abundant Scolytinae species were *Hylastes porculus* (Erichson), *Scolytus piceae* (Swaine) and *Polygraphus rufipennis* (Kirby) which accounted, respectively, for 52, 21 and 11% of insects belonging to this subfamily. Only eight Buprestidae individuals belonging to three species were collected. Bark beetle predators *Thanasimus dubius* (F.) and *Thanasimus undulatus* (Say) (Cleridae) were also abundantly captured throughout the burned areas. These two species represented 39% of all insects collected.

The effect of fire severity at the stand scale was assessed on total Cerambycidae, total Scolytinae, total *Thanasimus* spp. and seven individual species (Table 4.3). No differences between burned stands of low- and high-severity classes were found in total captures of Cerambycidae (Mann-Whitney test, $Z = -0.367$, $P = 0.714$; Fig. 4.4) or in captures of individual cerambycid species. Scolytinae abundance was higher in low- than in high-severity burned stands, although this difference was only marginally significant (Mann-Whitney test, $Z = -1.826$, $P = 0.068$; Fig. 4.4). Each individual Scolytinae species tested was more abundant in low- than in high-severity burned stands, although these differences were not significant except for *P. rufipennis*, for which the difference was marginally significant (Mann-Whitney test, $Z = -1.768$, $P = 0.077$). Trends in Scolytinae abundance were supported by similar effects of fire severity on bark beetle predators *Thanasimus* spp. (Mann-Whitney test, $Z = -2.739$, $P < 0.01$; Fig. 4.4).

Most specimens captured from the bole segments 8 years after fire (snag dissection) were *A. foveicollis* (95% of all Cerambycidae; Table 4.4). We observed no significant difference in total Cerambycidae densities between lightly charred jack pine and black spruce 8 years after fire (Mann-Whitney test, $Z = -0.076$, $P = 0.939$; Fig. 4.5). *A. foveicollis* was also the main species collected from the bole segments 11 years after fire: these insects were found in different stages (adults, larvae and pupa) and represented 78% of all Cerambycidae captured (Table 4.4). Lightly charred spruce snags contained higher numbers of Cerambycidae when compared with severely charred ones (Mann-Whitney test, $Z = -2.5$, $P < 0.05$; Fig. 4.5).

4.6 Discussion

The mixed-severity burned forests we studied were characterized by high variability in tree characteristics many years after fire, which likely affected habitat conditions for bark-foraging birds and saproxylic insects. Portions of these burns were covered by burned stands of low and moderate severity which supported mixed proportions of live, declining and dead trees. Conditions of snags were also very variable, these being affected to varying degrees by fire, even in high-severity burned stands (i.e. stands characterized by total tree mortality). Our results show that these mixed-severity burns supported the presence and, in some cases, a high abundance of many deadwood-associated species. Several of these species have been typically associated with initial post-fire habitat conditions following severe stand-replacing fires (references below). Our results suggest that the overall low severity of these fires likely contributed to the long-term occupancy of these burns by bark-foraging birds and saproxylic insects.

The black-backed woodpecker was the most abundant of the three bird species examined in these old burns. The black-backed woodpecker is a well-known fire specialist that typically occupies recently burned North American conifer forests (Hutto 1995, 2008; Murphy and Lehnhausen 1998; Saab *et al.* 2007). The high abundance of this woodpecker in recent post-fire forests is tightly linked to the high densities of saproxylic insects in burned conifer trees (Nappi *et al.* 2003; Saint-Germain *et al.* 2004b), in particular the cerambycid *M. scutellatus*, which is often the black-backed woodpecker's main prey (Villard and Beninger 1993; Murphy and Lehnhausen 1998; Nappi and Drapeau In press). In the North American boreal forest, the population decrease of black-backed woodpeckers in high-severity burned forests has been linked to the decrease of this insect in the first 3 years following fire (Nappi and Drapeau In press). We found a relatively high abundance of the black-backed woodpecker 6 and 8 years after fire, a pattern that contrasts sharply with the short-term occupancy of this species documented in burns of the boreal spruce forest (Murphy and Lehnhausen 1998; Nappi and Drapeau In press; but see Hoyt and Hannon 2002). This high abundance suggests that these lower-severity burns provided extended foraging opportunities for this species. Our results suggest two factors that were likely responsible for this observed prolonged occupancy of the black-backed woodpecker.

First, our results suggest that low fire severity created delayed tree mortality which likely maintained appropriate tree hosts for many saproxylic insects, thereby contributing to their long-term occupancy of these burns. Indeed, the presence of live trees in a declining stage in low- and moderate-severity stands shows that tree mortality was still ongoing within the burned landscapes. Many of the wood-feeding species we captured in these 8-year-old burns, such as *A. proteus*, *M. scutellatus* and *P. rufipennis*, are typically associated with early post-fire conditions (Gardiner 1957; Saint-Germain *et al.* 2004a, 2004b; Boulanger and Sirois 2007). For instance, 11 of the 17 species of Cerambycidae and 9 of the 13 species of

Scolytinae collected at our sites were also captured the first year following a severe fire in a conifer forest about 500 km south-east of our sites (Saint-Germain *et al.* 2004a). Most coniferophagous wood-feeding Coleoptera found in the Canadian eastern boreal forest, including the aforementioned species, are closely associated with the very first stages of decay of their tree hosts (Saint-Germain *et al.* 2007b). In experimental trials, ovipositing females of *Monochamus* rejected hosts that were dead for over 1-2 months (Alya and Hain 1985). This association is likely due, in most cases, to the dependence of early-instar larvae on simple sugars still found in recently dead subcortical tissues. Most species we captured frequently have life cycles of at most 3 years (i.e. *Monochamus* in colder climate; Rose 1957). Therefore, the fact that these species were captured 8 years after fire in such abundance confirms that appropriate hosts (i.e. recently dead trees) were still available through delayed mortality several years after the fire.

The second factor likely responsible for the long-term occupancy of the black-backed woodpecker was the high abundance of *A. foveicollis*. This insect was, by far, the most abundant saproxylic insect found in dissected snags, many of which were used by foraging woodpeckers prior to dissection. Larvae of this species were mostly longer than 1 cm, thus representing a substantial food resource for black-backed woodpeckers. Very little is known of the habits and life history of this species (formerly *A. agrestis*), but it was also found in recent burns in northern Ontario (Gardiner 1957) and in northern Quebec (Boulanger and Sirois 2007), suggesting an association of this cerambycid with post-fire forest conditions. The closely related *Arhopalus tristis* responds to smoke compounds of burned pines (Suckling *et al.* 2001) and colonization by *Arhopalus* spp. typically occurs in the first weeks after tree death (Chararas 1981). Life cycle of *A. foveicollis* is not well-known but we collected high numbers in burned trees 8 and 11 years after fire. Considering that all but two of the burned trees used for wood dissection died in the year of fire (based on dendrochronological analysis), this suggests that *A. foveicollis* larvae may remain in the wood for a much longer period (up to at least 11 years) than many other cerambycids.

Fire severity, at the tree scale, had a significant effect on the abundance of Cerambycidae larvae (the majority of these being *A. foveicollis*). The effect of fire severity on host quality (i.e. burned snags) for immediate colonizers has been well documented (Richmond and

Lejeune 1945; Ross 1960; Furniss 1965; Saint-Germain *et al.* 2004b). However, few studies have investigated the long-term effect of fire severity on host quality. Fire severity may influence the decay process itself, and thus host quality in the longer term for species with larval development that spans several years (e.g. *A. foveicollis*). In our study, severely charred trees typically lost their bark earlier than lightly charred trees. Maintenance of bark cover can alleviate variations in temperature and water content of underlying woody tissues – both these factors affect wood-boring beetles by influencing survival rates of larvae or fitness of survivors (Savely 1939; Chararas 1981, Hanks *et al.* 2005). Higher numbers of Cerambycidae in lightly versus severely charred spruce snags could be explained either by a higher density of colonists following fire or by lower mortality rates of insects in lightly charred snags. In any case, our results suggest fire severity at the tree scale may have an important influence on the long-tem abundance of species with long life cycles such as *A. foveicollis*.

In burned forests of Alberta, Hoyt and Hannon (2002) also found a high abundance of black-backed woodpeckers 8 years after fire. They attributed this result to the presence of jack pines which they hypothesized could survive longer and provide more suitable conditions for wood-borers. Although the thicker bark of pines may be more efficient than spruce in preserving moist conditions for saproxylic insects (Gardiner 1957; Saint-Germain *et al.* 2004b), we found no effect of tree species on densities of Cerambycidae (i.e. mostly *A. foveicollis*) in lightly charred trees. We did not investigate differences between severely charred jack pine and black spruce, but we observed similar external wood conditions (extensive bark loss, high desiccation) for severely burned trees of these two species, which suggests the effect of increased protection in jack pine may be limited. Although more studies are needed to clarify the interaction of tree species and fire severity on the long-term quality of wood substrates for saproxylic insects, our results emphasize that less severely burned trees of both species (black spruce and jack pine) are more likely to provide suitable foraging substrates for woodpeckers.

At the scale of the burned landscapes, low fire severity likely favoured the long-term presence of suitable foraging trees (i.e. recently dead and less severely charred trees) for the black-backed woodpecker, and may explain the overall high abundance of this species within the burns. Contrary to our expectations, however, we found no effect of fire severity on the abundance of this species at the stand scale. This pattern may be, in part, explained by the high heterogeneity of tree characteristics at the stand scale and the widespread distribution of lightly and moderately charred trees (which represented high-quality substrates for *A. foveicollis*) in burned stands of all severity. In other words, foraging trees which contained *A. foveicollis* larvae were present in similar abundance within or in proximity to most sampling stations. Yet, we would have expected a higher abundance of insect species associated with recent snags (and thus of total Cerambycidae) in low-severity burned stands given the ongoing recruitment of snags in these stands. However, results obtained from our sampling approach (funnel traps) probably reflected habitat use by these insects on a scale larger than the one used to characterize fire severity (>1.8 ha) (e.g. by capturing insects in dispersal; Saint-Germain *et al.* 2006; Webb *et al.* 2008). This may be especially true for Cerambycidae given that this family has been shown to be less efficient than other wood-feeding taxa in identifying the sources of local host volatiles (Saint-Germain *et al.* 2007a); host finding may thus require more dispersal in this family. We can hypothesize that heterogeneity in fire severity was high at this larger scale which would explain the lack of difference in Cerambycidae abundance. The fact that these insects, and thus foraging opportunities for woodpeckers, were likely present within or in proximity to most burned stands may also explain the similar abundance of black-backed woodpecker among burned stands of different fire severity.

The black-backed woodpecker has been typically associated with high-severity burned forests (Hutto 2008; Koivula and Schmiegelow 2008). Indeed, high snag densities within severely burned stands (i.e stands with total tree mortality) provide, immediately after fire, important concentrations of potential foraging trees for this deadwood-dependent species. In the long-term however, our results show that only the less severely charred trees in these stands are likely to represent suitable substrates for some saproxylic insects. While burned stands of low- and moderate-severity may provide less foraging opportunities in the short-term than high-severity burned stands, prolonged recruitment of recent snags and relatively higher proportions of lightly charred trees in such stands likely maintain suitable habitat conditions over the longer term for saproxylic insects, and thus, for the black-backed woodpecker. Our results suggest, therefore, that the black-backed woodpecker may be more strongly associated with low to moderate severity burned forests than with high severity burned forests beyond the first few years post-fire.

The American three-toed woodpecker was rarely observed in our burned landscape. Although this species has often been reported in recent burns, this woodpecker is generally associated with old-growth forests (Hutto 1995; Imbeau *et al.* 1999; Hoyt and Hannon 2002; Imbeau and Desrochers 2002). Because of the short fire cycle in our study region (Lefort *et al.* 2004; Bergeron *et al.* 2006), old-growth forests occupy a smaller proportion of the forested landscape in comparison with other regions of the Quebec's spruce-moss boreal forest (Bergeron *et al.* 2001). It may thus be hypothesized that population size is low at a regional scale, which would explain the low abundance of this species in these burns.

American three-toed woodpeckers forage mainly on recently dead spruce by flaking off pieces of bark and exposing Scolytinae beetle prey (Murphy and Lehnhausen 1998; Imbeau and Desrochers 2002). In burned spruce forests, Murphy and Lehnhausen (1998) found that American three-toed woodpeckers fed mainly on uncharred portions of lightly to moderately burned spruce trees where Scolytinae beetle larvae were abundant. Although no significant difference was found in relation to fire severity, the few observations of these birds were made in burned stands of low and moderate severity, which suggests that these retained better habitat conditions relative to high severity stands many years after fire (i.e. higher abundance of lightly charred trees, declining trees and Scolytinae). Indeed, we observed an effect of fire severity at the stand scale for Scolytinae species. For *H. porculus*, this effect of fire severity was probably caused by the higher proportion of live trees in low severity stands, this species being known to feed on the roots of living trees (Erbilgin *et al.* 2001). In contrast, species such as *S. piceae* and *P. rufipennis* are bole-feeders associated with heavily stressed and recently dead trees (Saint-Germain *et al.* 2007b). Since life cycles of Scolytinae are typically short ($\leq$1 year), their presence in these stands was likely associated with the delayed mortality of trees that provided declining trees and recent snags. Our results suggest that low fire severity provided more favourable habitat conditions for these bird and insect species, which has contributed to their presence in these burned landscapes many years after fire.

Brown creepers are typically found in mature and old-growth conifer and mixedwood forests where they forage superficially on trunks of large trees and snags (Imbeau *et al.* 1999; Hejl *et al.* 2002). This species also uses recent burns, although this pattern is inconsistent among studies (see Hutto 1995; Schieck and Song 2006). In western boreal forests, this species is uncommon in burned forests without residual live trees but common in burns with large live trees (Schieck and Song 2006). Our results are consistent with this pattern as we found the brown creeper to increase in abundance with lower fire severity. Given that Scolytinae may be an important component of the brown creeper's diet (Otvos and Stark 1985), the higher occurrence of this species in lower-severity burned stands could be partially linked to higher foraging opportunities relative to high-severity burned stands.

4.7 Conclusion and management implications

Our results show that fire severity may be an important factor influencing the long-term presence of trophic webs associated with post-fire conditions that involve saproxylic insects and, in turn, several bark-foraging birds in burned forest landscapes. Variations in fire severity induce varying patterns of tree mortality and snag conditions many years after fire. Delayed mortality in burned stands of lower severity seems to have contributed to the presence of several saproxylic species associated with heavily stressed or recently dead trees many years after fire. Variation in fire severity at the tree scale also had an important effect on the abundance of insect species with long life cycles in dead wood such as the deep-borer *A. foveicollis*. As its main food source, the collective presence of these saproxylic insects in the burned landscapes contributed greatly to the high abundance of the black-backed woodpecker 6 and 8 years after fire. At the stand scale, fire severity influenced the abundance of Scolytinae and their insect predators (*Thanasimus* spp.), which were more abundant in low- than in high-severity burned stands. Bark-foraging birds such as the American three-toed woodpecker and the brown creeper that feed on Scolytinae responded similarly and tended to be more abundant in burned stands of lower severity. These results suggest that fires of lower severity may provide suitable long-term post-fire habitat conditions for deadwood-associated species in the boreal conifer forest. Our study further supports the idea that fire severity may be an important determinant of species responses to fire and, as suggested by Smucker *et al.* (2005), may explain the inconsistent response patterns of some species to fire among studies when fire severity and time since fire are not taken into account.

Our findings suggest that fire severity is an important factor to consider in the management of burned forests. As in many parts of the world (Lindenmayer *et al.* 2004), there is increasing economic pressure to intensify post-fire salvage logging in the boreal forest (Nappi *et al.* 2004; Schmiegelow *et al.* 2006). This management practice is often conducted with few guidelines targeting the conservation of post-fire legacies and natural processes (Morissette *et al.* 2002; Nappi *et al.* 2004; Hutto 2006; Schmiegelow *et al.* 2006). Results of this and other recent studies show that fire severity has a major influence on species responses to fire (Smucker *et al.* 2005; Kotliar *et al.* 2007). Because species found in post-fire forests have different habitat requirements, we consider that a coarse-filter approach which focuses on conserving large forest patches representative of all severity classes (including merchantable stands) is necessary to maintain biodiversity and natural processes in managed burned forest landscapes (see also Koivula and Schmiegelow 2007). Differences in species composition or responses among post-fire studies also emphasize the need for conservation strategies to be applied to all burns under management (Nappi *et al.* 2004). For instance, one of the most abundant saproxylic insects present in this study (*A. foveicollis*) was not present in another study conducted approximately 500 km from our study area (Saint-Germain *et al.* 2004a, 2004b). Further studies are clearly needed to better understand the effects of factors such as pre-fire composition, fire severity, time since fire and fire location on species responses to fire. These studies would contribute to the development of science-based strategies for post-fire harvesting that maintain fire-associated biodiversity.

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4.9 Tables

Table 4.1. Area covered by each fire impact class for the two studied burns.

		Fire 392		Fire 481	
Fire impact class	Description	Area (ha)	% of total area	Area (ha)	% of total area
No impact	Islands of green trees (not affected by fire)	1642	6.6	397	8.6
Light impact	Mixed patches (green trees > trees with reddish crowns)	10743	43.0	2394	51.5
Moderate impact	Mixed patches (trees with reddish crowns > green trees)	886	3.5	53	1.1
High impact	Trees with reddish crowns and generally < 25% blowdown	84	0.3	0	0.0
High impact	Charred trees with burned crowns, often with detached bark; generally < 40% blowdown	11301	45.2	1562	33.7
High impact	Charred trees with burned crowns, bark is detached; generally > 40% blowdown	339	1.4	235	5.1
Total fire area		24995	100.0	4641	100.0

Table 4.2. Tree characteristics for different classes of fire severity based on field estimates 6 years after fire. Fire severity classes: unburned (0% dead), low (1-50%), moderate (51-99%) and high (100%). Values are means (± 1 S.E.).

	Fire severity in forest stands (% of crown cover dead)			
Tree characteristics (% of trees in the stand)	Unburned (*n* = 10)	Low (*n* = 17)	Moderate (*n* = 32)	High (*n* = 21)
Tree condition	8.8 (2.0)	8.0 (1.5)	4.1 (0.8)	0.4 (0.2)
Live	84.1 (2.3)	60.6 (2.8)	17.7 (2.6)	0.1 (0.1)
Declining	8.7 (2.0)	8.0 (1.5)	4.1 (0.8)	0.4 (0.2)
Dead	7.1 (1.4)	31.3 (2.6)	78.2 (3.1)	99.6 (0.2)
Trunk charring				
Uncharred	99.4 (0.4)	64.0 (4.7)	14.7 (2.4)	0.0 (0.0)
Lightly charred	0.4 (0.3)	18.4 (3.0)	27.4 (3.3)	9.2 (2.1)
Moderately charred	0.1 (0.1)	10.3 (1.9)	33.2 (2.7)	38.8 (4.5)
Severely charred	0.1 (0.1)	7.2 (1.8)	24.7 (3.5)	52.0 (6.0)
Bark loss				
< 26% of bark lost	97.5 (0.8)	88.7 (2.1)	60.7 (3.5)	20.7 (3.4)
26-50% of bark lost	1.1 (0.5)	5.4 (1.4)	17.8 (1.5)	23.2 (2.2)
51-75% of bark lost	0.7 (0.2)	2.5 (0.5)	12.9 (1.6)	27.3 (2.2)
> 75% of bark lost	0.6 (0.2)	3.3 (1.2)	8.5 (1.8)	28.8 (3.8)
Tree species				
Black spruce	84.3 (5.8)	75.9 (6.1)	50.5 (5.2)	44.3 (6.8)
Jack pine	11.1 (5.5)	22.0 (6.3)	47.4 (5.5)	55.1 (6.8)

Table 4.3. Saproxylic insects captured in Lindgren funnel traps (n = 11) 8 years after fire.

Taxon[A]	Total number	% of total
Cerambycidae	**514**	**38.0**
Acanthocinus pusillus	2	0.1
Acmaeops proteus	**79**	**5.8**
Anastrangalia sanguinea	4	0.3
Arhopalus foveicollis	**46**	**3.4**
Asemum striatum	2	0.1
Cosmosalia chrysocoma	5	0.4
Evodinus monticola	5	0.4
Gnathacmaeops pratensis	17	1.3
Monochamus mutator	9	0.7
Monochamus scutellatus	**142**	**10.5**
Neoclytus leucozonus	0	0.0
Pygoleptura nigrella	2	0.1
Rhagium inquisitor	**187**	**13.8**
Tetropium cinnamopterum	1	0.1
Tetropium n. sp.	5	0.4
Trachysida mutabilis	1	0.1
Xylotrechus undulatus	7	0.5
Buprestidae	8	0.6
Chrysobothris sp.	1	0.1
Dicerca sp.	5	0.4
Melanophila fulvoguttata	2	0.1
Curculionidae	282	20.9
Dendroctonus rufipennis[B]	1	0.1
Dryocoetes autographus[B]	4	0.3
Hylastes porculus[B]	**107**	**7.9**
Ips latidens[B]	3	0.2
Ips perroti[B]	11	0.8
Ips perturbatus[B]	1	0.1
Ips pini[B]	1	0.1
Orthotomicus caelatus[B]	4	0.3
Pityokteines sparsus[B]	2	0.1
Pityophthorus sp.[B]	4	0.3
Polygraphus rufipennis[B]	**23**	**1.7**
Procryphalus utahensis[B]	1	0.1
Scolytus piceae[B]	**43**	**3.2**
Scolytinae total	**205**	**15.2**
Pissodes sp.	76	5.6
Not identified	1	0.1

Taxon[A]	Total number	% of total
Cleridae	547	40.5
Thanasimus dubius	265	19.6
Thanasimus undulatus	267	19.7
***Thanasimus* spp. total**	**532**	**39.3**
n. Enoclerus	15	1.1
Anobiidae	1	0.1
Microbregma abbreviata	1	0.1
Total	1352	100.0

[A] Effect of fire severity at the stand scale was assessed for taxa in bold.

[B] Subfamily Scolytinae.

Table 4.4. Saproxylic insects captured in 1-m bole segments of snags collected 8 years (2004 boles; *n* = 20) and 11 years (2007 boles; *n* = 24) after fire.

	2004 boles		2007 boles	
Taxon	Total number	% of total	Total number	% of total
Cerambycidae	140	68.0	41	85.4
Acmaeops proteus	1	0.5	0	0.0
Anastrangalia sanguinea	1	0.5	0	0.0
Arhopalus foveicollis	133	64.6	32	66.7
Stictoleptura canadensis	0	0.0	8	16.7
Trachysida sp.	0	0.0	1	2.1
Lamiinae	2	1.0	0	0.0
Not identified	3	1.5	0	0.0
Buprestidae	2	1.0	0	0.0
Cleridae	2	1.0	0	0.0
Elateridae	1	0.5	0	0.0
Melandryidae	2	1.0	0	0.0
Salpingidae	16	7.8	0	0.0
Staphylinidae	2	1.0	0	0.0
Formicidae[A]	26	12.6	0	0.0
Others	15	7.3	7	14.6
Total	206	100.0	48	100.0

[A] Often found in colonies. Real abundance was higher than reported.

4.10 Figures

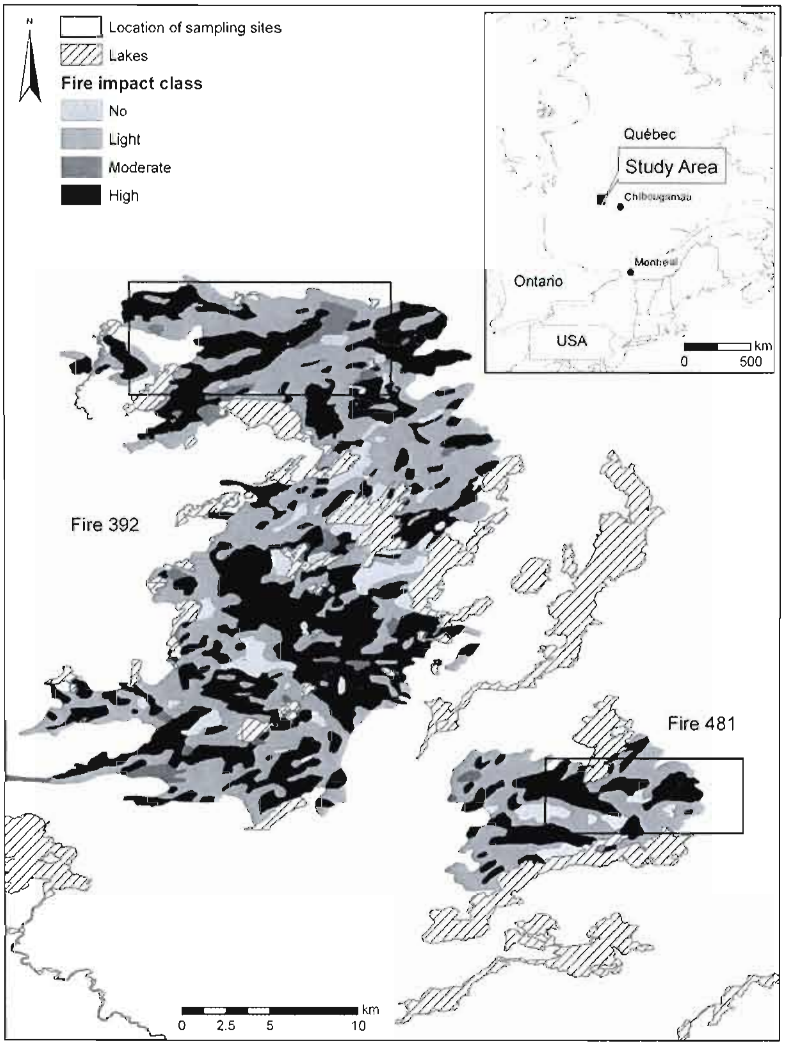

Figure 4.1. Fire impact maps and location of study burns in Quebec, Canada. See Table 4.1 for descriptions of the fire impact classification.

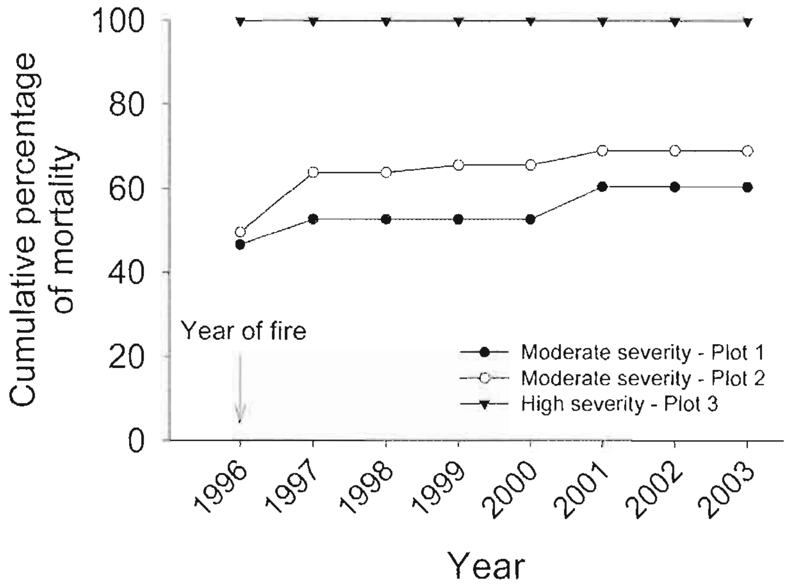

Figure 4.2. Cumulative tree mortality in relation to fire severity. Ratios are based on basal area.

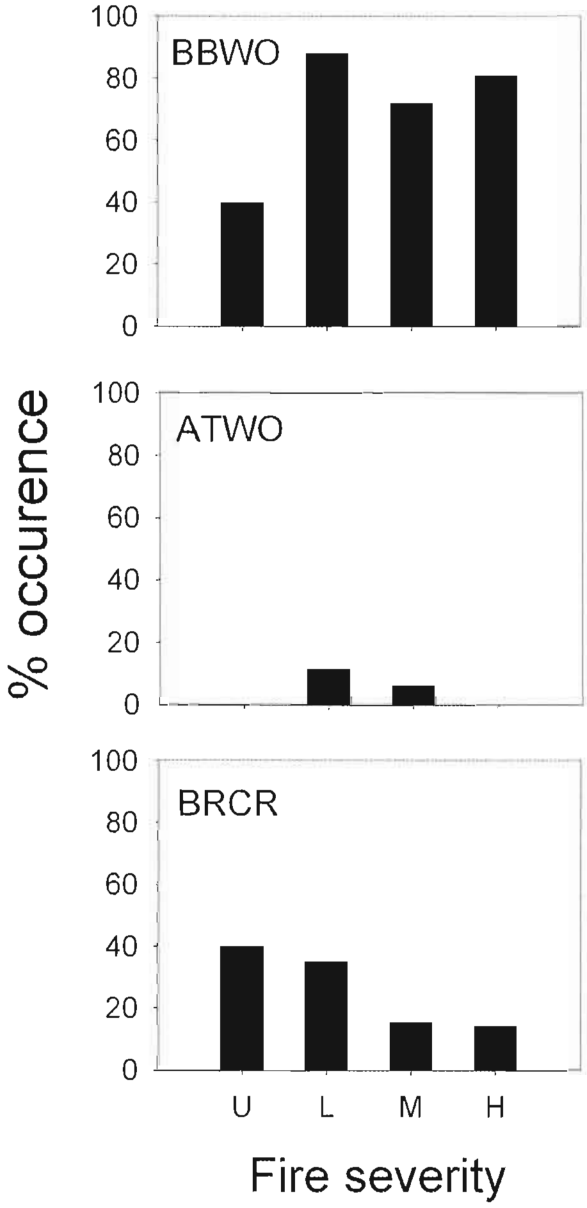

Figure 4.3. Percentage of occurrence of the black-backed woodpecker (BBWO), American three-toed woodpecker (ATWO) and brown creeper (BRCR) in unburned stands (U; *n* = 10) and burned stands of low (L; *n* = 17), moderate (M; *n* = 32) and high (H; *n* = 21) severity 6 years after fire.

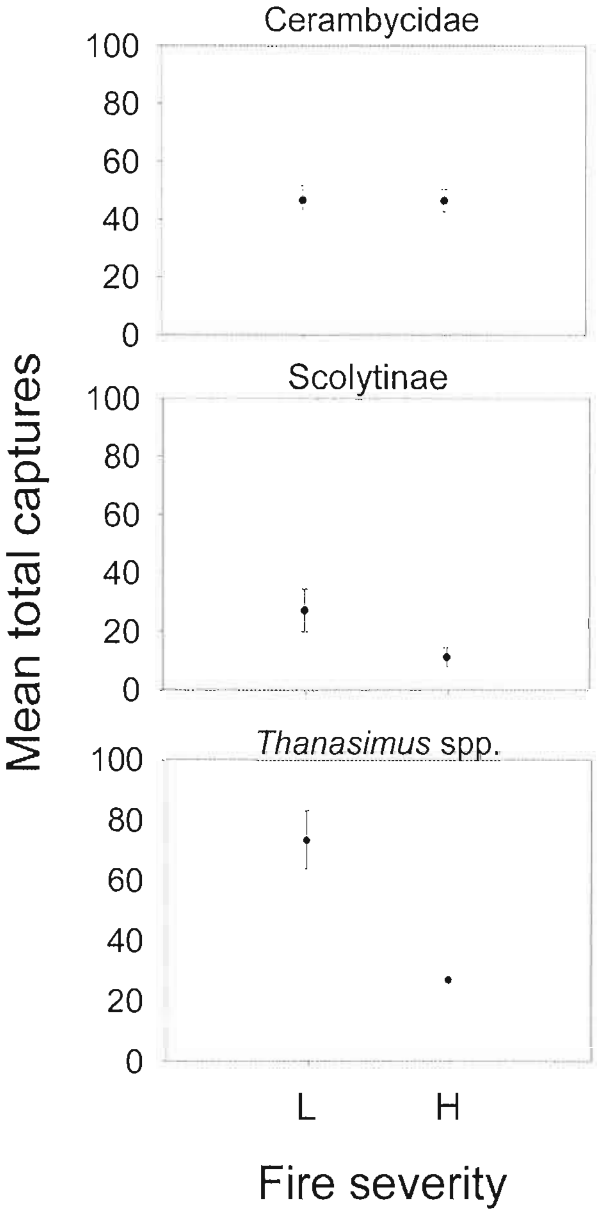

Figure 4.4. Mean captures (± S.E.) of Cerambycidae, Scolytinae (Curculionidae) and *Thanasimus* spp. (*T. dubius* and *T. undulates*; Cleridae) in Lindgren funnel traps for burned stands of low (L; $n = 5$) and high (H; $n = 6$) severity.

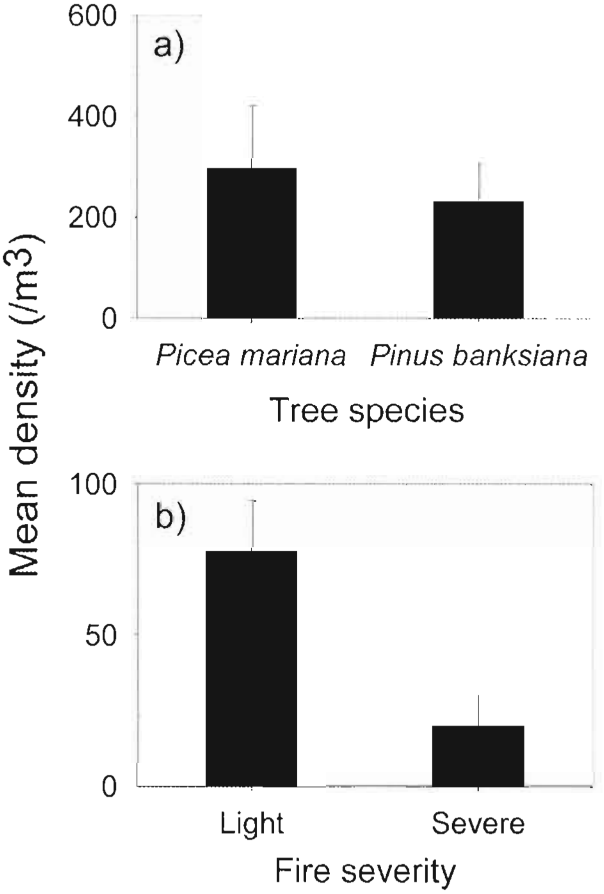

Figure 4.5. Mean density (± S.E.) of total Cerambycidae for a) dissected bole segments from lightly charred black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) trees collected 8 years after fire ($n = 20$) and b) dissected bole segments from lightly and severely charred spruce trees collected 11 years after fire ($n = 24$).

CONCLUSION GÉNÉRALE

Le feu est de plus en plus reconnu comme un élément clé de la biodiversité dans plusieurs écosystèmes forestiers du globe (Smith 2000, Brown et Smith 2000, Conner *et al.* 2001, Saab et Powell 2005, Noss et Lindenmayer 2006). En forêt boréale cependant, la plupart de nos connaissances sur l'occupation des forêts brûlées par la faune et la flore ont porté, jusqu'à présent, sur la comparaison de l'abondance de certaines espèces entre les forêts brûlées et non brûlées. Bien que ceci ait permis de décrire la réponse générale de ces espèces au feu, nous possédons encore peu de connaissances sur les facteurs qui influencent cette occupation des forêts brûlées et sur le rôle du feu dans le maintien et la dynamique des populations fauniques et floristiques qui sont associées à ce type d'habitat.

Cette thèse montre que le feu peut jouer un rôle important dans le maintien et la dynamique des populations de pic à dos noir dans les écosystèmes forestiers boréaux. Dans la première partie de cette thèse, je montre que le pic à dos noir est l'espèce la plus fortement associée aux arbres récemment morts et que, par conséquent, cette espèce est favorisée par l'abondance de ce substrat dans les forêts récemment perturbées par le feu. La deuxième partie de la thèse confirme que les forêts brûlées constituent un habitat d'alimentation et de nidification important pour cette espèce, bien que la qualité de cet habitat varie temporellement et spatialement à l'intérieur d'un même événement de feu.

Utilisation du bois mort pour l'alimentation des pics en forêt boréale

Bien que le bois mort soit généralement reconnu comme un élément clé de la biodiversité forestière, peu d'études portant sur la sélection du bois mort par la faune vertébrée en forêt boréale ont été menées. À cet effet, le chapitre 1 a permis de quantifier et de comparer l'utilisation du bois mort par les six espèces de pics qui s'alimentent sur les arbres et qui sont présentes en forêt boréale. Quatre des six espèces étudiées soient le pic à dos noir, le pic à dos rayé, le pic chevelu et le grand pic montraient une sélection significative pour les arbres morts. Une cinquième espèce, le pic mineur, bien qu'utilisant surtout les arbres vivants, passait près du tiers de son temps à s'alimenter sur les substrats morts (ex. branches mortes). Mes résultats montrent également que chaque espèce est généralement spécialisée quant aux stades de dégradation et aux types de proies utilisées. Ces différentes affinités au bois mort et ces spécialisations alimentaires constituent des connaissances fondamentales sur l'écologie des pics qui peuvent nous permettre de mieux comprendre les différentes réponses des pics aux perturbations naturelles.

Le pic à dos noir était l'espèce qui montrait la plus forte association aux arbres morts pour l'alimentation. Cette espèce sélectionnait principalement les conifères récemment morts, une préférence qui s'explique par sa spécialisation pour certains insectes saproxyliques (surtout Cerambycidae) présents en grande densité dans les premiers stades de dégradation des conifères (Saint-Germain *et al.* 2007). Ces résultats montrent que le pic à dos noir dépend, pour son alimentation, du recrutement d'arbres morts, qu'ils soient issus de mortalité individuelle de tiges ou de perturbations naturelles de grande ampleur tels que les feux. À cet effet, les résultats du chapitre 1 permettent d'expliquer la forte abondance de cette espèce dans les brûlis récents.

Utilisation temporelle et spatiale des forêts brûlées

Bien que la forte abondance du pic à dos noir dans les forêts brûlées ait été largement documentée, les études menées jusqu'à présent n'ont permis que de dresser un portrait général de l'association de cette espèce aux forêts brûlées. Peu d'études ont examiné l'utilisation fine de l'habitat et la démographie des populations de pics dans ce type de forêt. À cet effet, les résultats qui découlent de la deuxième partie de la thèse (chapitres 2 à 4) permettent de mieux comprendre les facteurs qui influencent la qualité des forêts brûlées pour le pic à dos noir ainsi que la démographie des populations après feu.

Le chapitre 2, qui porte sur la sélection des arbres de nidification et d'alimentation, montre que la qualité des forêts brûlées peut varier grandement à l'intérieur d'un même événement de feu. En effet, bien que les forêts brûlées supportent typiquement de grandes densités d'arbres morts, tous les arbres n'ont pas la même susceptibilité d'être utilisés comme substrats d'alimentation et de nidification. Pour la nidification, les pics choisissaient préférentiellement des arbres de plus de 20 cm de diamètre à hauteur poitrine (seuil minimal = 15 cm), fortement dégradés (ex. arbres morts avant le feu) ainsi que des feuillus. En revanche, les arbres d'alimentation étaient presque exclusivement constitués de conifères morts suite au feu. Tant pour la nidification que pour l'alimentation, le diamètre des arbres était un facteur déterminant dans la sélection des substrats d'alimentation. Un second volet de l'étude a notamment permis de montrer que les pics concentraient leurs sites de nidification et d'alimentation dans les portions de forêts qui étaient matures avant feu et évitaient les portions plus jeunes du paysage brûlé (forêts ~ 40 ans au moment du passage du feu). D'autre part, la sévérité du feu à l'échelle de l'arbre était un facteur important dans la sélection des arbres d'alimentation. Ces résultats montrent que la combinaison des conditions présentes avant le feu (i.e. composition, structure et âge des forêts) et de la sévérité du feu influence la qualité des forêts brûlées pour l'alimentation et la nidification du pic à dos noir.

Le chapitre 3 constitue le cœur de cette deuxième partie de la thèse. Ce chapitre aborde plus spécifiquement la dynamique et le succès reproducteur d'une population de pic à dos noir pendant trois années successives après feu. Les résultats de ce chapitre montrent clairement que les forêts brûlées représentent un habitat de nidification important pour le pic à dos noir. Les résultats basés sur la densité de nids montrent cependant que l'occupation de cet habitat peut être éphémère, étant limitée dans notre étude aux deux premières années suivant le feu. Le succès reproducteur, qui est un paramètre démographique très peu documenté pour cette espèce, repose sur un effectif de plus d'une centaine de nids. Ces données ont non seulement permis de mesurer le succès reproducteur de cette espèce dans les forêts brûlées, mais elles ont permis d'examiner les effets de la qualité temporelle et spatiale de l'habitat sur celui-ci. D'une part, les résultats montrent que le succès reproducteur diminue significativement avec le temps depuis la perturbation, une tendance qui semble attribuable à une augmentation du taux de prédation et à la diminution des ressources alimentaires (i.e. abondance de l'insecte *Monochamus scutellatus*, la proie principale du pic à dos noir) au cours de ces trois années. Les résultats sur le succès reproducteur montrent également que celui-ci varie en fonction des conditions présentes dans les forêts brûlées : le succès étant plus élevé dans les peuplements matures que dans les peuplements jeunes brûlés et plus élevé à proximité de la bordure des forêts non brûlées. Ces résultats viennent corroborer les résultats obtenus dans le chapitre 2 et montrent que les conditions présentent dans les forêts brûlées ainsi que les patrons spatiaux dans la sévérité du feu peuvent influencer la qualité de cet habitat pour le pic à dos noir.

Les données sur le succès reproducteur dans ce chapitre ont été analysées à la lumière de la théorie sur la dynamique source-puit (Pulliam 1988). Une comparaison de la productivité des pics avec des scénarios de taux de survie de juvéniles et d'adultes tirés de la littérature ont permis d'évaluer le potentiel des forêts brûlées à constituer un habitat source ou puit pour les populations de pics et d'examiner l'effet de la variabilité temporelle et spatiale de la qualité de l'habitat sur ce statut. Les résultats montrent que les forêts brûlées sont susceptibles de représenter un habitat source pour les deux premières années suivants le feu. Ce statut d'habitat source se maintient plus longtemps dans les habitats de plus haute qualité (forêts matures brûlées). Bien que la qualité des forêts brûlées soit variable et éphémère, les résultats de ce chapitre supportent l'hypothèse que les forêts brûlées peuvent constituer des habitats sources pour les populations de cette espèce en forêt boréale.

Les résultats du chapitre 3 sur l'occupation temporelle du pic à dos noir sont basés sur des forêts brûlées sévèrement. Cependant, les feux en forêt boréale peuvent montrer une grande variabilité quant à leurs patrons de sévérité. D'autre part, bien que nos résultats obtenus au chapitre 3 corroborent des résultats d'études antérieures, d'autres études montrent que l'occupation des forêts brûlées par le pic à dos noir peut s'étendre jusqu'à plus d'une dizaine d'années après le feu. Dans le chapitre 4, je montre que la sévérité du feu peut affecter l'occupation temporelle des brûlis par le pic à dos noir ainsi que par deux autres espèces qui s'alimentent sur les insectes saproxyliques, soient le pic à dos rayé et le grimpereau brun. Les résultats de ce chapitre montrent que la sévérité du feu a pu affecter l'occupation des forêts brûlées par ces oiseaux de deux manières. D'une part, les secteurs brûlés légèrement étaient généralement associés à une mortalité différée des arbres, ce qui a probablement contribué à la persistance, plusieurs années après feu, d'insectes saproxyliques typiquement associés aux conditions des premières années post-feu. Ceci se reflétait notamment par la plus grande abondance des Scolytes et de leurs prédateurs (*Thanasimus* spp.) dans les peuplements de plus faible sévérité. Les oiseaux prédateurs de ces insectes, le pic à dos rayé et le grimpereau brun, étaient généralement plus abondants dans les secteurs brûlés plus légèrement. À l'échelle de l'arbre, la sévérité du feu a eu un effet important sur *Arhopalus foveicolis*, le Cerambycidae le plus important 8 à 11 ans après feu. La plus grande abondance de cet insecte dans les arbres légèrement brûlés est probablement la principale cause de la forte abondance du pic à dos noir dans ces vieux brûlis.

Les résultats combinés des parties 1 et 2 de la thèse montrent que le pic à dos noir n'est pas dépendant des forêts résineuses brûlées en tant que tel, mais plutôt du recrutement de conifères récemment morts. Les conifères récemment morts auxquels cette espèce est associée peuvent provenir autant du recrutement individuel de tiges (chapitre 1) que de peuplements affectés par des perturbations naturelles (chapitre 2). Néanmoins, les résultats du chapitre 3 montrent que le succès reproducteur du pic à dos noir dans les forêts brûlées est très élevé, possiblement en raison de la faible pression de prédation mais également de la forte concentration des ressources alimentaires. Parce que la faible prédation est causée, entre autres, par le faible couvert arbustif et que la concentration d'arbres morts est typiquement beaucoup plus élevée dans les brûlis que dans d'autres types d'habitats, on peut supposer que cette combinaison de conditions favorables génère un succès reproducteur plus élevé que dans d'autres types d'habitats. Ceci est d'autant plus probable que les résultats du chapitre 3 montrent également que le succès reproducteur est sensible aux variations dans les conditions d'habitats, même au sein des habitats brûlés qui peuvent être considérés comme optimaux. Ces résultats laissent croire que le pic à dos noir est non seulement une espèce spécialiste (Saab et Powell 2005) ou associée (Hannon et Drapeau 2005) au feu, mais également une espèce favorisée par cette perturbation naturelle.

Bien que l'utilisation des forêts brûlées soit éphémère, la forte récurrence des feux en forêt boréale et la forte qualité de cet habitat pour la nidification du pic à dos noir suggèrent que le feu joue un rôle important dans la dynamique des populations à l'échelle régionale. À l'annexe 1, je montre que cette contribution pourrait être particulièrement élevée dans les régions où le cycle de feu est court. Ceci découle du fait que les forêts brûlées occupent une plus large proportion des superficies forestières dans ces régions mais également du fait que les forêts anciennes qui constituent l'habitat alternatif pour cette espèce se font plus rares lorsque le cycle de feu est court. À titre d'exemple, les estimations suggèrent qu'environ le quart des populations régionales pourraient occuper les forêts récemment brûlées (≤ 2 ans) pour une région avec un cycle de feu de 100 ans (Annexe 1).

Implications en aménagement forestier

Cette thèse montre clairement que le bois mort, qu'il soit dispersé dans la matrice forestière non brûlée ou concentré dans des peuplements brûlés, constitue un substrat alimentaire important pour plusieurs espèces de pics en forêt boréale. Par conséquent, le maintien de ces espèces dans les forêts aménagées requiert nécessairement le maintien de bois mort de qualité pour l'alimentation. Parce que les exigences écologiques des pics en matière d'alimentation peuvent être considérablement différentes de celles pour la nidification (e.g. Harestad et Keisker 1989, Martin *et al.* 2004, Drapeau *et al.* sous presse, chapitre 2) et parce qu'elles nécessitent le maintien d'une grande quantité de bois mort en comparaison avec les besoins en nidification, les résultats de cette thèse suggèrent que les stratégies pour le maintien de bois mort orientées sur les arbres à cavités sont assurément inadéquates afin de maintenir des habitats de qualité pour l'alimentation des pics en forêt boréale (voir également Weikel et Hayes 1999, Imbeau et Desrochers 2002, Hutto 2006).

Les résultats des chapitres 1, 2 et 4 montrent clairement que les caractéristiques du bois mort, en particulier l'état de dégradation, influencent grandement la qualité de ces substrats pour l'alimentation. Le maintien de substrats alimentaires implique différentes stratégies pour les feuillus et les conifères. Dans le cas des feuillus, le maintien de bois mort de qualité pour les pics peut être assuré à la fois par la mortalité partielle des arbres vivants (ex. branches mortes sur les arbres) ainsi que par les arbres morts de dégradation avancée. Pour les conifères cependant, la fenêtre de qualité des arbres pour l'alimentation est généralement limitée aux arbres mourants ou récemment morts (ex. < 5 ans après la mort de l'arbre). Ces résultats soulignent l'importance d'assurer un recrutement constant en arbres morts, en particulier pour les pics associés aux forêts résineuses tels que le pic à dos noir et le pic à dos rayé.

Parce que les forêts brûlées représentent une importante source de bois mort à l'échelle régionale et un habitat de qualité pour la nidification et l'alimentation de plusieurs espèces, les stratégies de récupération devraient assurer le maintien d'habitats adéquats pour les espèces associées au feu. À cet effet, l'annexe 2 (article publié en 2004) énonçait plusieurs recommandations qui se voulaient essentiellement des mesures de précaution à l'égard de l'aménagement des forêts brûlées et du maintien de la biodiversité associée à ce type d'habitat. Les résultats de cette thèse viennent grandement appuyer les recommandations proposées à l'annexe 2. Les conclusions tirées de cette thèse ont également constitué la base de l'élaboration de lignes directrices pour une approche écosystémique lors de la récupération des bois brûlés (Nappi *et al.* 2007).

Importance de la qualité de l'habitat. Les résultats de cette thèse montrent clairement que la qualité des forêts brûlées pour le pic à dos noir varie en fonction des conditions présentes avant le feu et de la sévérité du feu. Étant donné l'importance du diamètre des arbres tant pour l'alimentation que pour la nidification, les peuplements matures brûlés constituent les habitats de plus haute qualité pour les pics (plus grande densité de nids, plus fort succès reproducteur). Parce que ce sont ces peuplements qui sont ciblés par la récupération, il est important de s'assurer que les peuplements brûlés non récupérés seront constitués en partie de ces types de peuplements. D'autre part, mes résultats suggèrent également que les zones brûlées en bordure des forêts vertes constituent des habitats d'alimentation (arbres moins sévèrement brûlés) et de nidification (succès reproducteur plus élevé) de haute qualité qui devraient être maintenus lors des opérations de récolte. La combinaison des conditions avant feu (ex. information tirée des cartes écoforestières) et de la sévérité du feu (ex. information tirée des cartes d'impact du feu) pourrait être utilisée afin de déterminer les habitats de qualité pour le pic à dos noir et d'assurer leur maintien à travers l'élaboration des plans de récupération. Parce que plusieurs autres taxons et espèces sont également influencés par les conditions forestières avant feu et la sévérité du feu (Purdon *et al.* 2004, Jayen *et al.* 2006, Koivula et Spence 2006), je suggère que la combinaison de ces deux éléments constitue la base d'une approche de filtre brut lors de l'élaboration de stratégies de récupération visant le maintien d'habitats adéquats pour les espèces associées au feu (Nappi *et al.* 2007).

Importance du temps depuis le feu. La qualité des forêts brûlées étant éphémère pour le pic à dos noir, il faut que le maintien de forêts brûlées dans le paysage soit planifié sur un horizon annuel afin de maintenir la disponibilité de cet habitat pour cette espèce dans le temps. En d'autres mots, ceci signifie que la présence de vieilles forêts brûlées ne peut compenser pour le maintien de forêts récemment brûlées. Parce les caractéristiques des forêts brûlées (ex. types de peuplements brûlés, sévérité du feu) peuvent varier grandement sur une base annuelle (Bergeron *et al.* 2002), cette approche permet également d'assurer davantage le maintien de l'ensemble du spectre de conditions présentes dans les forêts brûlées.

Importance de l'échelle spatiale pour établir les cibles de conservation. Les résultats de cette thèse viennent également appuyer l'importance de bien définir des cibles de maintien de forêts brûlées à une échelle régionale (ex. en considérant la classification écologique du territoire) et non provinciale. En effet, les différences observées quant à la présence de certaines espèces d'insectes entre les deux secteurs de feux à l'étude (chapitre 3 vs. chapitre 4) illustrent l'importance de maintenir des forêts brülées sur l'ensemble du territoire forestier, et ce, afin d'assurer le maintien de l'ensemble des populations d'espèces associées au feu.

Les pics peuvent représenter de bons modèles en aménagement forestier et en biologie de la conservation (Mikusiński 2006, Virkkala 2006), notamment comme espèces « fonctionnelles », « indicatrices » et « parapluies » (Martikainen *et al.* 1998, Martin et Eadie 1999, Mikusiński *et al.* 2001, Roberge et Angelstam 2006, Drever *et al.* 2008). L'association de plusieurs espèces de pics au bois mort pour l'alimentation mais également leurs affinités aux divers stades de dégradation du bois suggèrent que les pics pourraient représenter de bons indicateurs de la présence et de la dynamique naturelle du bois mort dans les écosystèmes forestiers aménagés. Parce que le pic à dos noir est particulièrement dépendant du processus de recrutement des arbres morts et qu'il semble favorisé par le feu, cette espèce pourrait être un bon indicateur du maintien des processus naturels en forêt boréale. Compte tenu que l'aménagement écosystémique implique, entre autres, le maintien des processus naturels afin de maintenir ou d'améliorer l'intégrité écologique des écosystèmes, le pic à dos noir pourrait ainsi représenter un « indicateur écosystémique » en forêt boréale. Du même coup, la protection de cette espèce bénéficierait probablement à une variété d'espèces fauniques et floristiques dont la présence est limitée par ces processus naturels (« umbrella process-limited species » *sensu* Lambeck 1997).

Perspectives futures de recherche

Cette thèse ainsi que plusieurs études récentes montrent que de nombreux facteurs (conditions avant feu, sévérité du feu, âge du feu, taille, localisation, régime de feu) peuvent influencer la réponse des vertébrés, des arthropodes et des plantes au feu. Tout comme le suggèrent Saab et Powell (2005), d'autres études seront nécessaires afin de comprendre les effets de cet éventail de conditions et afin de dégager une compréhension globale des effets du feu. En outre, ces facteurs devraient constituer le cadre de référence de toute étude portant sur les effets du feu; chaque étude devrait décrire clairement les caractéristiques du feu étudié afin de permettre une meilleure mise en contexte des résultats et des conclusions de l'étude. En forêt boréale, beaucoup plus d'études seront nécessaires afin de mieux comprendre les effets de la variabilité des régimes de feu (fréquence, sévérité, taille, etc) sur la dynamique des espèces associées au feu.

La quantification des paramètres démographiques (natalité, mortalité, immigration, émigration) des espèces associées au feu constituent une des carences d'information les plus importantes à combler dans les prochaines années. Parce que la plupart des espèces de plantes, d'arthropodes et de vertébrés peuvent également occuper d'autres types d'habitats, il est important de quantifier ces paramètres dans les forêts brûlées ainsi que dans les forêts non brûlées soumises à d'autre types de perturbations naturelles (épidémies d'insectes, chablis, etc). Parce que les conditions forestières (dont notamment l'abondance de bois mort) dans les forêts non brûlées sont, par défaut, plus variables que dans les forêts brûlées, il est probable que beaucoup plus de données seront nécessaires afin de couvrir cet éventail de conditions rencontrées (gradient de densités de bois mort, différents types de perturbations naturelles). Seule une meilleure quantification des paramètres démographiques de ces populations permettra de valider et raffiner les hypothèses liées aux modèles de dynamique de population (ex. dynamique source-puit).

Dans un contexte d'aménagement durable des forêts, les orientations et lignes directrices d'aménagement concernant le bois mort et les forêts brûlées devront être testées dans une optique d'amélioration continue des pratiques forestières. Étant donné le manque de connaissances quant aux effets du feu et de la récupération des forêts brûlées, il est important d'explorer et de comparer différentes stratégies de récupération, notamment en ce qui a trait aux caractéristiques de peuplements brûlés à maintenir, à leur quantité ainsi qu'à leur répartition dans les paysages forestiers. Une des informations les plus critiques concerne la détermination de cibles d'aménagement quant à la quantité de certaines ressources (ex. bois mort) et aux proportions d'habitats à conserver au sein des paysages forestiers aménagés.

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ANNEXE 1

CONTRIBUTION OF BURNED FORESTS TO REGIONAL POPULATIONS OF THE BLACK-BACKED WOODPECKER (*PICOIDES ARCTICUS*)

A1.1 Note

Although fire is recognized as the main natural stand-replacing disturbance in the Canadian boreal forest, fire cycle (time required to burn an area equal to the study area) has been shown to vary widely among regions. This variability inevitably affects the availability of post-fire habitats but also the availability of alternative older mature forests for the black-backed woodpecker. Here, we provide a simple model to evaluate the relative proportion of a regional population that could occupy burned and unburned forest habitats in boreal regions that vary in their fire cycle.

As reviewed by Bergeron *et al.* (2004), fire cycle in the Canadian boreal forest ecosystem has historically (last three centuries) varied from 50 years (West central Alberta; Van Wagner 1978) to more than 500 years (Southern Labrador; Foster 1983). Fire cycle is also known to vary greatly among regions of the boreal forest of Quebec (Fig. A1.1; Lefort *et al.* 2004).

Using this range of variability as a reference, we may estimate the mean annual proportion of a given region that would burn on an annual basis (1/fire cycle) and derive the mean proportion occupied by suitable burns (i.e. 2 years, based on Chapter 3). Figure A1.2a shows that for a fire cycle of 50 years, an annual average of 4% of the region would be occupied by recent burns (≤ 2 years) whereas this proportion is less than 1% for regions with fire cycles longer than 200 years. Because fire cycle also influences forest age structure, the proportion of forest of a given age will also vary as a function of fire cycle. This will affect the proportion of alternative unburned forest habitats for black-backed woodpeckers. Because of their dependence on dead wood, it is reasonable to expect black-backed woodpeckers to mainly occupy mature and old-growth forests (i.e. > 100 years). The proportion of a given region that is covered by overmature forest (> 100 years) increases with longer fire cycle; for instance, overmature forests represent 14% of the forest landbase with a fire cycle of 50 years whereas they represent 82% of the forest landscape with a fire cycle of 500 years (Fig. A1.2a; Bergeron *et al.* 1999; Cyr *et al.* In press).

Although it is clear that recent burns always cover a smaller proportion of the landscape as compared to mature and old-growth forest types, burned forests generally support much higher densities of woodpeckers (Hutto 1995, Hoyt and Hannon 2002) and may thus support a significant proportion of a regional population on a annual basis. Yet, it is important to consider that the quality of burned forests for black-backed woodpeckers will also depend on the fire cycle. Indeed, with a fire cycle of 50 years, fires will inevitably burn higher proportions of young stands than in regions with longer fire cycles. For example, with a fire cycle of 50 years, more than 50% of the forests are younger than 40 years. These burned forests are unlikely to represent suitable habitats to woodpeckers (chapter 2 and 3). Our data suggest that nest density in burned forests will vary as a function of age prior to fire and time since fire (Table A1.1). Based on density data of burned and unburned forests, we weighted habitat proportions to take into account differences in habitat-specific nest densities. Therefore, the relative proportion of a regional population that may occupy each potential woodpecker habitat on an annual basis will depend on both the relative abundance of each habitat and their associated relative bird densities.

As shown in Figure A1.2b, in boreal regions where fire is as short as 50 years, as much as 50% of a regional population could potentially occupy recent burns on a mean annual basis. This proportion is about 25% in regions with a 100-year fire cycle and becomes more marginal as fire cycle increases (e.g. 500 years). Of course, habitat quality varies within and among burns (as shown in Chapter 3) and is also likely to vary in unburned habitats. However, this simple model illustrates that recent burns may thus contribute significantly to regional populations, especially in regions with short fire cycles.

The source-sink dynamic as proposed by Hutto (1995) for the black-backed woodpecker assumes that the net surplus of individuals produced in source (burned) habitats would compensate for the net loss of individuals in sink (unburned) habitats (Pulliam 1988). This equilibrium in a closed population (no emigration, no immigration) will depend on both population growth in each habitat ($\lambda > 1$ in sources, $\lambda < 1$ in sinks) and on the relative proportion of the population in these habitats (Pulliam 1988). In regions with a short fire cycle, this source-sink dynamic is plausible given that recent burns support an important portion of the population and may thus compensate for potential deficits in unburned habitats.

However, in regions where fire cycle is longer, the net surplus generated by burned forests in these regions is unlikely to compensate for deficits generated in unburned habitats. Two scenarios are thus possible. First, it is plausible that reproduction is high enough in these unburned forests to ensure population persistence. For instance, these regions are covered by a larger proportion of old-growth forests (Bergeron *et al.* 2002) and fire is replaced by secondary disturbances such as insect outbreaks (Bergeron *et al.* 1995, Bergeron and Leduc 1998) which provide both increased levels of dead wood and potentially high-quality habitats. An alternative (non-mutually exclusive) is that regions with short fire cycles would serve as regional sources from which surplus individuals disperse into less fire-prone forest ecosystems (regional sinks).

A1.2 References

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A1.3 Table

Table A1.1. Nest density estimations used to assess the relative proportion of a black-backed woodpecker population that would occupy burned and unburned forest habitats.

Habitat type	Year since fire	Stand age prior to fire (years)	Nest density (no./100 ha)	Comments
Burned forests (≤ 2 years after fire)	1	0-40	0	Unsuitable habitat [1]
	1	40-80	5	About half the density observed in burned > 80-year-old stands [2]
	1	> 80	10	Highest observed density [2]
	2	0-40	0	Unsuitable habitat [1]
	2	40-80	2.5	Two-fold decrease by year 2 [2]
	2	> 80	5	Two-fold decrease by year 2 [2]
Unburned mature forests (> 100 years)	-	-	0.7	Based on home ranges estimated in boreal forests of Quebec [3]

[1] Based on chapters 2 and 3

[2] Based on chapter 3

[3] Tremblay, J. and J. Ibarzabal (unpublished results): mean home-range = 150 ha (*n* = 7).

A1.4 Figures

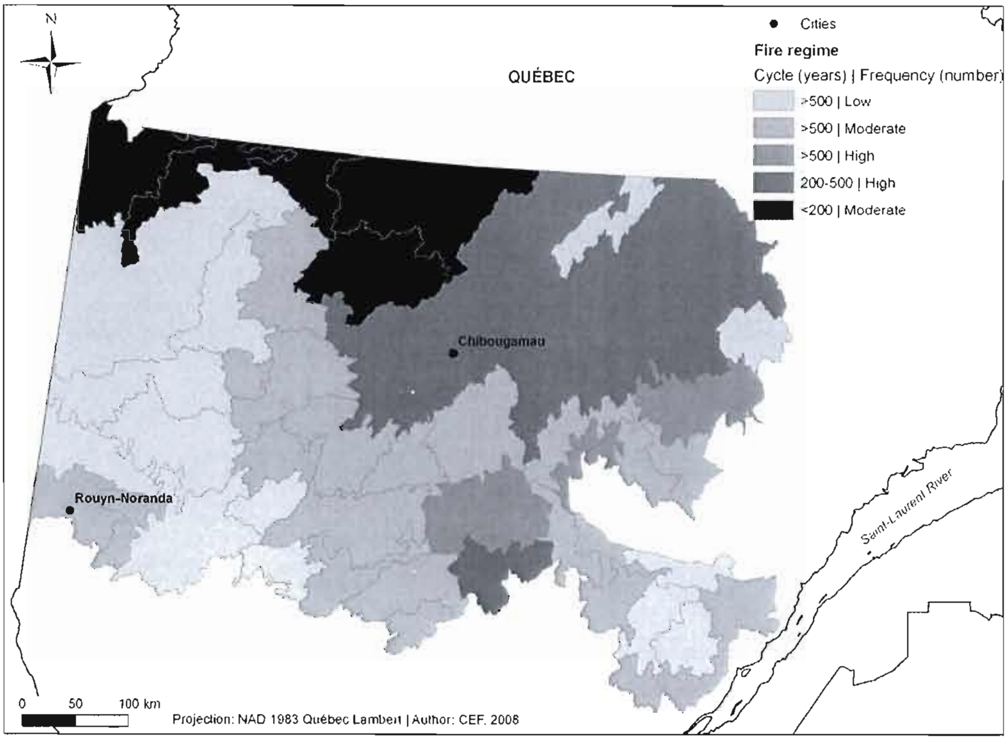

Figure A1.1. Recent fire regimes (1945-1998) in the western portion of the boreal forest of Quebec (adapted from Lefort *et al.* 2004).

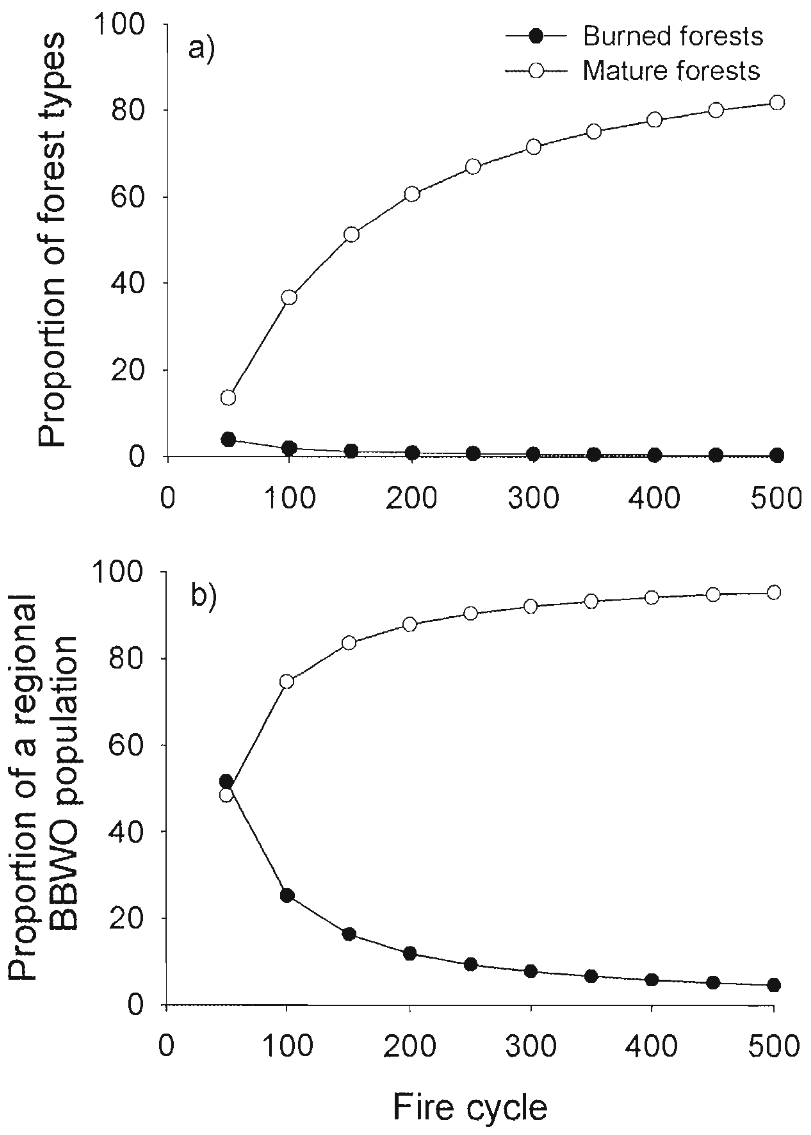

Figure A1.2 Relative contribution of burned forests to regional populations of the black-backed woodpecker on an annual basis: a) relative proportion of a region occupied by potential burned and mature forest habitats, b) relative portion of a regional population that would occupy burned forest habitats given their relative difference in densities in each habitat.

ANNEXE 2

SALVAGE LOGGING AFTER WILDFIRE IN THE BOREAL FOREST: IS IT BECOMING A HOT ISSUE FOR WILDLIFE?

A2.1 Résumé

Au cours des dernières années, la demande accrue en matière ligneuse et sa raréfaction, l'expansion nordique de la coupe forestière, ainsi que la perception générale que les feux créent des désastres écologiques ont favorisé l'intensification de la coupe de récupération dans les forêts brûlées de l'écosystème boréal. En parallèle, des études récentes ont montré que ces forêts brûlées peuvent constituer des habitats importants pour plusieurs espèces animales et que la coupe de récupération intensive, en éliminant les chicots debout, entraîne plusieurs impacts sur la faune associée à cet habitat. Jusqu'à maintenant, la problématique des effets de la coupe de récupération sur la diversité biologique a été peu considérée dans l'aménagement des forêts brûlées. Cet article présente la problématique de la coupe de récupération pour la faune en forêt boréale. Nous utilisons la situation du Québec comme un exemple de l'aménagement actuel des forêts brûlées dans l'est de la forêt boréale. Nous décrivons l'état actuel de nos connaissances quant à l'utilisation de ces forêts par la faune et quant aux impacts de la coupe de récupération sur ces habitats. Nous concluons que la rétention de chicots à différentes échelles spatiales et temporelles dans les forêts récemment brûlées soumises à la coupe de récupération constitue une pratique sylvicole qui se doit d'être implantée afin de rencontrer les principes d'un aménagement forestier durable et le maintien de la biodiversité de la forêt boréale.

Mots-clés : forêt boréale, forêts brûlées, coupe de récupération, chicots, faune, oiseaux, avifaune cavicole, pics, mammifères, invertébrés, insectes xylophages, biodiversité.

A2.2 Abstract

In recent years, the increase in wood demand, the reduction in the availability of timber resources and the northern expansion of timber harvesting, along with the general perception that wildfires create ecological disasters, have favoured an increase in salvage logging in burned boreal forests. Concurrently, pioneer studies have shown that these post-fire forests may represent important habitats for several wildlife species and that intensive salvage logging, by removing standing snags, have several impacts on wildlife. However, the effects of salvage logging on biodiversity have yet to be considered in post-fire management plans. We examine the issue of salvage logging for wildlife in the boreal forest, with particular reference to Québec as an example. We describe our current state of knowledge on the use of burned forests by some wildlife and on the impacts of salvage logging on these habitats. We conclude that snag retention at multiple spatial and temporal scales in recent burns that will be salvage-logged is a prescription that must be implemented to meet the principles of sustainable forest management and the maintenance of biodiversity in the boreal forest.

Keywords : boreal forest, post-fire forests, salvage logging, snags, wildlife, birds, cavity-nesting birds, woodpeckers, mammals, invertebrates, xylophagous insects, biodiversity.

A2.3 Introduction

Over the last century, wildfires have been mainly perceived by the public, forest managers and ecologists as catastrophic events (Kuuluvainen 2002). Because forest fires represent a threat for lives, property and forest resources, most of the attention has focused on preventing, detecting and fighting them (Blanchet 2002, Drolet 2002). While this threat is still of topical interest, the role of fire in forest ecology has undergone an important re-evaluation in recent years. In the boreal forest, as in many other North American forest ecosystems, fire is now recognized as a major process in forest dynamics (Rowe and Scotter 1973, Johnson 1992). For instance, in many pine ecosystems, prescribed burning is now a useful management tool to restore forests that were historically under a regime of frequent low-intensity understorey fires (Ford *et al.* 1999, Conner *et al.* 2001, Quenneville and Thériault 2002). In the boreal forest, there is also an increasing interest in using natural disturbances as a guide for sustainable forest management (Bergeron and Harvey 1997, Bergeron *et al.* 2002).

Despite the potential benefits to forest regeneration, wildfires often represent an important economic loss for forest industries. In coniferous forests of North America, the increase in wood demand and the reduction in the availability of timber resources have led to increased salvage logging of burned forests. Under a regime of stand-replacement fires, salvage logging consists mainly of clearcutting all merchantable (and accessible) timber within recently burned areas. While salvage logging may be unavoidable for economic reasons, from a sustainable forest management standpoint, it raises several questions about how this forestry practice is conducted and its effects on soil, streams, vegetation and wildlife (Saab and Dudley 1998, Morissette *et al.* 2002, Purdon *et al.* 2002).

In this paper, we examine why salvage logging may become an important issue in the boreal forest. We first provide several examples regarding the use of burned forests by wildlife. We then use the case of salvage logging in Québec as an example of how these post-fire habitats are currently managed in the eastern boreal forest. Finally, we deal with some of the impacts of salvage logging on burned forests and suggest ideas on how salvage logging might meet the principles of sustainable forest management in the maintenance of biodiversity.

We focus on the salvaging of burned forests because stand-replacement fires represent the main natural disturbance in the Canadian boreal ecozone (Rowe and Scotter 1973, Johnson 1992, Bergeron *et al.* 2001). However, in the absence of fire for long periods, other large-scale disturbances, such as insect outbreaks, may exceed the importance of fire as a natural disturbance (MacLean 1980, Bergeron and Leduc 1998) and thereby become important targets for salvage. Whereas these stand-replacement disturbances may be different ecologically, they are managed similarly in Québec.

A2.4 Burned forests: an ecological disaster or a bonanza for wildlife ?

While wildfires vary in frequency, size or severity, the natural fire regime of the boreal forest is typically characterized by large-scale stand-replacement fires (Bergeron *et al.* 2002). These wildfires create a mosaic of forest cover types of varying age to which the regional biodiversity is closely linked. However, the short-term impacts of fires on wildlife have received very little and only recent attention.

When recent burns are compared to other forest types (including recent clearcuts) one of the most striking difference is the number of standing snags (Angelstam and Mikusiński 1994, Hutto 1995, Drapeau *et al.* 2002). At the landscape level, disturbances such as fires and insect outbreaks represent the main source of dead wood in the boreal forest of North America. In the western portion of Québec's boreal forest (northern clay belt), the contribution of fire is even more important because old forests contribute very little to the abundance of dead wood, especially large snags (Drapeau *et al.* 2002), and insect outbreaks are scarce (Blais 1983, Morin *et al.* 1993, Bergeron and Leduc 1998). Wildfires also create open stands with warm and exposed mineral soils, and eventually, an increased shrub cover, all of which can benefit the wildlife species that require these habitat structures. While current knowledge of the impacts of fire on boreal wildlife is limited for certain taxa, we present, in the following sections, several examples of the response of wildlife to wildfires.

Invertebrates

Recent work on boreal invertebrates has shown that Coleoptera and spider assemblages in post-fire habitats are clearly distinct from those in other forest types (Buddle *et al.* 2000, Saint-Germain *et al.* 2003). Several insect species greatly benefit from the conditions created by fire such as habitats free of competitors, exposed soils and high abundance of snags (Wikars 1992, 1994, Saint-Germain *et al.* 2003). Burned forests are particularly important for wood-boring (Cerambycidae and Buprestidae) and bark (Scolytidae) beetles that rely on recently dead trees for their life cycles (Rose 1957, Ross 1960, Powell *et al.* 2002, Saint-Germain *et al.* 2004). Some pyrophilous species have also developed adaptations, such as the capacity to detect smoke or heat generated by fire, that help them track post-fire habitats (Evans 1966, Schütz *et al.* 1999, Suckling *et al.* 2001). Some soil-dwelling species (Elateridae) associated with stressed roots and some subcortical predators may also be found in high numbers in burned forests (Muona and Rutanen 1994, Saint-Germain *et al.* 2003).

Because of within-burn variability, not all stands offer the same quality of habitat. For xylophagous insects, several stand characteristics such as tree diameter and vigour before tree death, fire severity or site have been shown to influence their choice of substratum (Nappi *et al.* 2003, Saint-Germain *et al.* 2004).

Mammals

The response of small mammals to fire is principally associated with the structural complexity of the shrub cover, which is itself influenced by time since fire (Krefting and Ahlgren 1974, Crête *et al.* 1995), fire severity (Martell 1984, Kirkland *et al.* 1996, Ford *et al.* 1999) and the amount of coarse woody debris (Menzel *et al.* 1999, Simon *et al.* 2002). Small mammal diversity and abundance generally decrease immediately after fire and tend to increase with regeneration and increased shrub cover during the following years. However, some species, such as the Deer mouse (*Peromyscus maniculatus*), take immediate advantage of the newly created habitat. Several studies show Deer mice increase in abundance in recently burned areas and seem to benefit greatly from the abundant food resources provided by the massive seed bank of dead coniferous trees following fire (Sims and Buckner 1973, Krefting and Ahlgren 1974, Martell 1984, Crête *et al.* 1995). Years after a fire, changes in vegetation provide habitat conditions that are attractive for other species of mice, voles and shrews (Sims and Buckner 1973, Krefting and Ahlgren 1974, Crête *et al.* 1995, Simon *et al.* 2002). For instance, the Red-backed vole (*Clethrionomys gapperi*), which typically feeds on fungi and lichens (Gliwicz and Glowacka 2000) associated with late successional forests, will gradually recolonise post-fire forests as habitats become more suitable.

Some large mammals also take advantage of recently-burned stands. In their study in the northern boreal forests of Québec, Crête *et al.* (1995) found more Black bears (*Ursus americanus*) and Moose (*Alces alces*) in recently-burned stands than in older or unburned stands. Their presence was mainly related to abundance of food such as berries – an important component of Black bears' diet (Boileau *et al.* 1994) – which are usually abundant in burned forests. These young stands also provide abundant deciduous shrubs for Moose foraging (Crête and Jordan 1981). The abundance of small mammals may also provide good hunting opportunities for mammalian predators. Paragi *et al.* (1996) found higher marten abundance, hunting activity and small mammal biomass and diversity in a recent burn (6-9 years after fire) compared to older (25-28 years) or mature coniferous forests (100-115 years).

Birds

Forest bird assemblages have been studied in several areas of the boreal or other coniferous forests to compare burned forests with other forest habitats such as unburned and harvested stands (Raphael *et al.* 1989, Hutto 1995, Hobson and Schieck 1999, Imbeau *et al.* 1999, Morissette *et al.* 2002). Whereas the results of these studies vary according to forest cover type and time elapsed since fire, a consistent finding is the relatively high abundance of ground- and shrub-nesting birds (*e.g.* Hermit thrush (*Catharus guttatus*), American Robin (*Turdus migratorius*), Dark-eye junco (*Junco hyemalis*)), flycatchers (*e.g.* Olive-sided flycatcher (*Contopus borealis*)) and cavity-nesters (*e.g.* Woodpecker spp., Bluebird spp.) in recently-burned forests. The main divergence in bird community patterns between post-fire and post-logged stands seems to occur during the first few years following disturbance (Hobson and Schieck 1999), partly due to the high abundance of woodpeckers (*Picoides* ssp.), which are known to colonize recently disturbed forests following natural disturbances such as fire (Blackford 1955, Hutto 1995, Murphy and Lehnhausen 1998, Drapeau *et al.* 2002) and insect outbreaks (Crockett and Hansley 1978, Yunick 1985, Goggans *et al.* 1989).

One of the most striking and best-known examples of a burn-associated species is the Black-backed Woodpecker (*Picoides arcticus*). In different parts of North America where stand-replacement fires represent the main natural disturbance, this species is highly abundant during the first years following fire (*e.g.* Alaska (Murphy and Lehnhausen 1998); Rocky Mountains (Hutto 1995); Alberta (Hoyt and Hannon 2002); Québec (Imbeau *et al.* 1999, Nappi *et al.* 2003)). Its abundance is mainly linked to the increased availability of wood-boring (Cerambycidae and Buprestidae) and bark (Scolytidae) beetles on standing dead trees (Murphy and Lehnhausen 1998, Nappi *et al.* 2003).

Woodpeckers such as the Black-backed Woodpecker may play an important role in the nest-web (Martin and Eadie 1999) by excavating cavities that can then be used by several secondary cavity nesting species (species that cannot build their own cavity but require one for breeding). Because of this link, the presence of secondary cavity nesters such as the Eastern Bluebird and the Tree Swallow may be closely tied to initial woodpecker abundance. As most do not rely on snags for food (contrary to woodpeckers), secondary cavity nesters may persist in post-fire habitats for a longer period and will constitute an important and constant component of the avifauna during post-fire succession (Taylor 1979).

Burned snags that remain standing for several years following fire likely facilitate the use of these areas by perch hunting species such as small owls and accipiters by allowing them to exploit the post-fire increase in small mammals populations (Lyon *et al.* 1978, Spires and Bendel 1982).

Species relationships and population dynamics

As shown previously, recently burned forests with their mass recruitment of standing dead trees not only provide habitat for several individual species, but also play a key role in the functional organization of food webs (predator-prey relationships) and nest-webs (*sensu* Martin and Eadie 1999) for cavity nesting birds. Prey-predator relationships may be observed between xylophagous insects and insect predators and/or woodpeckers. Such relationships may also be observed between small mammal populations and mammalian predators (*e.g.* Mustelidae) or birds of prey.

A frequently asked question of forest ecologists is whether species associated with burns are either 1) opportunistic species who rely on mass recruitment of snags but also use other post-disturbance habitats or 2) "pyrophilous" species that have evolved in the presence of fire and are now fire-dependent. Although the answer to this question is currently unknown, it is clear that stand-replacement fires lead to mass colonisation by fire-associated species and that these fires represent the major natural disturbance in most of the boreal forest.

In parallel to this question is the interesting, but yet to be tested, hypothesis of source and sink dynamics (*sensu* Pulliam 1988). For the Black-backed Woodpecker for instance, Hutto (1995) suggested that populations of this species are maintained by a patchwork of recently burned forests whereas unburned forests support sink populations that emigrate from burns after they become less suitable (see also Murphy and Lehnhausen 1998). Such dynamics may apply as well to other fire-associated species such as wood-boring and bark beetles. High populations of these insects observed following recent forest fires would allow their persistence in sub-optimal unburned habitats until the next regional disturbance (Jonsell *et al.* 1998). Because of the relationships between some fire-associated species, recent burns do not contribute only to species diversity but they also may have a strong influence on the functional diversity of the boreal ecosystem, given that they are the template of complex trophic links between wildlife species that have evolved in a context of unpredictable, abundant but ephemeral resources (standing dead wood).

A2.5 Salvaging burned forests: the Québec case

With the northern expansion of forestry into ecological zones where fire cycles are shorter (< 100 years) than in southern areas (Fig. A2.1), it is likely that forest industries will have to deal more and more with the reality of wildfires in the future. While fire suppression has had limited success in northern portions of the boreal forest in the last 30 years (Leduc 2002, Lemaire 2002), the development of the road network will probably help increase fire control and salvage logging in these areas.

Before the adoption of a legal framework in Québec, salvage logging of forests affected by fire or severe insect outbreaks was sporadic (Fig. A2.2). However, the Québec Forest Act of 1986 and its recent modifications have provided several incentives to intensify salvage logging (Québec Government 2003). Specifically, Article 79 of the Québec Forest Act states that land tenure holders must comply (under penalties of quota reduction) with special management plans created at the provincial government's discretion, to salvage forests after a natural disturbance The law specifies that these special management plans are exempted from the obligation to apply current forest regulations (*e.g.* minimal buffer strips) normally used in undisturbed forests. In actuality, these plans primarily result in the clearcutting of burned stands with no retention of individual burned trees or patches within the logged areas, except those that are not merchantable or accessible. Forest companies have also adapted their management practices to optimize harvest operations in burned stands. For example, it is now possible and economically feasible for forest companies to salvage-cut old burned forests up to 12 years after fire (data from Saint-Félicien management unit).

The combination of all these elements has already favoured an increase in salvage logging over the last decade (Fig. A2.2). The last four years of our data set illustrate situations where fires were abundant. In Québec's commercial forest, from 13 to 40 % of large fires (>1000 ha) within the management units were salvage logged between 1995 to 1998. This period includes most of the total burned areas that have been salvaged up to then. During the same period, the intensity of salvaging within burned areas also increased; one third of these burned forests have been harvested on more than 50% of their burned areas, while this situation rarely occurred before 1995. While the proportion of burned forests that have been salvage logged still remains low, it will likely increase as road access is developed. Until now, the limited access to burns has concentrated salvage logging mainly in the southern portions of the boreal forest (Fig. A2.3).

A2.6 How should burned forests be managed ? an emerging challenge

Present knowledge on the use of burned forests by wildlife raises several concerns regarding the long-term maintenance of this habitat type. In the eastern boreal forests of North America, recent burns are still common on the natural landscape but their regional importance may decrease in the future due to a climate-related decrease in fire frequency, accompanied by an increased efficiency of fire suppression and intensity of salvage logging.

The impacts of salvage logging

The emergence of the salvage logging issue has generated interest in evaluating the impacts of the practice (Saab and Dudley 1998, Purdon *et al.* 2002). However, the number and characteristics of fire-killed trees to be left in salvage cuts differs according to local and regional management prescriptions and social and economic conditions. For example, in a study that compared responses of cavity-nesting birds to different salvage-logging treatments (standard-cut salvage logged; wildlife-prescription salvage logged; unlogged controls) in Southwestern Idaho, even the most intensive standard-cut stands included the retention of 15 large trees (>25 cm DBH) per hectare (Saab and Dudley 1998). When retention prescriptions are lacking, salvage logging may be more intensive. In Québec for example, all merchantable wood (>8cm DBH) is harvested in burned forests that are accessible (Purdon *et al.* 2002). As a result, salvage-logged areas are clear-cuts and remaining patches or individual trees that are left are not merchantable.

It is doubtful that this level of retention will protect the structural attributes needed by wildlife. For instance, primary cavity nesters such as the Black-backed Woodpecker are known to use snags at least >10 cm for foraging (Nappi *et al.* 2003) and mostly >20 cm for nesting (Setterington *et al.* 2000). In their study on the effects of fire and salvage logging on birds, Morissette *et al.* (2002) found that salvage logging had a greater effect on the bird community than the fire alone. Species found in salvaged areas were mainly generalists, omnivores or shrub insectivores and ground and shrub nesters. Resident species, insectivores and canopy and cavity-nesting birds, which were associated with unburned and/or burned forests, were less likely to be found in salvaged areas.

From a vegetation and wildlife point-of-view, salvage logging, such as practiced in Québec, has been shown to have several negative impacts. Among them are the elimination of foraging and nesting habitat for wildlife, reduction of seed sources for regenerating species such as black spruce (*Picea mariana*) for several years after fire, unfavourable conditions for understorey vegetation and seed establishment and growth, and reduction in nutrients (Purdon *et al.* 2002).

The past and present experience of intensive forestry in Fennoscandia provides some insights on the long-term effects of these kinds of management practices on wildlife (Imbeau *et al.* 2001). In Sweden and in Finland, efficient fire suppression is thought to be the cause of decline of several fire-associated invertebrates (Wikars 1992, Ahnlund and Lindhe 1992, Jonsell *et al.* 1998). Most woodpecker species of Sweden have declined in response to changes in forest structure, such as the decrease in the availability of large trees or dead wood (Angelstam and Mikusiński 1994). In North American boreal forests, these population trends are difficult to assess, even for relatively well-studied taxa such as birds because of limited access and few long-term data (Imbeau *et al.* 2001). For some species, however, some trends may be negative, such as that already observed for Black-backed Woodpeckers in Canada (-9.0% for the period 1980-1996; Sauer *et al.* 1997). Currently, we have no understanding of the impact of salvage logging on long-term persistence of post-fire associated species. Until we learn more about wildfire-wildlife associations, a precautionary approach requires maintaining a good representation of the natural conditions within fires scheduled to be salvage-logged (Taylor 1991, Perrings 1995).

At a regional scale, the effect of salvage logging and fire suppression on the availability of post-fire habitats may be even more important in the context of a long-term decrease in fire frequency. Contrary to other parts of Canada, current climate change models predict a decrease in wildfire occurrence for eastern Ontario and western Québec (Flannigan *et al.* 2001). In western Québec, a decrease in fire frequency has already been observed since the mid-19th century (Bergeron *et al.* 2001).

Management prescriptions

Considering that burned forests are ecologically important, and salvage logging is likely to increase in the future, sustainable management of post-fire habitats should thus integrate ecological and economic values. To achieve the goal of maintaining biodiversity, management guidelines should be based on, and updated with, recent research results.

As shown previously, current knowledge on wildfire-wildlife associations is still incomplete for several taxa. Future effort should be directed towards a more comprehensive understanding of habitat use and population dynamics for the whole spectrum of wildlife species associated with post-fire habitats. For instance, using "umbrella" species such as the Black-backed Woodpecker for burned forests may be quite attractive and useful from a wildlife monitoring perspective. However, managing for this species alone may not necessarily maintain all the biodiversity associated with burned forests.

Filling data gaps may be challenging for some areas of the boreal forest. In Québec for instance, access to burns is limited by the poor road network in northern portions of the boreal forest. When accessible, burned forests (or parts that are accessible within the burn) are often intensively salvage-logged. Stands that remain are often less representative of what has been salvaged (unmerchantable stands) or too small to maintain large territorial species. Because of limited access, it is also difficult to sample more than one fire, which is often needed for comparative studies requiring replication.

In this perspective, we should take the opportunity, while burned areas are still available, to increase our knowledge of species associations with burned forests and implement innovative retention strategies. To answer the question of "how much should be left, where, and how?", such strategies should be designed to assess their effectiveness in the maintenance of biodiversity. It is crucial that this objective address both stand and landscape scales as well as at multiple temporal scales.

Within-burn retention.- Because wildlife species may be associated with different habitat features, retained snags should represent the full range of structure present before and after fire. This includes characteristics such as diameter (including large merchantable trees that are also the ones used by wildlife), tree species composition, before-fire decay conditions and fire severity. Field experiments should be designed to test the effectiveness of different levels of retention (from individual or clumped snags to large patches) on different wildlife species or group of species.

The use of a *xylophagous insect spatial model* is an example of what could be done at this spatial scale to help in the selection of burned forest stands to be maintained. The spatial pattern of wood-boring beetle colonisation such as for the widespread *Monochamus* species could help in the identification of areas to be precluded from salvage logging. On the one hand, this would help to identify burned stands of high conservation value for *Monochamus* species and other fire-associated insects with similar ecological requirements (as well as for woodpeckers and other secondary cavity nesters). On the other hand, this could help forest managers in the identification of areas that are less affected by wood-boring beetles, which are known to affect the quality of timber products.

Delayed salvaging.- Rapid changes occur in species composition and dynamics in the early stages following fire (*e.g.* loss and decay of standing snags, accumulation of coarse woody debris, regeneration of fire-adapted species such as jack pine). These first post-fire years are particularly important for several burn-associated species such as woodpeckers and xylophagous insects. However, to warrant harvesting that involves considerable field costs, forest companies need to promptly salvage burned stands before xylophagous insects significantly reduce timber value. In the cases where forest companies can harvest burned areas for pulp wood rather than saw logs or other timber products, delayed-salvaging can be a good alternative for both economic and ecological values. First, it increases the window of habitat availability for species that require post-fire structures. Second, it allows forest managers to reduce regeneration costs by providing the time needed to identify areas that regenerate well and thereafter implement harvesting practices that protect established regeneration.

Regional considerations.- It is often argued that salvage logging does not affect biodiversity because large burns remain mostly unsalvaged in northern areas of the boreal forest. First, the issue is not only how much burned habitat remains unsalvaged, but rather how salvage-logged areas comply to principles of sustainable forest management. Second, it is dangerous to rest the maintenance of biodiversity on the assumption that northern burned forests may compensate for the intensive salvaging of southern burns. We still know little about species composition and dynamics, and even less on the influence of a north and south gradient on species associated to post-fire habitats. Given this perspective, it may be prudent to maintain burned habitat across regions.

A2.7 Conclusions

The current state of knowledge and data gaps on the importance of burned forests for wildlife imply that forest managers need to be cautious in the management of post-fire habitats. The current intensification of salvage logging in several parts of the boreal forest, such as in Québec, may not meet the principles of sustainable forest management, including the maintenance of biodiversity. It is critical to seize the opportunity, while unsalvaged burned areas may still be available, to better document the diversity and dynamics of fire-associated species and thereby foster the development and implementation of innovative retention strategies that meet both ecological and economic objectives in this neglected but important habitat type for boreal wildlife.

A2.8 Acknowledgements

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A2.10 Figures

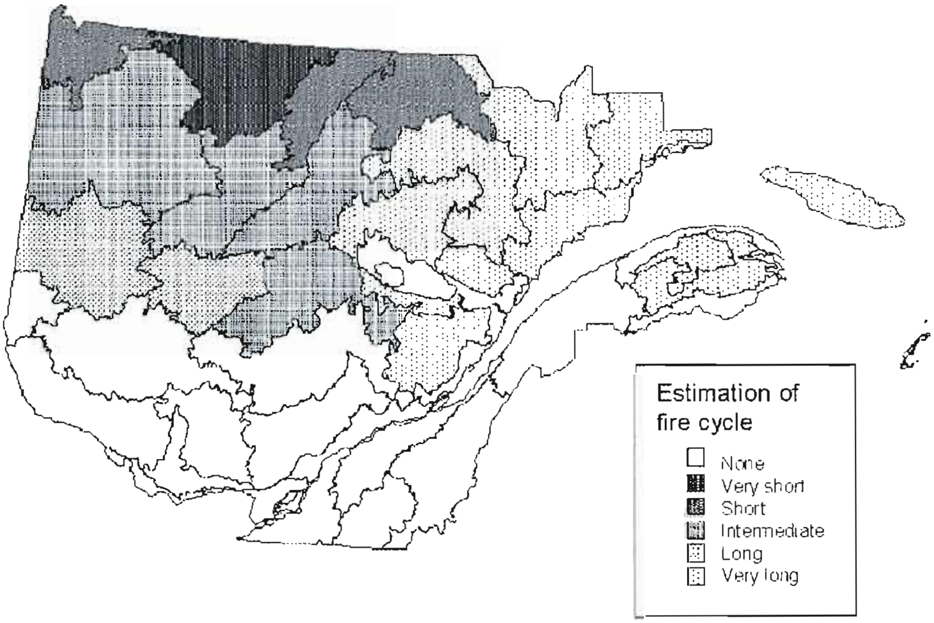

Figure A2.1. Estimation of fire cycles in ecological boreal zones of Québec. Adapted from Gauthier *et al.* (2001) by permission from Le Naturaliste Canadien.

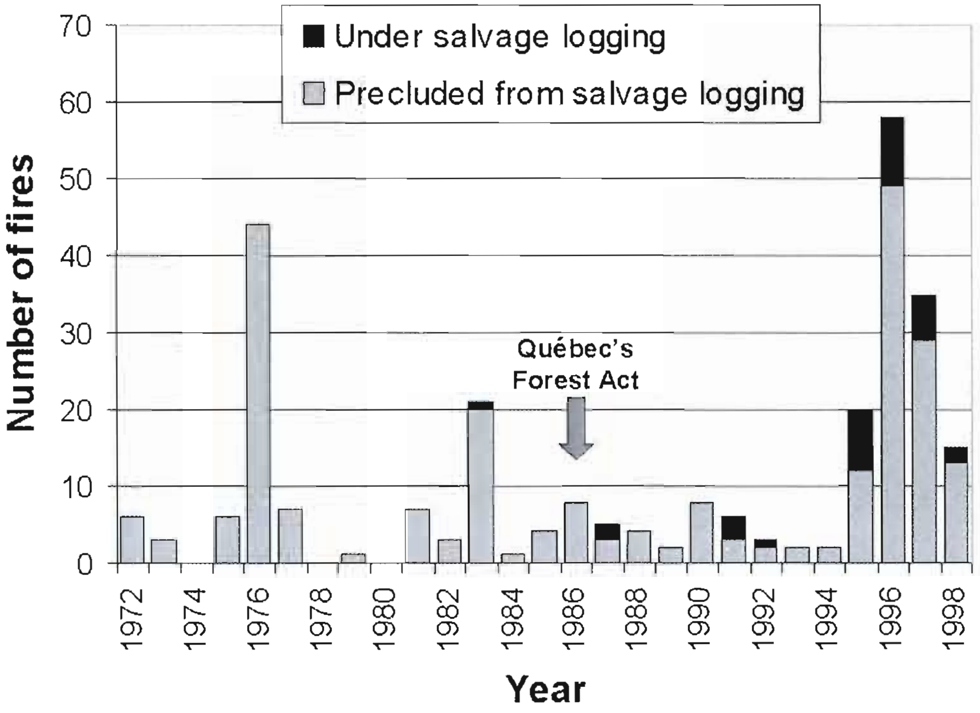

Figure A2.2. Progression of salvage logging in Québec from 1972 to 1998: number of wildfires (>1000 ha) precluded from or under salvage logging, south of the 52° parallel in Québec. The period covered corresponds to one of intensive fire suppression. The zone south of the 52 o parallel corresponds to management units and includes the merchantable forests. Data for fires and salvage logging have been provided by the Québec's Ministry of Natural Resources (number of fires under salvage logging is minimum, information on salvage logging is missing for one management unit).

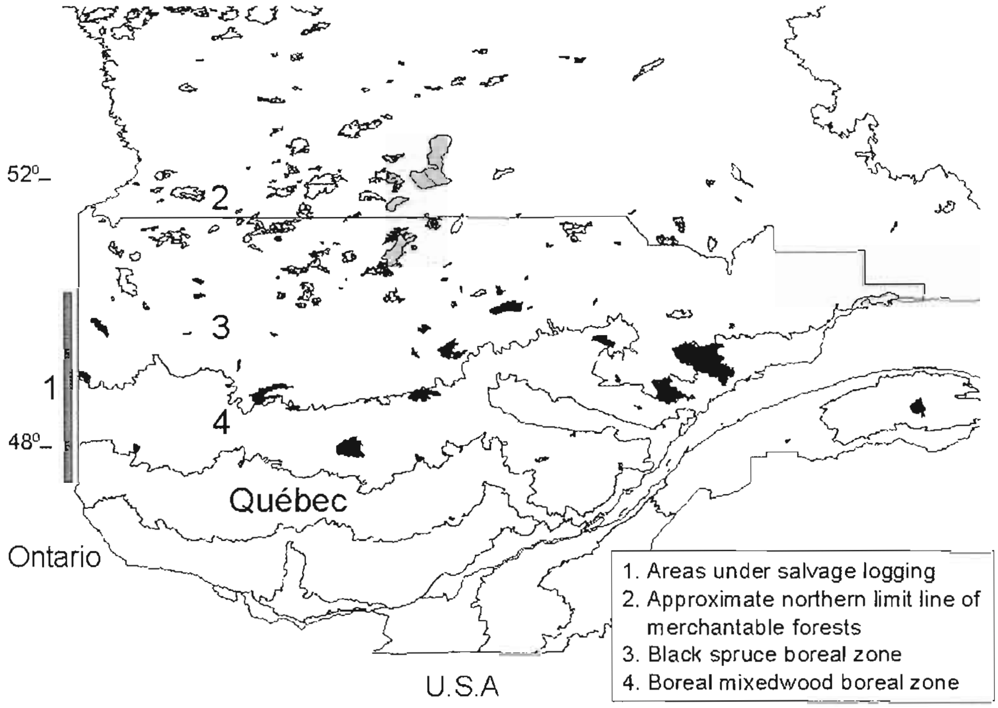

Figure A2.3. Spatial distribution of salvage logging for burned forests (>1000 ha) in Québec. In black: burned forest that have been under salvage logging. In grey : burned forests precluded from salvage logging.

Photo. Pic à dos noir femelle, nichant dans une forêt brûlée à environ 100 km au nord-ouest de Chibougamau, Québec. Le pic a été photographié à sa cavité alors qu'il transportait une larve d'insecte pour ses jeunes (photo par Antoine Nappi, 2004)