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ECOLOGIE DE NIDIFICATION DU PIC À DOS NOIR (*PICOIDES ARCTICUS*) EN FORÊT BOREALE NON BRULÉE

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AVANT-PROPOS

Cette thèse est constituée de cinq chapitres : une introduction générale, une conclusion générale et trois articles originaux dont je suis l'auteur principal. Mon directeur, Dr. Jacques Ibarzabal, et mon co-directeur, Dr. Jean-Pierre Savard, sont co-auteurs pour ces trois articles. Pour chacun des articles, j'ai établi la méthodologie, mené les travaux de terrain avec des assistants et fait les analyses statistiques appropriées. J'ai rédigé les premiers jets de toute la thèse. Pour le chapitre III, M. Christian Dussault apparaît comme co-auteur et sa participation à l'article fut principalement à titre de support pour les analyses statistiques. La version finale qui suit est le fruit d'une collaboration fidèle avec mes directeurs. Toutes les autres personnes qui ont collaboré à cette thèse, que ce soit sur le terrain, par des discussions ou financièrement, sont remerciées dans les articles respectifs.

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RÉSUMÉ

Le Pic à dos noir (*Picoides arcticus*) se trouve en plus grande densité dans les forêts brûlées que les forêts non brûlées et certains auteurs ont associé intimement le Pic à dos noir avec les forêts brûlées. Ces derniers ont émis l'hypothèse que les forêts non brûlées représentent des habitats puits pour le Pic à dos noir. Les objectifs de cette thèse de doctorat consistaient à définir le rôle des forêts non brûlées dans l'écologie de nidification et dans la démographie du Pic à dos noir dans un paysage issu de l'exploitation forestière et de feux de forêts en milieu boréal. La thèse est structurée selon trois chapitres principaux qui représentent des articles scientifiques publiés ou à être soumis (Chapitres II, III et IV), d'une introduction générale (chapitre I) et d'une conclusion générale (Chapitre V). Le Chapitre II compare l'écologie de nidification du Pic à dos noir dans les forêts brûlées et non brûlées et évalue l'hypothèse selon laquelle les forêts brûlées constituent des habitats puits pour cette espèce. Afin d'évaluer l'hypothèse source-puits, des nids ont été suivis dans les deux types de forêts et le taux d'accroissement intrinsèque a été estimé dans ces habitats sous divers scénarios d'estimés de survie d'adultes et de juvéniles. Le succès pendant les périodes d'incubation et de nidification, ainsi que le développement des jeunes au nid étaient similaires entre les nids des forêts brûlées et non brûlées. Cependant, les nids dans les forêts brûlées ont produit davantage de jeunes par nid achevé que les nids dans les forêts non brûlées (forêts brûlées : 3,0 ± 0,0 [moyenne ± erreur-type] ; forêts non brûlée : 2,1 ± 0,3). Le taux d'accroissement intrinsèque des populations des forêts brûlées et non brûlées était semblable selon les divers scénarios d'estimés de survie d'adultes et de juvéniles. Les résultats du Chapitre II suggèrent que le Pic à dos noir maintient des populations nicheuses dans les forêts non brûlées à proximité de forêts récemment brûlées et que les deux types de forêts sont comparables dans leur apport à la dynamique des populations. Ainsi, les forêts non brûlées constituent des habitats importants dans la démographie du Pic à dos noir et la dépendance de cette espèce aux forêts brûlées est ambiguë. Le Chapitre III se concentre sur la sélection d'habitat et à évaluer la taille du domaine vital du Pic à dos noir en forêt boréale non brûlée. La sélection d'habitat par cette espèce a été spécifiquement étudiée lors de l'établissement de son domaine vital et la quête alimentaire. Les résultats de ce chapitre indiquent que le Pic à dos noir établit son domaine vital dans des secteurs où des habitats ouverts et de vieilles forêts sont disponibles. Toutefois, lors de sa quête alimentaire, les individus sélectionnent fortement les secteurs dominés par les vieux peuplements de conifères. De plus, les résultats du Chapitre III suggèrent que la distribution spatiale des vieux peuplements de conifères influence l'utilisation de l'espace du Pic à dos noir ; la superficie des domaines vitaux augmente avec la distance médiane entre les peuplements de vieux conifères disponible dans le paysage. Finalement, les résultats de ce chapitre suggèrent que, pour nicher avec succès dans la forêt boréale non brûlée, le Pic à dos noir nécessite un minimum de 35 m^{3} • ha^{-1} de bois mort, lequel était constitué dans l'étude de 40% (14 m^{3} • ha^{-1}) de bois récemment mort. Dans le Chapitre IV, je décris le comportement alimentaire du Pic à dos noir dans la forêt boréale non brûlée et non affectée par une épidémie d'insectes. Il a été observé que le Pic à dos noir s'alimente sur les arbres vivants, les chicots et les débris ligneux au sol et principalement sur le tronc des chicots récemment morts (67,2 %) ayant un diamètre à hauteur de poitrine moyen de 18.3 ± 0.4 cm. Les résultats de ce chapitre suggèrent que le diamètre et le stade de dégradation sont des prédicteurs importants des substrats d'alimentation du Pic à dos noir dans les forêts boréales non brûlées étudiées. Également, le Pic à dos noir s'alimentait davantage par excavation que dans des études en milieux brûlés ou touchés par des épidémies d'insectes. Cette espèce devrait être considérée comme un spécialiste de l'alimentation par excavation, mais les diverses techniques utilisées lors de sa recherche alimentaire en font un oiseau opportuniste qui peut varier ses sources alimentaires. Les résultats de cette thèse montrent que le Pic à dos noir est davantage un spécialiste des habitats associés aux insectes xylophages accessible par excavation qu'un spécialiste strict des forêts brûlées, tel que précédemment suggéré dans la littérature. Les résultats de cette thèse supportent également que les efforts de conservation pour le Pic à dos noir, et par conséquent les autres espèces dépendantes du bois mort récent, devraient prioriser le maintien de blocs intacts de forêts de conifères surannées (affichant un recrutement régulier de bois mort récent) dans le paysage et, devraient favoriser les pratiques sylvicoles irrégulières qui conservent des arbres vivants et morts coniférien ≥18.0 cm, particulièrement dans les pessières noires.

Mots-clés : dynamique source-puits ; survie au nid ; bois mort ; radio-télémétrie ; utilisation de l'habitat ; écologie alimentaire ; utilisateur de cavité ; chicots.

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INTRODUCTION GÉNÉRALE

La forêt boréale constitue le plus vaste biome terrestre au monde. Elle représente près de 32 % de la surface totale des forêts mondiales et environ 58 % du territoire canadien (Burton et al., 2003). Anciennement, la configuration du paysage boréal était principalement modelée par les feux de forêts (Bergeron et al., 2001), qui consument annuellement la superficie moyenne de 2,5 millions d'hectare de forêt au Canada (McRae et al., 2001). La fréquence des feux, leur intensité et l'intervalle entre ceux-ci façonnent la répartition et la configuration des peuplements forestiers (Gauthier et al., 2008a). À plus petite échelle, les épidémies d'insectes, les chablis, les maladies et la sénescence engendrent des taux de mortalité moins sévères que ceux associés aux feux, mais génèrent également une diversité structurale des peuplements et diversifient la composition des espèces forestières (McCarthy, 2001). Toutes ces perturbations naturelles entraînent un renouvellement, total ou partiel, de la couverture forestière des peuplements touchés et créent un apport important d'arbres morts. En outre, ces derniers offrent des habitats à une vaste gamme d'espèces animales et végétales (Thomas, 1979 ; Harmon et al., 1986 ; Grove, 2001).

Avec l'avènement de l'exploitation forestière à grande échelle, la configuration des peuplements s'est vue altérée ; l'exploitation forestière est désormais la perturbation la plus importante en forêt boréale (McRae et al., 2001). Comme elle est généralement pratiquée sous forme de juxtapositions de coupes totales de grande superficie, le paysage exploité présente un rajeunissement de la matrice forestière et une homogénéisation des classes d'âges. Ces caractéristiques contrastent avec la variabilité naturelle associée aux paysages forestiers régulés par des cycles de feux (Bergeron et al., 2001, 2006). En fait, sous une révolution forestière théorique de 100 ans, les peuplements ont une moyenne d'âge de 50 ans et aucun peuplement est plus vieux que 100 ans, alors que sous un régime de feux de même révolution, la moyenne d'âge des peuplements sera la même mais plus de 35% du territoire est occupé par des peuplements âgés de plus de 100 ans. (Gauthier et al., 2008b). Cette différence dans la répartition des classes d'âges est expliquée en partie par la nature stochastique des feux de forêts. À l'échelle du peuplement, le prélèvement systématique des arbres matures lors de l'exploitation forestière engendre une raréfaction des arbres, chicots et débris ligneux de gros diamètres. Par ailleurs, ces éléments représentent des attributs clés, souvent associés aux vieilles forêts, dont dépendent plusieurs espèces dites saproxyliques. Ainsi, la structure végétale et les espèces qui y sont associées diffèrent remarquablement entre les peuplements issus de perturbations naturelles et ceux issus de l'exploitation forestière (Hobson et Schieck, 1999 ; Imbeau et al., 1999 ; Drapeau et al., 2002). Les impacts de l'exploitation forestière sont ressentis à au moins deux échelles distinctes : 1) à l'échelle du paysage par la juxtaposition des aires de coupes et de la raréfaction des vieilles forêts et 2) à l'échelle du peuplement par le prélèvement du bois mort et des arbres de gros diamètre des parterres de coupe. Actuellement, l'exploitation forestière oriente ses pratiques sylvicoles pour favoriser un aménagement écosystémique ; l'objectif principal étant de minimiser l'écart entre les conditions forestières naturelles et celles engendrées par les pratiques sylvicoles dans le but d'atténuer les impacts sur la biodiversité et la productivité des écosystèmes (Vaillancourt et al., 2008). Pour ce faire, il est impératif de connaître les exigences écologiques des espèces sensibles à l'exploitation forestière et les impacts éventuels de cette dernière sur ces espèces.

EXIGENCES ÉCOLOGIQUES DES PICIDAE

La famille des pics (Aves : Picidae) est connu pour ses exigences écologiques particulières. La plupart des espèces de pics sont insectivores et les deux groupes d'insectes les plus largement consommés sont les fourmis et les insectes xylophages (Backhouse, 2005). Les insectes xylophages pondent leurs œufs au niveau de l'écorce des arbres morts ou sénescents au moment où leurs mécanismes de défense naturels sont faibles. Dans cet état, ces arbres dégagent même divers composés chimiques qui attirent ces insectes, par exemple des monoterpènes ou de l'éthanol (Allison et al., 2004). D'autre part, les pics nidifient dans une cavité qu'ils excavent généralement dans des arbres de gros diamètre (Backhouse, 2005), souvent déjà morts. Ainsi, la présence de bois mort récent, d'arbres de gros diamètre et d'une diversité structurelle à l'intérieur des peuplements leurs sont nécessaires (Angelstam et Mikusinski, 1994 ; Mikusinski et Angelstam, 1997 ; Roberge et Angelstam, 2006 ; Virkkala, 2006 ; Roberge et al., 2008). Les pics occupent une place importante dans les écosystèmes forestiers et, en ce sens, ils sont considérés comme des espèces clé de voûte (keystone species ; Paine, 1969) : ils offrent des opportunités de nidification aux utilisateurs secondaires de cavités (nest-web : Martin et Eadie, 1999 ; Martin et al., 2004), des occasions d'alimentation pour certaines espèces par leur excavation (Aubry et Raley, 2002) et peuvent contribuer à la dégradation du bois comme vecteur des champignons (Jackson et Jackson 2004). De plus, à cause de leur susceptibilité aux modifications de leur habitat, les pics peuvent être utilisés comme des indicateurs de la diversité des oiseaux forestiers et également des indicateurs d'autres groupes d'espèces forestières (Mikusinski et al., 2001 ; Roberge et Angelstam, 2006 ; Drever et al., 2008). Il a été observé que le déclin de certaines populations de pics est lié à la perte d'habitat et à la fragmentation (Mikusinski et Angelstam, 1998 ; Imbeau et al.,

2001) ; deux répercussions connues de l'exploitation forestière (Schmiegelow et Mönkkönnen, 2002 ; Hannon et Drapeau, 2005). Dans les pays de l'Europe du Nord, certaines populations de pics ont décliné et d'autres ont disparu des forêts intensivement aménagées (Angelstam et Mikusinski, 1994 ; Mikusinski et Angelstam, 1998 ; Roberge et al., 2008). Roberge et al. (2008) ont observé que l'occurrence des pics à l'échelle du paysage est positivement associée au degré de naturalité des forêts. Le concept de naturalité implique l'intégrité fonctionnelle des écosystèmes et classifie le niveau d'altération anthropique de l'écosystème (Vallauri, 2007). De plus, la présence des pics à l'échelle du peuplement est liée principalement à la quantité de bois mort (Angelstam et al., 2003 ; Bütler et al., 2004 ; Roberge et al., 2008). Or, ce sont les vieilles forêts et les forêts issues de perturbations naturelles qui peuvent offrir les meilleurs apports en bois mort.

LE PIC À DOS NOIR : UNE ESPÈCE BORÉALE

Le Pic à dos noir (*Picoides arcticus*) est une espèce forestière qui s'alimente et niche sur des arbres récemment morts ou sénescents dans la forêt boréale de l'Amérique du Nord (Raphael et White, 1984 ; Goggans et al., 1989 ; Villard et Beninger, 1993 ; Villard, 1994 ; Murphy et Lehnhausen, 1998 ; Powell, 2000 ; Nappi et al., 2003). Son aire de répartition et celle de la forêt boréale de conifères se chevauchent presque intégralement (Figure 1.1 ; Bock et Bock, 1974). Le Pic à dos noir sélectionne principalement des larves d'insectes xylophages (Coleoptera: Buprestidae, Cerambycidae) qu'il extrait en excavant dans le xylème des arbres (Apfelbaum et Haney, 1981 ; Harris, 1982 ; Villard et Beninger, 1993 ; Murphy et Lehnhausen, 1998 ; Powell, 2000 ; Nappi et al., 2003). Il est trouvé majoritairement dans les forêts récemment brûlées mais également dans les vieilles forêts; la densité du Pic à dos noir dans les habitats brûlées peut être jusqu'à 20 fois plus élevée que dans les forêts non brûlées (Bock et Lynch, 1970; Apfelbaum et Haney, 1981; Harris, 1982; Hutto, 1995; Murphy et Lehnhausen, 1998).

Figure 1.1. Aire de répartition du Pic à dos noir (trait oblique '/' vert) et de la forêt coniférienne boréale et montagnarde (trait oblique '\' noir), adaptée de Bock et Bock (1974).

Les habitats récemment brûlés sont caractérisés par une abondance de chicots (presque tous morts simultanément) et une colonisation massive par les insectes xylophages (Murphy et Lehnhausen, 1998 ; Nappi et al., 2003 ; Saint-Germain et al., 2004). Le Pic à dos noir profite de cette abondance d'insectes xylophages en peuplant les forêts brûlées rapidement, normalement dès la première année (Huot et Ibarzabal 2006). Il y demeure sur une période variant de trois à sept ans, soit le temps où persistent ces conditions propices (Hutto, 1995; Murphy et Lehnhausen, 1998; Saab et al., 2007; Vierling et al., 2008), et cela varie, en fonction de l'intensité du feu, des caractéristiques avant-feu des peuplements touchés (Stepnisky, 2003 ; Lentile et al., 2006 ; Koivula et Schmiegelow, 2007 ; Vierling et al., 2008), de même que des espèces d'insectes impliqués dans cette colonisation.

Cette abondante et rapide utilisation des forêts brûlées par le Pic à dos noir a amené les chercheur à le percevoir comme une espèce principalement associée, voire restreinte, aux forêts récemment brûlées qui ne pourrait survivre en l'absence de feux de forêts en région boréale (Hutto, 1995 ; Murphy et Lehnhausen, 1998 ; Hoyt et Hannon, 2002). En ce sens, Hutto (1995) a émit l'hypothèse que les habitats non brûlés représentent des habitats puits pour le Pic à dos noir alors que les forêts récemment brûlées constituent des habitats sources. Théoriquement, un habitat puits est un habitat où la reproduction est insuffisante pour compenser la mortalité locale, mais où ces populations peuvent subsister conditionnellement à une immigration provenant d'un habitat source, là où la reproduction excède la mortalité locale (Pulliam 1988). L'hypothèse de Hutto (1995) provient de la comparaison de densité de Pic à dos noir entre les deux types d'habitats. Or, une différence de densité entre deux habitats ne témoigne pas nécessairement d'un taux de reproduction inégal entre ces habitats. Pidgeon et al. (2006) mentionnent que l'abondance relative d'individus n'est pas un bon indicateur de la qualité d'un habitat et que l'utilisation du succès de reproduction constitue une mesure plus adéquate pour évaluer la qualité d'un habitat au niveau de la population. D'autre part, la détectabilité du Pic à dos noir semble être plus élevée dans les forêts brûlées que dans les forêts non brûlées (Ibarzabal et Desmeules, 2006). Ainsi, un observateur devrait consacrer un effort plus important pour détecter la présence de l'espèce en milieu non brûlé. Toutes les comparaisons entre ces deux habitats sur la base de recensements auditifs (passifs ou actifs) de même durée devraient sérieusement être mis en doute. Ainsi, dans la perspective d'examiner les possibilités de subsistance à long terme du Pic à dos noir en milieu non brûlé, il est impératif d'utiliser une méthodologie adaptée à la détectabilité de l'espèce dans ce milieu.

OBJECTIFS DE L'ÉTUDE ET STRUCTURE DE LA THÈSE

Le Pic à dos noir étant une espèce fortement associée à la forêt boréale, brûlée ou non, ses habitats sont soumis à des modifications importantes, provenant principalement de l'exploitation forestière (Imbeau et al., 1999 ; Hannon et Drapeau, 2005). Cette pression exercée sur l'habitat est importante dans les forêts brûlées (coupes de récupération), mais également dans les forêts non brûlées où ces dernières sont sujettes à l'exploitation forestière. Les coupes de récupération ont un impact négatif sur l'abondance des Pics à dos noir dans les brûlis récents (Koivula et Schmiegelow, 2007 ; Saab et al., 2007) et il est probable que l'exploitation forestière présente également des impacts négatifs sur les populations de Pics à dos noir en forêts non brûlées. Cette thèse vise à documenter la sélection d'habitat du Pic à dos noir dans un paysage boréal aménagé et à évaluer les impacts potentiels de l'exploitation forestière sur les besoins écologiques de cette espèce. L'aire d'étude de ce projet de recherche se situe dans la forêt boréale de l'est du Canada, plus spécifiquement dans le centre du Québec, aux confins de l'exploitation forestière. Dans le paysage étudié, les parterres de coupe et les blocs de forêts résiduelles se juxtaposent, ce qui est caractéristique de la première passe de la coupe en mosaïque. Lors de cette première passe, la forêt résiduelle représente environ 50 % du territoire alors qu'après la deuxième passe (qui est entamée lorsque la régénération des parterres de coupe atteint 3 m de hauteur), la forêt résiduelle devra constituer minimalement 10 % du territoire (MRNF, 2008). L'étude s'est ainsi déroulée dans un paysage boréal avec la première passe de la coupe en mosaïque comme perturbation principale et les feux de forêts comme perturbation secondaire.

Cette thèse est structurée en cinq chapitres : le premier et le cinquième sont respectivement l'introduction générale et la conclusion générale. Les trois autres chapitres constituent le corps de la thèse et sont présentés sous forme d'articles scientifiques indépendants. Le Chapitre II porte sur la reproduction du Pic à dos noir dans les forêts brûlées et non brûlées. Spécifiquement, il présente la caractérisation des besoins pour la nidification du Pic à dos noir en forêt boréale non brûlée et fait la comparaison du succès de reproduction et de la croissance des jeunes au nid entre les forêts brûlées et non brûlées. De plus, ce chapitre évalue l'hypothèse de la dynamique source-puits et le rôle des forêts non brûlées dans la démographie du Pic à dos noir. Les Chapitres III et IV traitent de la sélection de l'habitat du Pic à dos noir dans un paysage exploité de la forêt boréale non brûlée. La sélection de l'habitat par une espèce peut être observée selon un échelonnage hiérarchique. Johnson (1980) identifie un ordre dans le processus de sélection d'habitat d'une espèce donnée lequel s'établit selon quatre échelles : (1) l'aire de répartition de l'espèce, (2) l'établissement du domaine vital des individus, (3) l'utilisation des composantes d'habitat dans le domaine vital et, (4) la sélection alimentaire dans les habitats. Ainsi, le Chapitre III se concentre sur les deuxième et troisième échelles de Johnson (1980) de même que sur l'estimation de la superficie des domaines vitaux de Pic à dos noir et sur la relation du Pic à dos noir avec la quantité de bois mort dans le paysage. Dans le Chapitre IV, la sélection alimentaire à fine échelle est détaillée (échelle 4 ; Johnson, 1980), c'est-à-dire que les substrats d'alimentation sélectionnés et les techniques utilisées par le Pic à dos noir sont caractérisés. De plus, des cibles de *conservation sont présentées.*

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CHAPITRE II

DO UNBURNED FOREST STANDS REALLY CONSTITUTE A SINK FOR BLACK-BACKED WOODPECKERS

RÉSUMÉ

Le Pic à dos noir (*Picoides arcticus*) se trouve en plus grande densité dans les forêts brûlées que les forêts non brûlées et certains auteurs ont émis l'hypothèse que les forêts non brûlées représentent des habitats puits pour le Pic à dos noir. La présente étude, réalisée dans un paysage issu de l'exploitation forestière et de feux de forêts, compare l'écologie de nidification du Pic à dos noir dans les forêts brûlées et non brûlées et évalue l'hypothèse selon laquelle les forêts non brûlées constituent des habitats puits pour cette espèce. Afin d'évaluer l'hypothèse source-puits, des nids ont été suivis dans les deux types de forêts et le taux d'accroissement intrinsèque (λ) a été estimé dans ces habitats sous divers scénarios d'estimés de survie d'adultes et de juvéniles. Le succès pendant les périodes d'incubation et de nidification, ainsi que le développement des jeunes au nid étaient similaires entre les nids des forêts brûlées et non brûlées. Cependant, les nids dans les forêts brûlées ont produit davantage de jeunes par nid achevé (3.0 ± 0.0 [moyenne ± erreur-type]) que les nids dans les forêts non brûlées (2.1 ± 0.3). Le taux d'accroissement intrinsèque des populations des forêts brûlées et non brûlées était semblable selon les divers scénarios d'estimés de survie d'adultes et de juvéniles ($\lambda_{\text{brûlée}} = \lambda_{\text{non brûlée}} + 0.02$). Les résultats de la présente étude suggèrent que le Pic à dos noir maintient des populations nicheuses dans des peuplements non brûlés à proximité de peuplements récemment brûlés. Également, les forêts non brûlées ne sont pas plus des habitats puits que les forêts brûlées. Ainsi, les forêts non brûlées constituent des habitats importants dans la démographie du Pic à dos noir. De plus, le Pic à dos noir pourrait ne pas être un spécialiste des forêts brûlées, tel que précédemment suggéré dans la littérature mais plutôt un spécialiste des habitats associés aux insectes xylophages.

ABSTRACT

The Black-backed Woodpecker (*Picoides arcticus*) occurs at higher densities in burned than in unburned forest stands. This has led to the hypothesis that unburned tracts of forest are a sink for this species. The present study, conducted in boreal forests shaped largely by timber harvesting and wildfire, seeks to compare the breeding ecology of Black-backed Woodpeckers in both unburned and burned stands, and to examine the hypothesis that unburned forest stands constitute a sink habitat. To investigate the source/sink hypothesis, nests were monitored in both stand types, and the finite rate of population increase (λ) was estimated for the two habitat types under diverse survival scenarios. Incubation and nesting successes, and nestling development were similar in unburned and burned stands, but more nestlings fledged from successful nests in burned stands (3.0 ± 0.0 [mean ± standard error]) than from those in unburned stands (2.1 ± 0.3 [mean ± standard error]). The finite rate of increase in unburned and burned stands was similar for the range of adult and juvenile annual survival estimates tested ($\lambda_{burned} = \lambda_{unburned} + 0.02$). The results of the present study suggest that Black-backed Woodpeckers maintain breeding populations in mature / over mature stands within proximity of recent burns, that unburned tracts of forest are not more likely to act as a sink habitat than burned tracts, and that the former are important in the overall demography of the population. This implies that the Black-backed Woodpecker may not be a 'burn specialist', as previously suggested in the literature, but rather a specialist of areas populated by xylophageous insects.

Keywords: Nest survival; sink/source dynamic; boreal forest; cavity-nesting birds; avian reproduction

INTRODUCTION

In the eastern boreal forest, wildfires are frequent and often extensive (Bergeron et al., 2001). These major disturbances play an important role in the boreal ecosystem, and many avian species are closely associated with the habitat that is subsequently created. This is particularly true for cavity-nesting birds, especially during the first five years following the fire (Saab and Powell, 2005). This period coincides with a high density of xylophagous insect larvae (Saint-Germain et al., 2004), which offer abundant foraging opportunities for species such as the Black-backed Woodpecker (*Picoides arcticus*). This species feeds predominantly on the wood-boring larvae of members of the Buprestidae and Cerambycidae (Coleoptera) (Murphy and Lehnhausen, 1998; Nappi et al., 2003).

Black-backed Woodpeckers occur at low densities in unburned forests, and are mainly associated with mature / over mature stands, or those damaged by insect epidemics (Bull et al., 1986; Goggans et al., 1989; Chapitre III). Several authors have stressed the importance of the association between Black-backed Woodpeckers and recently burned forest stands (Hutto, 1995; Murphy and Lehnhausen, 1998; Hoyt and Hannon, 2002). This view is based on studies reporting densities of Black-backed Woodpeckers between 6 and 20 times higher than those in unburned stands (Apfelbaum and Haney, 1981; Harris, 1982; Hutto, 1995). Hutto (1995) hypothesized that Black-backed Woodpeckers in unburned forests are sink populations maintained by birds emigrating from burned stands. Moreover, Murphy and Lehnhausen (1998) suggested that Black-backed Woodpeckers use an 'island-hop' strategy, exploiting one high-quality burn after another and, when recently burned habitats are scarce, 'survive' in unburned forests until recently burned stands become available (Murphy and Lenhausen, 1998; Hoyt and Hannon, 2002). This suggests that unburned forests are only important to Black-backed Woodpeckers at times when suitable recently burned forests are unavailable (Murphy and Lehnhausen, 1998; Saab and Dudley, 1998; Hoyt and Hannon, 2002). Because of this view, the practice of post-fire salvage logging has been strongly criticized, as it is perceived as eliminating potential optimal habitat for this species (Hannon and Drapeau, 2005).

Despite the assumptions outlined above, little information exists regarding the nesting ecology of Black-backed Woodpeckers in burned (but see Saab and Dudley, 1998; Saab et al., 2004, 2007; Vierling et al., 2008) and unburned habitats (but see Goggans et al., 1989; Bonnot et al., 2008). Theoretically, lower foraging opportunities in unburned forest stands could reduce the amount of food delivered to nestlings, so increasing inter-nestling competition (Hadow, 1976). This could result in a lower nestling growth rate and, ultimately, nestling death. Nesting success is highlighted as one of the key indicators of habitat quality (Pidgeon et al., 2006). Furthermore, nesting success and survival in recently burned and unburned forest stands is considered important in determining source/sink dynamics for this species (Murphy and Lehnhausen, 1998). To test the assumption that unburned stands are sink habitat for Black-backed Woodpeckers, we hypothesised that the potentially lower food availability in unburned forest stands would result in nests with a smaller clutch size, a reduction in nestling growth-rate and a lower number of fledglings, compared to nests in burned forest stands.

To the best of our knowledge, this is the first study to compare the breeding ecology of Black-backed Woodpeckers in burned and unburned forests. The objectives were to: (1) define nest characteristics of this species in unburned forest stands, (2) compare breeding success and nestling growth in burned and unburned stands, and (3) test the hypothesis that unburned forest stands are a sink for this species.

METHODS

Study area

Field work was conducted from May to July over three breeding seasons (2004-2006). Two study areas approximately 170 km apart were used: one near St-Thomas-Didyme (48° 59'N, 73° 03'W), which included a 2003 burn of 6,500 ha, and one 200 km north-west of Lac Saint-Jean, Québec (50° 34'N, 72° 10'W; hereafter referred to as the Rivière Daniel site), which included a 2005 burn of 36,000 ha. Both areas were within the black spruce (*Picea mariana*)-moss forest of the Canadian boreal forest ecological domain (Saucier et al., 1998). The stands were composed mainly of black spruce, or black spruce mixed with jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*) and, occasionally, tamarack (*Larix laricina*). The topography was undulating and forest fires were the major natural forest disturbance, although smaller areas were affected by spruce budworm (*Choristoneura fumiferana*) outbreaks. Commercial timber harvesting began during the last decade and the area was logged using mosaic harvesting, which favoured an interspersion of logged and residual forested blocks in the landscape. Even-aged management (cut with protection of regeneration and soil, CPRS) was practiced in the southern part of the study area and uneven-aged management (cut with protection of small merchantable trees, CPSMT) in the northern part.

We followed nests in burned and unburned forest stands. However, because habitat quality and Black-backed Woodpecker densities decreases rapidly in post-burn sites (Hutto, 1995; Murphy and Lehnhausen, 1998; Vierling et al., 2008) due to a decline in the densities of beetle larvae three to four years after fire (Saint-Germain et al., 2004), we monitored breeding success in 2004 in the St-Thomas-Didyme area burn (2003 burn), and breeding success and nestling growth in 2006 in the Rivière Daniel area burn (2005 burn). Breeding success and nestling growth were monitored in unburned forests in the Rivière Daniel area in all three years of the project.

Trapping and tracking

Trapping and tracking methods differed between habitat types. In burns, transects were established and playbacks of the Black-backed Woodpecker's rattle call (employed against conspecifics (Dixon and Saab, 2000)) was used to attract individuals. Nest cavities were located by visual observation. In unburned forests, birds were located using roadside surveys with playbacks of 20 min (or less if detection occured) of calls and drumming of Black-backed Woodpeckers (Ibarzabal and Desmeules, 2006). Playback stations were established at 1 km intervals along major roads, which allowed sampling of habitat types in proportion to their availability. However, burned areas and a 2 km buffer zone surrounding them, were not sampled. Woodpeckers were captured using mist nets and individuals showing signs of breeding (i.e., presence of a brood patch) were fitted with a radiotransmitter (2.3 g, Model PD-2, Holohil Systems Ltd., Carp, Ontario) that was attached at the base of the two central rectrices. The released birds were followed to locate their nests. Transmitter batteries lasted between 8 and10 weeks.

The location of each nest was marked using flagging tape at a distance > 3 m from the nest tree. Nest location coordinates were recorded using a global positioning system (GPS Garmin Legend, Garmin Coporation, Olathe, Kansas). To obtain nestling growth data, an inspection hole was drilled approximately 5 to 8 cm below the cavity entrance using an 18 V wireless drill equipped with a 10 cm hole saw. This procedure allowed clear access to nestlings and the block of wood that was removed was used to create a weatherproof door (see Ibarzabal and Tremblay (2006) for further details). Only cavities at < 3 m were opened.

Nest characteristics

The characteristics of each nest tree in unburned stands were recorded. As only one Black-backed Woodpecker nest was located in a live tree, this nest was removed from the analysis. Nine physical characteristics of the snags that could influence nest selection (Raphael and White, 1984; Bull et al., 1986; Goggans et al., 1989) were measured. These were: (1) species, (2) height, (3) diameter at breast height (dbh), (4) decay stage (see Table 2.1), (5) condition of the top (intact or broken), (6) percentage of bark cover, (7) cavity-hole height, (8) orientation of the cavity-hole (corrected for true north), and (9) diameter at cavity-hole. Snag height was measured with a clinometer, and dbh with a tree-calliper. Other available snags were sampled in 0.04 ha circular plots (one for every 20 ha of home range area) randomly distributed within each Black-backed Woodpecker home range. The same characteristics were recorded for these snags as for the nest snags, with the exception of cavity-hole height and cavity-hole aspect.

Breeding success and nestling growth

Where possible, nests were visited every two days until the nestlings fledged or the nest failed; any loss of eggs or nestlings was noted. Because of logistical problems, some nests were checked every three days. In addition, in 2005, the forest fire in the Rivière Daniel area prevented nest visits for four days. When nest cavities were higher than 3 m, nestlings were observed using a wireless camera mounted on a telescopic pole (Dudley and Saab, 2003) and only breeding success data were collected.

The nestlings used for the biometric study were identified using a spot of nail varnish on one of the claws; this provided each individual with a unique colour code until it was large enough to be banded. The sex of nestlings was determined using the yellow feathering on the crown, which is less extensive and paler in females, but as it is difficult to clearly distinguish sex of Black-backed Woodpecker nestlings (Pyle, 1997) we did not consider it in our analysis . Five growth parameters were recorded during the three week period in the nest: (1) body mass to the nearest 0.1 g, using a digital balance (Ohaus model CS200); (2) tarsus length and (3) culmen length to the nearest 0.01 mm, using a digital calliper (Mitutoyo model CD-6B); and (4) wing length (the distance from the anterior surface of the radiocarpal joint to the tip of the longest primary) and (5) length of the medial tail feather to the nearest 1 mm, using a wing ruler. All manipulations were done according to Authorized animal care committee approvals (No 0351, 0564 and 0668) issued by the Université du Québec à Chicoutimi.

Statistical analyses and source-sink assessment

Correlation analyses were performed on the six characteristics taken for nesting and available snags to identify and remove highly correlated characteristics (Pearson $r > 0.70$). Snag height was correlated with dbh and was eliminated. The five variables retained for use in logistic regressions were: dbh, decay class, top condition, bark cover and species. A stepwise logistic regression (PROC LOGISTIC; SAS Institute, 2008) was used to examine the influence of snag characteristics on nest selection. Independent variables were entered or removed from the model at the 0.05 significance level using Wald's test. Comparative use of snag species was analysed with the Kruskal-Wallis test, and the orientation of cavity-holes was compared with a random circular distribution using Rayleigh's test (Zar, 1999).

Nest success was calculated using Johnson's (1979) method (modified from Mayfield, 1961, 1975) to correct for biases attributable to unequal periods of nest observations, and to include the standard error of the success estimator (maximum likelihood estimator). Hence, estimated daily survival rates and overall nesting success were compared between burned and unburned forest stands with 95 % confidence intervals (CI) (Johnson, 1979). Non-overlapping confidence limits for estimates of daily survival rates and overall nesting success indicate significant differences in survival between burned and unburned stands. Nests that fledged at least one young were considered successful. Mayfield estimates of daily survival do not account for partial nest losses (i.e., a nest fledging one young is scored the same as a nest fledging four young – both are scored as successful). To calculate the overall nesting success, we assumed that the median length of the nestling period from hatching to the end of the nestling period was 24 days (Dixon and Saab, 2000). For uncertain nest fates, the exposure period was considered to end on the last day that a given nest was known to be active (a visit with at least one young in the nest). In contrast, for successful and unsuccessful nests, the exposure period ended at the midpoint between the last day the nest was observed to be active and the first day the nest was observed to be inactive ('Last-Active-B' approach (Manolis et al., 2000)). Because nest success rates can vary between nesting stages, the daily rate of success and overall nesting success were calculated separately for the incubation and nestling stages.

Only data from nestlings that survived to fledging were used for the analyses of nestling growth. We worked on mean nest value of each parameters by pooling nestling data. Nestlings were measured at each visit providing a mixed longitudinal sample (Ricklefs, 1983). To analyze growth, growth parameters were investigated using logistic, von Bertalanffy and Gompertz curves (Ricklefs, 1967). The growth constant (K_L) and the $t_{10\text{-}90}$ value (the time a chick required to grow from 10 % to 90 % of its asymptotic size) were determined. These are considered the most useful parameters for comparing growth rates (Ricklefs, 1967; Bradley et al., 1984). The determination of the asymptote is a subjective procedure, which is influenced by the duration over which data are obtained. As the increase in body mass was not continuous (it plateaued between day 16 and day 18 in this study (day 0 being hatching) and sometimes dropped for a few days before resuming), the analysis was restricted to the day corresponding to 90 % of the asymptote. No limit was placed on determining asymptotes for other body characteristics, except for tail length that did not reach asymptote and was not included in subsequent growth rate analysis. We compared growth parameters between both habitats by calculating mean and 95 % CI for nests in unburned forest stands, and using the only nest monitored for nestling growth parameters in burned forests to provide threshold values (Scherrer, 2007). A significant difference was observed when growth parameter values of burned forest nestlings were not included in the 95 % CI of unburned forests nestlings. The relationship between tail length and nestling age was analyzed by using linear regression.

The source/sink status of the study populations was determined using the Pulliam (1988) model:

$$\lambda = P_{AF} + P_{JF}\,\beta$$

where λ is the finite rate of population increase, P_{AF} is the rate of adult female survival, P_{JF} is the rate of juvenile female survival from fledging to the next breeding season, and β is the number of female offspring per female per year. A value of $\lambda \leq 0.95$ indicates a sink population, $\lambda \geq 1.05$ a source population, and $0.95 < \lambda < 1.05$ a stable population. Following the procedure of Robles et al. (2007), female survival was used because the number of females ultimately limits population growth. We calculated the mean number of female offspring per female per year, based on the number of female offspring per successful nest. Renesting frequency and the production of multiple broods may bias estimates (Anders and Marshall, 2005); however, these have not been observed in Black-backed Woodpeckers (Dixon and Saab, 2000). Data on the adult and juvenile survival rate of Black-backed Woodpeckers are unavailable, therefore we used the range of survival estimates that Saab and Vierling (2001) developed for Lewis's Woodpecker (*Melanerpes lewis*), *i.e.* by using plausible range of survival estimates. We used a range of four annual adult survival values (minimum: 0.59, medium 1: 0.62, medium 2: 0.68, maximum: 0.75) and three annual juvenile survival values (lowest: 0.35, mean: 0.46, highest: 0.57). These adult survival ranges fit the relationship between survival rate and clutch size established by Wiebe (2006) for woodpeckers. In this relationship, an adult survival rate between 0.55 and 0.70 is realistic when the clutch size reaches 3.9, like the one found in the present study for Black-backed Woodpecker. The number of female offspring per female per year (β) was determined by our nest survey in burned and unburned stands.

All statistical tests were carried out using SAS 8.0 (SAS Institute, 2008), with the exception of Rayleigh's test, which was done using the R 2.7.1 software (R Development Core Team, 2008). The values given are means ± SE unless otherwise stated. Differences were considered significant at $P < 0.05$. As there were no significant differences in the studied parameters between years ($P > 0.05$ for all), the data were pooled for the comparison tests.

RESULTS

During the three-year study, 18 nests were found in unburned forests (9 in cut stands and 9 in old coniferous stands) and 38 in burned forests. In the Rivière Daniel burn, the largest of the two, the nearest nest found in unburned forest was about 8 km from the edge of the burn.

Nest characteristics in unburned forests

Nest cavities were all in dead trees (snags) ($n = 17$), except one that was in a live jack pine (dbh, 23.1 cm; height, 11.6 m; top intact). The mean dbh of cavity snags (23.8 cm ± 1.1 cm) was greater than the mean dbh of other available snags (12.4 cm ± 0.2 cm; Table 2.2) in the home range. The smallest nest cavity snag was in a black spruce with a dbh of 17cm. Jack pine was the preferred nest cavity tree species, black spruce was used proportionally to its availability and balsam fir was not used (Table 2.2). The mean cavity snag height was 7.8 ± 1.1 m and the cavity-holes were situated at a mean height of 5.0 ± 0.7 m above ground level. The mean diameter at the cavity hole was 19.3 ± 0.6 cm. Aspect of cavity entrances was 112 ± 27°(east) and differed from a random circular aspect distribution ($z = 0.65$, $P < 0.001$, $n = 18$).

Breeding success

During the incubation stage, daily nest survival rate (burned: 0.959 [CI = 0.879 – 1.039]; unburned: 0.984 [CI = 0.953 – 1.015]), overall nesting success (burned: 0.558 [CI = 0.165 – 1.712]; unburned: 0.802 [CI = 0.512 – 1.238]), percentage of nests predated ($Z = -0.609$, $P = 0.2714$, $n_{burned} = 3$, $n_{unburned} = 7$) and clutch size ($Z = 1.143$, $P = 0.1265$, $n_{burned} = 2$, $n_{unburned} = 6$), did not differ between burned and unburned stands (Table 2.3). A red squirrel (*Tamiasciurus hudsonicus*) predated one nest in an unburned stand and Tree Swallows (*Tachycineta bicolor*) usurped two nests during the incubation stage, one in a burned stand and one in unburned stand. During the nestling stage, daily nest survival rate (burned: 0.972 [CI = 0.949 – 0.995]; unburned: 0.984 [CI = 0.968 –

0.999]), overall nesting success (burned: 0.505 [CI = 0.288 – 0.877]; unburned: 0.681 [CI = 0.463 – 0.997]) and percentage of nests predated ($Z = -0.5683$, $P = 0.2849$, $n_{burned} = 24$, $n_{unburned} = 16$), did not differ between burned and unburned stands (Table 2.3). However, the number of fledglings per successful nest was higher in burned (3.0 ± 0.0) than unburned stands (2.1 ± 0.3; $Z = 1.8208$, $P = 0.0343$, $n_{burned} = 4$, $n_{unburned} = 10$).

Nestling growth

All growth parameters measured best fitted logistic curves, with the exception of tail length, which best fitted a linear regression (unburned: $r^2 = 0.9821$, slope = 4.5151, intercept = - 28.862; burned: $r^2 = 0.9947$, slope = 4.8085, intercept = -36.774) (Figure 2.1). Two nests were monitored in burned forest but one failed. The development pattern of nestlings in the only nest in the burned forest for which biometric measurements were taken, fell within the range of that of nestlings in unburned stands (Figure 2.1). All analysed growth parameters of nestlings in the burned stand nest also fell within the CI of those from nests in unburned stands, except for the tarsus asymptotic size (A) that was lower than the CI of nestlings in unburned stands (Table 2.4).

Source-sink assessment

The average number of female offspring produced by every adult female per breeding season (β) was 0.715 in unburned forests and 0.758 in burned forests (Table 2.3), and the ratio of male to female nestlings was 1:1. Among the 12 survival scenarios offered by the range of values of adult and juvenile survival estimates (see Methods section), four scenarios in unburned forest stands and three in burned stands had

λ values of < 0.95, suggesting sink habitat (Table 2.5). Three scenarios in unburned stands and four in burned stands had λ values > 1.05, suggesting source habitat. Finally, both habitat types had five scenarios of stable populations ($0.95 < \lambda < 1.05$; Table 2.5). The relationship between burned and unburned λ was relatively constant in the range of juvenile survival rate covered here, with $\lambda_{burned} = \lambda_{unburned} + 0.02$.

DISCUSSION

This study provides new information about Black-backed Woodpecker breeding ecology and the role of unburned forests in its demography. In eastern unburned boreal forest stands, Black-backed Woodpeckers preferentially nest in tall, large-diameter, solid, jack pine snags with broken tops, and the cavity entrance is oriented east. Incubation and nesting successes, and nestling development were similar in unburned and burned stands, but nests in burned stands produced more young per successful nest than those in unburned stands. The finite rate of population increase in unburned and burned habitats reacted similarly to the range of adult and juvenile annual survival estimates tested. Our results suggest that unburned stands are not more likely to be sink habitats than burned stands, and that they are important in the demography of Black-backed Woodpeckers.

Nest characteristics in unburned forests

Most of the nests found in unburned stands (either in mature / over mature forest or recent cuts) were in a more open part of the home range. This result supports the findings of others studies within mature / over mature forests that suggest that Black-backed

Woodpeckers use more open, drier sites (Goggans et al., 1989; Mohren, 2002). Black-backed Woodpeckers nested in larger snags than those typically available in their home range; however, the other physical characteristics of the snags were similar. The results of the present study show that dbh is the best predictor of snag use by nesting Black-backed Woodpeckers in unburned areas within the eastern boreal forest. Although Black-backed Woodpeckers are known to nest in relatively small snags compared to other cavity nesters (Raphael and White, 1984; Saab and Dudley, 1998; Dixon and Saab, 2000; Mohren, 2002), Raphael and White (1984) showed, using an adjusted mean diameter for tree species, that, of the cavity nesting bird species tested, the Black-backed Woodpecker exhibits the strongest preferences for nest tree diameter. However, our mean nest snag dbh cannot be compared to values reported in western North America, where mean tree height and snag dbh are larger. In our study area, snags ≥ 20 cm represent only 10.1 % of the available snags and snags ≥ 30 cm, only 0.3 % (Chapitre IV). Moreover, in the eastern boreal forest, the smallest snag sizes occur in black spruce stands (Vaillancourt et al., 2008). Similarly to Raphael and White (1984), the results of the present study show that Black-backed Woodpeckers select the largest snags available. The availability of large snags may limit nesting of this species in burned and unburned stands in the eastern boreal forest where trees have a mean dbh < 17 cm.

The present study supports the findings that Black-backed Woodpeckers often excavate their nests in solid snags (primarily in decay classes 4 and 5) (Raphael and White, 1984; Goggans et al., 1989; Saab and Dudley, 1998; Dixon and Saab, 2000). However, in the present study, they also used >20 cm dbh mid-term decayed snags (decay class 6), which are quite abundant in the eastern boreal forest region of Québec, (Vaillancourt et al. 2008).

In the present study, Black-backed Woodpecker cavity entrance holes were oriented toward the east. This supports the findings of Harris (1982); however, in a study by Goggans et al. (1989), entrance holes were randomly oriented. An eastern orientation maximises exposure to the sun, which may be an advantage early in the day. The selection of nest snags in more open stands (Goggans et al., 1989) may also increase sun exposure. Nests of the Acorn Woodpecker (*Melanerpes racemosa*) and Northern Flicker (*Colaptes auratus*) also tend to be oriented towards the warmest average temperatures (Hooge et al. 1999; Wiebe 2001). At night, temperatures in central Québec can drop below 0°C during the breeding season (May to July) (Environment Canada, 2008). Therefore, orientation of the nest entrance towards the rising sun could induce a rapid temperature increase in the cavity during the coldest period of the day. Furthermore, as prevailing winds in central Québec are typically from the northwest (Environment Canada, 2008), an eastern orientation of the cavity entrance would reduce wind exposure.

Breeding success and nestling growth

Daily survival rates and overall nesting success were similar in unburned and burned forest stands, but successful nests in burned stands produced more young. Daily survival rates were comparable to those recorded in a four years study by Vierling et al. (2008) of Black-backed Woodpeckers at a site after fire, which ranged from 0.982 to 0.995. The overall nesting success of Black-backed Woodpeckers in a range of habitats (i.e., burned, mixed, and unburned forests) was > 0.60 (Goggans et al., 1989; Dixon and Saab, 2000; Bonnot et al., 2008; Vierling et al., 2008). However, Saab et al. (2007) report overall nesting success ranging from 0.30 to 0.95 in recent to late (≤ 12 years) unlogged burned stands in Idaho and Bonnot et al. (2008) report overall nesting success as low as 0.44 in mountain pine beetle (*Dendroctonus ponderosae*) outbreak forests in South Dakota. In the present study, overall nesting success in burned stands was relatively low (0.558) for nests in a one-year-old burn. Because there was a longer period between nest visits in burned forests, this resulted in the larger CI for survival estimates in this habitat type.

The mean number of fledglings per successful nest in burned and unburned stands was higher than the average of 1.7 (range 1.6 - 1.8) reported by Dixon and Saab (2000) and those reported by Bonnot et al. (2008; 2.0 youngs per nesting attempt in 2004 and 1.2 in 2005). Although the average mean for unburned stands was slightly higher than the above values, the average in burned stands was considerably higher. In the present study, data for burned stands is exclusively from one-year-old burns, which have been shown to have the highest insect biomass (Saint-Germain et al., 2004). This would result in greater foraging opportunities in burned stands and may explain why these stands produced more fledglings per successful nest than unburned forest stands, even though clutch sizes were similar. In the present study, the parent birds delivered food to the first nestling encountered (results not shown). Since food is presented from above, smaller or weaker nestlings that were unable to reach as high as their siblings would have received less food, leading to inter-nestling competition and selection (Hadow, 1976). This selection pressure was probably higher in unburned stands and resulted in the lower number of young per successful nest. However, contrary to our hypothesis, this pressure did not appear to affect fledgling growth; no differences in growth rate were observed between burned and unburned stands. However, this may be due to a bias introduced by the fact that only one nest was monitored in burned habitat. Further studies are needed to confirm or disprove these results.

The percentage of nests predated was similar in both stand types and was comparable to the predation rate (27.9%; 17 predation events on 61 nests) reported by Bonnot et al. (2008). Lower predator pressure has been advanced as one of the reasons favouring nest site selection in burned stands (Vierling et al., 2008). In a study done by Saab and Vierling (2001), the authors concluded that unburned habitats serve as a source habitat for nest predators. This is further supported by the observations of Fisher and Wilkinson (2005), who noted that higher densities of sciurids (squirrels) were found in unburned habitat, where forage and cover were more abundant. The results of the present study partly support these conclusions. Of the nests predated, one nest predator and one nest competitor was observed. In an unburned stand, a red squirrel predated one nest and Tree Swallows usurped two nests during the incubation stage, one in a burned stand and one in an unburned stand. While mammalian predator pressure might be higher in unburned forests (Saab and Vierling, 2001; Saab et al., 2004), the results from this study suggest that nest competition is similar in both stand types. More detailed studies are needed to clarify predator and competition pressures on this species in burned and unburned stands.

Source-sink assessment

The twelve scenarios evaluated (three juvenile survival estimates • four adult survival estimates (Table 2.5)) indicated a similar λ for burned and unburned tracts of forest. Survival estimates for adults and juveniles greatly influence λ values. Hairy Woodpeckers (*Picoides villosus*), like Black-backed Woodpecker, are known to positively respond to fire (Raphael et al., 1987; Hobson and Schieck, 1999; Covert-Bratland et al., 2006; Saab et al., 2007) and their annual adult survival probability varies from 0.524 to 0.807, with 0.807 being the estimate for the northeast region (Michel et al., 2006). If we substitute this value into the equation for Black-backed Woodpecker, the value of λ is generally ≥ 1 in both stand types, independent of annual juvenile survival. If this was the case, both burned and unburned stands would be source habitats. However, annual juvenile survival of Black-backed and Hairy Woodpecker are unknown. Robles et al. (2007), reviewed a number of woodpecker studies and found that juveniles tended to experience survival rates that were often half that of adults. To correctly reply to the question concerning source/sink habitats, further studies are needed to determine the survival rates of adult and juveniles in burned and unburned stands.

Demography of Black-backed Woodpecker

The number of sightings (data not shown) and the nest discovered in an unburned stand ≤ 8 km from a burn boundary, indicates that Black-backed Woodpeckers do maintain breeding populations in mature / over mature stands, even in close proximity to recently burned tracts of forest. Hoyt and Hannon (2002) only observed Black-backed Woodpeckers in old growth forests at > 75 km from burns. The authors suggested that

Black-backed Woodpeckers leave unburned stands to take advantage of higher food and nest site availability in recent adjacent burns. However, even if some individuals may have moved from unburned to burned stands, the general results of the present study do not support these authors' assumption. It is also possible that the difference between the two studies is due to differences in the methods used to detect woodpeckers. Hoyt and Hannon (2002) diffused playbacks of calls and drumming for 20 sec in each of the four cardinal directions (which may not have been long enough (Ibarzabal and Desmeules, 2006)), while the present study used similar playbacks, but for 20 min (or less if detection occurred). The argument for burn selection by Black-backed Woodpecker is not clear. Even if burned stands represent higher foraging opportunities (Murphy and Lehnhausen, 1998; Powell, 2000; Nappi et al., 2003), some individuals still selected unburned stands over burned ones. Black-Backed Woodpecker habitat quality in burned forest stands is quite variable, being related to pre-fire forest characteristics (e.g., tree size, tree density and slope), fire severity and time since fire (Stepnisky, 2003; Lentile et al., 2006; Koivula and Schmiegelow, 2007; Vierling et al., 2008). The results of the present study allow us to hypothesize that if a given habitat presents sufficient foraging opportunities for nesting, be it burned or unburned, it will be selected, even if foraging opportunities are theoretically more densely distributed in burned areas.

The existing Black-backed Woodpecker sink/source hypothesis is supported by presence/absence data, and nest density in burned and unburned forests (Hutto, 1995; Murphy and Lehnhausen, 1998; Hoyt and Hannon, 2002). However, the relative abundance of adults and nest density are not good indicators of population level habitat quality (Pidgeon et al., 2006). For individuals, nest success is an adequate measure of habitat quality, but for populations, nest success and nest density considered together provides the best indicator (Pidgeon et al., 2006). Our results suggest that at the individual level, habitat quality of burned and unburned stands is similar ($\lambda_{burned} = \lambda_{unburned} + 0.02$). However, at the population level, habitat quality of recently burned stands may be higher than unburned stands due to the higher nest density (Saab et al., 1998; Dixon and Saab, 2000; Saab et al., 2004; Saab et al., 2007). Key considerations that must be taken into account when considering source/sink scenarios are the number of years that a burned tract of forest represents a source habitat, and how fire distribution in the landscape and dispersal processes regulate the demography of Black-backed Woodpeckers. The results of this study suggest that Black-backed Woodpecker demography should not be considered on a source/sink basis because the pulse of individuals coming from recently burned forests may not be significant over a longer time scale (e.g., decades). On such time scales, burns would have to be extremely productive to compensate for the habitat loss following a wildfire. Burns are suitable habitat for Black-backed Woodpeckers for a relatively short time period (Saab and Powell, 2005) and then are unsuitable until stands present senescence characteristics that produce recently decayed dead wood (> 120 years in black spruce stands (Imbeau et al., 1999)). The definition of sources and sinks based on local production of new individuals may be too simplistic a view (Reid et al., 2006); further data are needed to fully resolve this question (i.e., adult and juvenile survival rates, emigration and predation).

Recently burned and unburned tracts of forest should be considered similarly important for Black-backed Woodpecker at the landscape scale. Black-backed Woodpeckers may not be the 'burn specialist' as suggested before (Hutto, 1995; Murphy and Lehnhausen, 1998; Dixon and Saab, 2000; Hoyt and Hannon, 2002), but rather a specialist of areas populated by xylophageous insects (especially members of the Cerambycidea, Buprestidae and Scolytidae). Perhaps habitat selection by this species should be considered on a scale of beetle larvae density (Powell, 2000; Mohren, 2002), as it responds opportunistically to beetle increases created by wildfire and insect outbreaks (Blackford, 1955; West and Speirs, 1959; Apfelbaum and Haney, 1981; Yunick, 1985). We therefore support the recommendation of Koivula and Schmiegelow (2007), who suggested that the 'natural spectrum' of forested habitat should be maintained in boreal landscapes, which includes a mosaic of burned patches and mature / over mature stands with sufficient dead wood volume for foraging and nesting.

Study limitations

This study was limited by the lack of previous information regarding the demography, adult and juvenile survival rates, nest predation and dispersal rates for Black-backed Woodpeckers. The study was further limited by the spatial configuration of available and accessible early post-fire habitats (one-year-old burns). Only one nest was monitored in burned habitat for nestling growth and this limited our comparison between both habitats. Furthermore, Black-backed Woodpeckers occurred in low densities in mature / over mature forests, resulting in small sample sizes and low statistical power. However, we believe that our results identify important issues that deserve further study.

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Table 2.1. Characteristics used to determine different standing tree decay classes (live trees: 1-3; dead trees: 4-8) (modified from Tyrrell and Crow, 1994; Bergeron et al., 1997).

Class	Standing tree characteristics		
	Leaves	Bark	Top and height
Live trees			
1.	≥ 95%	100%	intact
2.	20 < x < 95%	> 90	intact
3.	< 20%	> 75%	intact
Dead trees			
4.	present but dead	present	intact
5.	absent	> 50 %	intact
6.	absent	< 50 %	broken
7.	absent	absent	broken, height > 50%
8.	absent	absent	< 2 m

Table 2.2. Characteristics of snags used for nesting by Black-backed Woodpeckers and other available snags in home ranges in unburned boreal forest stands in central Québec. Results are significant at the 0.05 level.

Characteristics	Cavity snags (n = 17)		Available snags (n = 747)		χ^2	p
	Mean (median)	S.E. (range)	Mean (median)	S.E. (range)		
Diameter at breast height	23.8	1.1	12.4	0.2	29.71	< 0.001
Decay class	(6.0)	(3.0-7.0)	(6.0)	(4.0-8.0)	0.49	0.993
Bark cover	(9.0)	(2.0-10.0)	(9.0)	(0.0-10.0)	0.03	0.864
Snag height	7.8	1.1	4.6	0.1	-	-
Top condition (% intact)	6.3	6.3	22.2	1.5	0.61	0.434
Tree species (%)						
Black spruce	70.6		78.5		0.55	0.459
Jack pine	29.4		5.4		15.00	< 0.001
Balsam fir	0.0		14.3		2.74	0.098
Others	0.0		1.9		0.32	0.575

Table 2.3. Mean daily nest survival rates (CI = 95 %), mean overall nesting success (CI = 95 %) and the percentage of nests predated by breeding stages, and the number of young per successful nest (± SE) in unburned and burned boreal forest stands in central Québec. Different letters indicate significant differences ($P < 0.05$, Wilcoxon test), numbers in bracket represents sample size, exposure days for the incubation stage are: burned = 24.5 and unburned = 64; and exposure days for nestling stage are: burned = 214 and unburned = 252.

	Daily survival rate	Overall nesting success	% of nests predated	Young per successful nest*
Incubation				
Unburned	0.984 (0.953-1.015) [7]	0.802 (0.512-1.238)	14 (1 of 7)	3.8 ± 0.1
Burned	0.959 (0.879-1.039) [3]	0.558 (0.165-1.712)	33 (1 of 3)	4.0 ± 0.0
Nestling				
Unburned	0.984 (0.968-0.999) [16]	0.681 (0.463-0.997)	25 (4 of 16)	2.1 ± 0.3^{b} [10]
Burned	0.972 (0.949-0.995) [24]	0.505 (0.288-0.877)	25 (6 of 24)	3.0 ± 0.0^{a} [4]

* : In incubation stage: number of hatched young per successful nest, and in nestling stage: number of fledged young per successful nest.

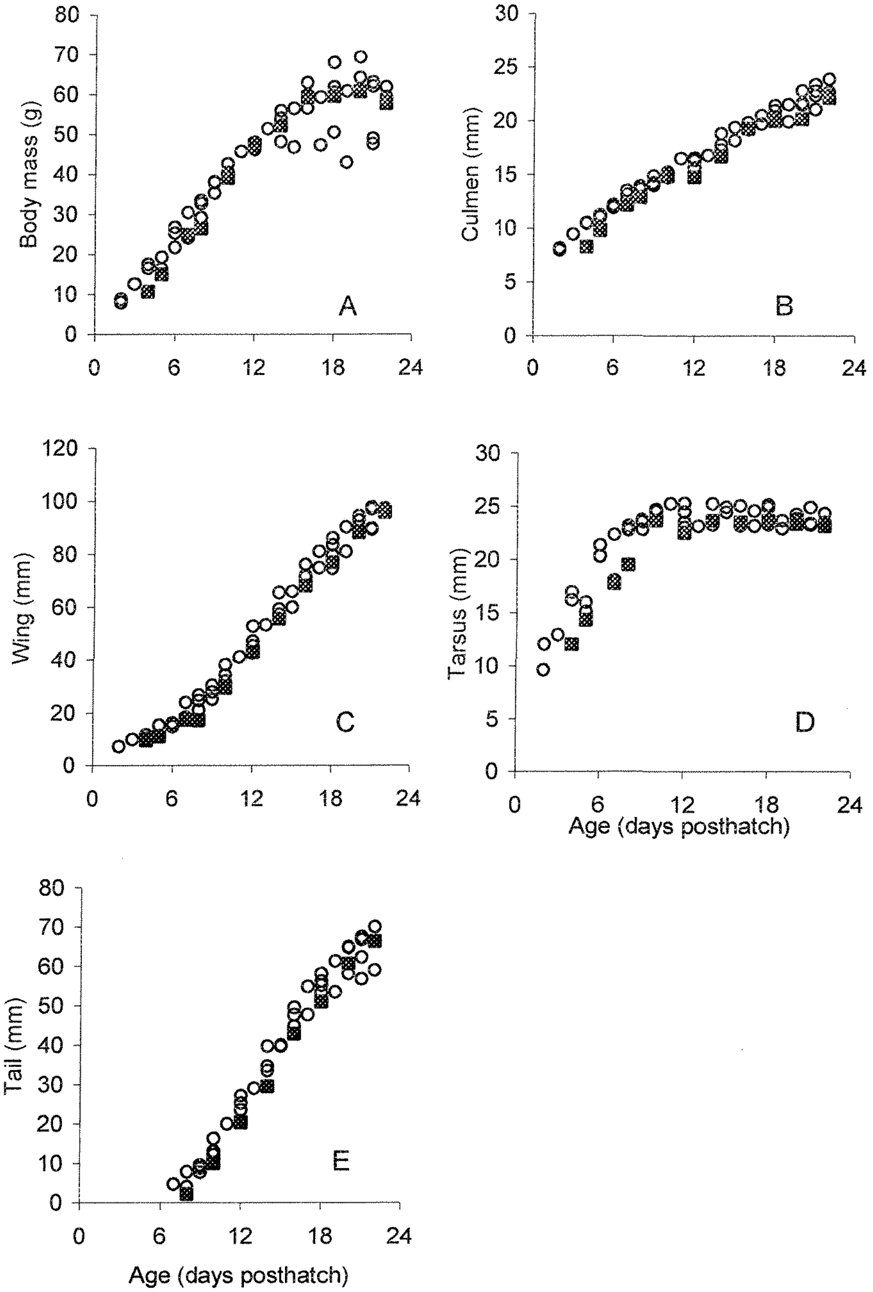

Figure 2.1. Nestling body mass (A), and culmen (B), tarsus (C), wing (D), and tail (E) length, as a function of age in nestlings of five nests in unburned forest stands (open circles) and one nest in a burned forest stand (black square).

Table 2.4. Asymptotic size (A), growth constant (k), growth period between 10% and 90% of asymptotic size (t_{10}-t_{90} in days), and coefficient of determination (r^2) of body mass (g), culmen, tarsus and wing length (mm) of nestlings from five nests (nestling mean values/nest; 13 nestlings) in unburned forest stands and one nest (nestling mean values; 3 nestlings) in a burned forest stand. All values were determined by logistic curves and are expressed as means (95% CI).

Habitat type	*A*	*k*	t_{10}-t_{90}	r^2
Unburned				
Body mass	60.8 (52.1 - 69.5)	0.381 (0.275 - 0.500)	12.3 (8.8 - 15.4)	0.955
Culmen	22.3 (21.3 - 23.2)	0.284 (0.247 - 0.320)	15.8 (14.0 - 17.6)	0.974
Tarsus	24.9 (24.1 - 25.8)	0.687 (0.391 - 0.919)	7.4 (4.0 - 11.7)	0.917
Wing	95.1 (88.7 - 101.6)	0.354 (0.324 - 0.387)	12.5 (11.0 - 13.8)	0.987
Burned				
Body mass	60.7	0.404	10.9	0.963
Culmen	22.1	0.253	17.4	0.938
Tarsus	23.9	0.745	5.9	0.933
Wing	96.0	0.372	11.8	0.989

Table 2.5. Finite rate of population increase (λ) in burned and unburned boreal forest stands in central Québec, based on four estimates of annual adult survival and three estimates of annual juvenile survival.

Habitat type	Annual juvenile survival	Annual adult survival			
		Lowest (0.59)	Med. 1 (0.62)	Med. 2 (0.68)	Highest (0.75)
Unburned	Lowest (0.35)	0.84	0.87	0.93	1.00
	Mean (0.46)	0.92	0.95	1.01	1.08
	Highest (0.57)	1.00	1.03	1.09	1.16
Burned	Lowest (0.35)	0.86	0.89	0.95	1.02
	Mean (0.46)	0.94	0.97	1.03	1.10
	Highest (0.57)	1.02	1.05	1.11	1.18

CHAPITRE III

HABITAT REQUIREMENTS OF BREEDING BLACK-BACKED WOODPECKER (*PICOIDES* ARCTICUS) IN MANAGED, UNBURNED BOREAL FOREST

Tremblay, J.A., J. Ibarzabal, C. Dussault, and J.P. Savard. 2009. Habitat requirements of breeding Black-backed Woodpecker (*Picoides arcticus*) in managed, unburned boreal forest. *Avian* Conservation and Ecology - Écologie et conservation des oiseaux 4(1): 2. [online] URL: http://www.ace-eco.org/vol4/iss1/art2/

RÉSUMÉ

Nous avons étudié les caractéristiques du domaine vital et la sélection de l'habitat chez le Pic à dos noir (*Picoides arcticus*) en forêt boréale non brûlée et aménagée par coupes en mosaïque, au Québec (Canada). La sélection de l'habitat a été tout particulièrement examinée afin de déterminer le domaine vital et les activités liées à l'alimentation chez cette espèce. Nous avons émis l'hypothèse selon laquelle le Pic à dos noir réagirait à la récolte de bois en modifiant la taille de son domaine vital selon la quantité de bois mort accessible. Vingt-deux oiseaux ont été suivis à l'aide de la télémétrie et des estimations fiables de la taille du domaine vital ont été obtenues pour sept individus nicheurs (six mâles et une femelle). La taille moyenne du domaine vital a été évaluée à 151,5 ± 18,8 ha (moyenne ± erreur-type ; étendue : 100,4–256,4 ha). Nos résultats indiquent que cette espèce établit son domaine vital là où des milieux ouverts et des milieux forestiers sont accessibles. Toutefois, au moment de s'alimenter, les individus sélectionnent préférablement les endroits où dominent les peuplements de vieux conifères. Les travaux ont également montré que la répartition spatiale des îlots d'habitat préférés pour l'alimentation du pic influence l'utilisation de l'espace : la taille du domaine vital augmente en fonction de la distance médiane entre les îlots de vieux conifères accessibles dans le paysage. Enfin, les résultats indiquent que le Pic à dos noir peut nicher avec succès en forêt non brûlée s'il y a un volume de bois mort d'au moins 35 $m^3 \cdot ha^{-1}$, dont 42 % (15 $m^3 \cdot ha^{-1}$) est en début de décomposition.

ABSTRACT

We investigated home-range characteristics and habitat selection by Black-backed Woodpeckers (*Picoides arcticus*) in an unburned, boreal forest landscape managed by mosaic harvesting in Quebec, Canada. Habitat selection by this species was specifically examined to determine home-range establishment and foraging activities. We hypothesized that Black-backed Woodpeckers would respond to harvesting by adjusting their home-range size as a function of the amount of dead wood available. Twenty-two birds were tracked using radiotelemetry, and reliable estimates of home-range size were obtained for seven breeding individuals (six males and one female). The average home-range size was 151.5 ± 18.8 ha (range: 100.4–256.4 ha). Our results indicate that this species establishes home ranges in areas where both open and forested habitats are available. However, during foraging activities, individuals preferentially selected areas dominated by old coniferous stands. The study also showed that the spatial distribution of preferred foraging habitat patches influenced space use, with home-range area increasing with the median distance between old coniferous habitat patches available within the landscape. Finally, these data show that Black-backed Woodpeckers may successfully breed in an unburned forest with at least 35 $m^3 \cdot ha^{-1}$ of dead wood, of which 42% (15 $m^3 \cdot ha^{-1}$) is represented by dead wood at the early decay stage.

Keywords: cavity-associated species management; dead wood; foraging ecology; habitat use; radiotelemetry

INTRODUCTION

The boreal forest is a dynamic ecosystem where natural and anthropogenic disturbances shape the landscape (Bergeron et al. 2001, 2002). Forest fires are the main source of natural disturbance in this biome, with millions of hectares of forest being consumed annually in Canada (Girardin et al. 2008). However, timber harvesting has recently become the main perturbation in this ecosystem (McRae et al. 2001). In harvested landscapes, a proportion of old-growth forest is being replaced by younger stands (Drapeau et al. 2005), which are characterized by a lower volume of dead wood (Darveau and Desrochers 2001). Furthermore, the distribution of harvested areas in the landscape alters the abundance and distribution of dead wood and is likely to influence movement patterns and space use by primary cavity-nesting species such as woodpeckers (*Picoides* spp.) (Pasinelli 2000, Pechacek 2004), which rely on decaying wood for foraging and nesting (Backhouse 2005). Significant changes in the abundance of primary cavity nesters could have a knock-on effect on various species of birds and mammals that are secondary users of tree cavities (Martin and Eadie 1999, Martin et al. 2004). Examples of species that regularly use woodpecker cavities in the eastern Canadian boreal forest include the Eastern Bluebird (*Sialia sialis*), Tree Swallow (*Tachycineta bicolor*), and red squirrel (*Tamiasciurus hudsonicus*).

There are relatively few primary cavity nesters in the conifer-dominated boreal forest of Canada, the most abundant being the American Three-toed Woodpecker (*Picoides dorsalis*) and Black-backed Woodpecker (*Picoides arcticus*). These species depend on snags at the early decay stage for foraging and nesting (Raphael and White 1984, Goggans et al. 1989, Villard and Beninger 1993, Villard 1994, Imbeau and Desrochers 2002b). American and European Three-toed Woodpeckers (*Picoides* *tridactylus*) are associated with old-growth spruce (*Picea* spp.) stands (Virkkala 1987, Imbeau et al. 1999), but the importance of mature and overmature forests in the ecology of Black-backed Woodpeckers is still unclear (Raphael and White 1984). Although many authors have associated Black-backed Woodpeckers with recent post-fire stands (Hutto 1995, Murphy and Lehnhausen 1998, Powell 2000), this may reflect the fact that most of the recent studies on this species have been conducted in these habitats (Murphy and Lehnhausen 1998, Nappi et al. 2003, Dudley and Saab 2007, Koivula and Schmiegelow 2007, Saab et al. 2007, Nappi and Drapeau 2009), and little information is available from mature and overmature forest stands (Goggans et al. 1989). Goggans et al. (1989), in one of the few studies dealing with the ecology of American Three-toed and Black-backed Woodpeckers in unburned forests, found that Black-backed Woodpeckers in lodgepole pine (*Pinus contorta*) forests in Oregon positively selected mature and overmature stands, and avoided younger stands and logged areas. As a result of this study, the authors recommended that the Black-backed Woodpecker, rather than the American Three-toed Woodpecker, be used as an indicator species for mature and old-growth lodgepole pine stands (Goggans et al. 1989). Studies on sympatric American Three-toed and Black-backed Woodpeckers in unburned forest stands have shown that Black-backed Woodpeckers use larger and less decayed trees than American Three-toed Woodpeckers (Bull et al. 1986, Villard 1994). Black-backed Woodpeckers appear to be old-growth dependent and more abundant than American Three-toed Woodpeckers in the eastern boreal forest (Thompson et al. 1999, Setterington et al. 2000) and could, therefore, serve as an indicator species in this forest type. The Black-backed Woodpecker occurs almost exclusively in ≥80-year-old forest stands and appears to be sensitive to the dead-wood removal typical of modern forestry (Thompson et al. 1999). Information about habitat and space use by, and the resilience of, Black-backed Woodpeckers in managed boreal forests is lacking, but is of primary importance in assessing the impact of large-scale forestry on this species, and on secondary cavity users in the eastern boreal forest of Canada. This is especially true given that forestry is now the dominant disturbance factor in the boreal forest and occurs in most parts of Black-backed Woodpecker's distribution range.

We investigated home-range characteristics and habitat selection of Black-backed Woodpeckers in unburned forest stands in order to identify quantitative targets for habitat management. Because of the Black-backed Woodpecker's association with recently decayed dead wood for nesting and foraging (Raphael and White 1984, Bull et al. 1986, Goggans et al. 1989, Murphy and Lehnhausen 1998), we hypothesized that its occurrence would be negatively influenced by timber harvesting. More specifically, we predicted that: (1) Black-backed Woodpeckers would establish their home range in old coniferous stands and avoid cut stands, (2) they would select old coniferous stands for foraging, and (3) their home-range size would be related to the amount of dead wood available, with home ranges shrinking as dead-wood volume increases. Our results provide information that should favor the conservation of this saproxylic species in landscapes shaped by modern forestry practices.

METHODS

Study Area

The study area, within the black spruce–feathermoss forest of the Canadian boreal forest ecological domain (Saucier et al. 1998), covered 650 km^2 and was located 200 km northwest of Lac Saint-Jean, Quebec, Canada (50° 34'N, 72° 10'W: 200–650 m a.s.l.: Fig. 3.1). Forest stands were composed mainly of black spruce (*Picea* *mariana*) or black spruce mixed with jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and aspen (*Populus tremuloides*), with a scattering of tamarack (*Larix laricina*). Forest fires were the major natural disturbances, followed by spruce budworm (*Choristoneura fumiferana*) outbreaks. Commercial timber harvesting and forest management at this latitude began in the last decade and the study area was logged using a mosaic harvesting regime, which resulted in logged and residual forested blocks interspersed over the landscape (Fig. 3.2). Even-aged stand management (cutting with regeneration and soil protection, CRSP) techniques were practiced in the southern part of the study area and uneven-aged stand management (cutting with little merchantable tree protection, CLMTP) in the northern part.

Trapping and Radio Tracking

Black-backed Woodpeckers were located from mid-May to mid-June in 2005 and 2006 using roadside surveys with playbacks of conspecific calls and drumming (Ibarzabal and Desmeules 2006). Playback stations were systematically established at 1-km intervals along major roads, which allowed habitat types to be sampled in proportion to their availability within the study area. Burned areas and a 2-km buffer zone around them were not sampled. Woodpeckers were captured using mist nets, and individuals showing evidence of breeding (i.e., presence of a brood patch) were fitted with a tail-mounted radiotransmitter (2.3 g; Model PD-2, Holohil Systems Ltd, Carp, Ontario) attached at the base of the two central rectrices. Transmitter batteries lasted about 8–10 weeks and the birds were followed from the hatching period up until the chicks fledged (i.e., 4–5 weeks). An individual that fledged at least one young was defined as a breeder.

Birds were located using the homing method (Mech 1983) with TRX-2000S radio receivers (Wildlife Materials, Murphysboro, Illinois) and three-element Yagi antennas. Individual woodpeckers were tracked at different times of the day to prevent bias related to cyclic behavior. For logistical reasons, we tried to alternate half days of data collection between woodpeckers wearing transmitters to collect data in both periods of the day (for instance, a woodpecker tracked before noon was tracked the next time after noon). Individuals were approached to within 10 m to establish visual or aural contact without disturbing them or, alternatively, to estimate location (± 5 m). The latter was recorded using hand-held GPS units (GPS Legend, Garmin Corp., Olathe, Kansas; ± 10 m) and the bird's behavior was classified as foraging or not foraging. When the bird flew, the observer tried to follow it to record further location points. The birds continued their normal activities as long as observers kept a >3-m distance. We considered consecutive location data points to be spatially independent if >100 m apart (Pechacek and Oleire-Oltmanns 2004). The breeding cavity was considered as a single independent location, and to avoid undue influence on home-range size, no other location data points were taken within a 100-m radius (Pechacek 2004).

Assessment of Home-Range Size and Habitat Selection

Individual home ranges were calculated with Range VI software (Kenward et al. 2003), using all independent locations (foraging or not) and the minimum convex polygon method (100% MCP; Hayne 1949). Although the MCP method can include unused areas and has been criticized (White and Garrott 1990, Powell 2000, Kenward 2001), it is an appropriate method to assess the composition of home ranges in terms of habitat type (i.e., habitat availability at a given home-range scale). In contrast, the Kernel estimator performs poorly when there are relatively few location points available

(Worton 1989), tending to break the home range into several parts, which does not allow a suitable description of the habitat matrix at the landscape scale. Furthermore, for management purposes, we feel that the MCP provides a suitable estimate of the area of boreal forest required by an individual Black-backed Woodpecker. The MCP size was estimated for individuals for which the relationship between home-range size and number of locations reached an asymptote ($n = 8$; seven breeders and one non-breeder) (Seaman et al. 1999). For habitat-selection analyses, only breeding individuals were considered [landscape (n = eight home ranges; the seven breeders indicated above plus another breeder for which the relationship between home-range size and number of locations did not reach an asymptote) and home-range scales (n = 128 foraging locations)]. The study-area boundaries were determined by creating a 4-km buffer zone (1 km playback carrying distance plus 3 km potential bird displacement) on both sides of the roads traveled during capture operations (Fig. 3.1). This was based on previous observations of Black-backed Woodpeckers up to 3 km from their roadside capture location (J.A.T. and J.I., unpublished data). The study area differed slightly between 2005 and 2006, and habitat maps were updated to incorporate disturbances (i.e., fires and logging; data provided by AbitibiBowater Inc.) that occurred between the two consecutive field seasons.

Habitat selection of Black-backed Woodpeckers was examined at two spatial scales to assess the possibility of hierarchical selection. At the larger scale, hereafter referred to as the landscape scale, habitat composition within home ranges was compared with that of random home ranges (second-order selection; Johnson 1980). At the smaller scale (home-range scale), habitat at telemetry locations used during their foraging activities was compared with habitat found at random locations within individual home ranges (third-order selection; Johnson 1980).

To assess habitat selection at the landscape scale, habitat composition (proportion of habitat types) within breeding woodpecker home ranges was compared with that of a control home range per individual (eight observed and eight random home ranges). The latter were randomly positioned within the study area (translation and rotation). To determine the composition of observed and random home ranges, these were overlaid onto digitized habitat layers. ArcView Geoprocessing Wizard (Environmental Systems Research Institute (ESRI) 1996) was used to clip habitat types within home-range boundaries and calculate their proportions. At the home-range scale, habitat use was assessed using only locations when individuals were classified as foraging, and availability was assessed by drawing one random location per observed location within each Black-backed Woodpecker home range. This provided a total of 128 observed and 128 random locations. Habitat types were established using 1:20 000 forest maps published by the Quebec Ministry of Natural Resources in 1992. These maps provide accurate information when conducting a simple classification based on cover type and stand age (Potvin et al. 1999, Dussault et al. 2001). Predominant habitat types in the study area were barren lands, defoliated stands (windthrows and spruce budworm outbreak stands), young (<90 years old) and old (>90 years old) coniferous stands, and recent (<5 years old) and old (>5 years old) cuts. Fragstats 3.3.5 (McGarigal et al. 2002) was used to calculate the median distance between each patch and the nearest neighboring patch of the same habitat type, based on the center-to-center distance (McGarigal et al. 2002), to characterize the distribution of habitat patches within each home range.

Sampling Dead Wood

Snag abundance was estimated on circular plots (0.04 ha) randomly distributed within the different home ranges. One plot was sampled for every 20 ha of home-range area and habitat types within woodpecker home ranges were sampled in proportion to their availability. The number of fallen logs were counted along three 20-m transects starting at 1 m from the plot center (Böhl and Brändli 2007). For snags and logs with a diameter at breast height (dbh) >5 cm, species, decay class, snag dbh and height, and log length and dbh at the line/log intersection point were recorded (Table 3.1). For snags that were severely leaning, an angle of 45° was used as the cutoff between a snag and a fallen log (Harmon and Sexton 1996). Log volume was calculated for each habitat type following Böhl and Brändli (2007). Even if Black-backed Woodpeckers showed a preference for snags, we noted that they were feeding on logs 20% of the time in the same study area (Tremblay et al., unpublished data). For this reason, we combined the volume of snags and logs in two categories: “all dead wood” and “dead wood at the early decay stage.” The latter included classes 1 and 2 for snags and logs (Table 3.1).

Statistical Analysis

Habitat selection was assessed at the landscape and home-range scales using resource selection functions (RSF). We used mixed-effects logistic regressions (PROC GLIMMIX; SAS Institute 2008) that allowed us to consider the non-independence between repeated measurements on the same individuals (i.e., observed and random data). We used individual ID as random factor and the proportion of the following habitat types within each woodpecker home range as variables to model habitat selection at the landscape scale: barren lands, young (<90 years old) and old (>90 years old) coniferous stands, recent (<5 years old) and old (>5 years old) cuts. At the home-range scale, we also used woodpecker ID as random factor but instead used the proportion of telemetry locations falling within the abovementioned habitat types as independent variables. Threshold-independent receiver operating characteristic curves (ROC, calculated using Glimmroc macro developed by Liu and Wu 2003) were used to assess regression model performance (Zweig and Campbell 1993). The ROC curve depicts sensitivity (proportion of true positives correctly predicted) and specificity (proportion of true negatives correctly predicted) pairs for the entire threshold range (Manel et al. 2001). It is generated by plotting sensitivity over one specificity. The area under this curve (AUC) provides an accurate measure of model performance. An AUC of 0.5 indicates that a model predicts no better than by chance, whereas an AUC of 1.0 indicates the model can perfectly distinguish between observed and random sites. Linear regression was used to examine the influence of dead wood on home-range size.

Statistical analyses were conducted using SAS version 9.1 (SAS Institute 2008) and effects with $p \leq 0.05$ were considered to be significant. Unless otherwise stated, the data shown are means ± 1 SE.

RESULTS

During the 2 years of the study, 38 Black-backed Woodpeckers were captured in unburned forests. Of these, 22 were fitted with radio transmitters. Signals were obtained from 17 birds and of those, four lost their radio transmitters. A sufficient number of locations were obtained to assess the home-range size of eight woodpeckers (i.e., the relationship between home-range size and number of locations reached an asymptote): seven breeders and one unsuccessful female (clutch failed to hatch). The average number of independent locations was 36 per bird (range: 28–50; n = 7). Mean home-range size was 151.5 ± 18.8 ha (range: 100.4–256.4 ha; n = 7) for successfully breeding woodpeckers. The home-range size of the bird that made an unsuccessful nesting attempt was 385.8 ha.

Old coniferous stands and recent cuts were the most abundant habitat types in the home ranges of breeding Black-backed Woodpeckers, each accounting for nearly a third of the area (Fig. 3.3). In contrast, defoliated stands and old cuts were almost absent (Fig. 3.3). At the landscape scale, woodpeckers non-significantly selected areas with a high proportion of recent cuts to establish their home range (Table 3.2).

Black-backed Woodpeckers foraged mostly in old coniferous stands and were never observed foraging in defoliated or in old cut stands (Fig. 3.4) and they also avoided recent cuts at the home-range scale (Table 3.2).

Habitat types differed greatly in terms of total volume of dead wood and volume of dead wood at the early decay stage (Table 3.3). Globally, old coniferous stands supported the highest volume of dead wood, snags, and fallen logs, whereas barren lands exhibited the lowest total dead-wood volume and recent cuts exhibited the lowest amount of dead wood at the early decay stage. The amount of dead wood was highly variable between sample sites in young and in old coniferous stands (Table 3.3).

No relationship was found between total dead-wood volume ($\beta j = -0.0302$; t-value = -0.41; r2 = 0.0323; p = 0.6999) or that at the early decay stage ($\beta j = 0.0093$; t-value = 0.28; r2 = 0.0157; p = 0.7890) and Black-backed Woodpeckers home-range size (n = 7). However, the median distance between the nearest old coniferous habitat patches influenced home-range size (βj = 0.2325; t-value = 2.23; r2 = 0.4987; p = 0.0761). Thus, home-range size tended to increase with distance between old coniferous habitat patches.

The home ranges of breeding woodpeckers contained more than 35 m3 • ha-1 of decayed dead wood and the mean dead-wood volume per home range was 42.4 ± 3.2 m3 • ha-1 (n = 7; Table 3.4). Dead wood at the early decay stage was abundant in home ranges, with a mean volume of 18 ± 1.4 m3 • ha-1 (Table 3.4). Snags represented approximately half of the volume of dead wood, the mean snag volume per home range was 19.8 ± 2.7 m3 • ha-1, of which 9.4 ± 1.4 m3 • ha-1 were snags at the early decay stage (Table 3.4).

DISCUSSION

This study provides new information on Black-backed Woodpeckers, with landscape management implications for this little-studied keystone species of the boreal forest. Although the results obtained were for a relatively small sample size (eight home ranges of breeding individuals), provided insight into habitat selection of breeding birds in unburned tracts of forest. This species established home ranges in areas with both open and forested habitats, but during foraging activities, patches of old coniferous forests were preferentially selected. No relationship was found between the amount of dead wood available and home-range size for successfully breeding Black-backed Woodpeckers in unburned boreal forest stands. However, the spatial distribution of the preferred foraging habitat (old conifer patches) seemed to influence the home-range size.

Home-Range Size

To the best of our knowledge, this study is the first to document foraging behavior and habitat use of the Black-backed Woodpecker in unburned, non-beetle-killed forests of North America. The home ranges described by Goggans et al. (1989) in beetle-killed lodgepole pine stands within commercial mature to overmature forests in Oregon, were similar to those described in the present study (*n* = 7) but slightly larger in size (mean = 174.7 ha, range = 72 - 328 ha, *n* = 3). Most locations recorded by Goggans et al. (1989) and subsequently used to estimate home-range size were taken after the young had fledged or after failed nesting attempts. In contrast, location points in this study were recorded between hatching and fledging. A recent study on European Three-toed Woodpeckers showed that this species increases home-range size after the chicks fledge (Pechacek 2004). Because we expect Black-backed Woodpeckers to behave in a similar manner, the mean home-range area of 151.5 ha estimated in our study should be considered as the minimum area required by this species during the breeding season, and probably on an annual basis in unburned tracts of eastern boreal forests. This assumption is further supported by the larger home range (385.8 ha) of the single non-breeding individual followed in the study.

Habitat Selection

At the landscape scale, Black-backed Woodpeckers tended to establish their home ranges in areas with a high proportion of recent cuts (*n* = 8; Fig. 3.3). This was unexpected, as many authors have reported Black-backed Woodpecker nests to be associated with areas of high tree or snag density (Raphael and White 1984, Saab and Dudley 1998, Saab et al. 2002). However, 51% of the Black-backed Woodpecker nests (*n* = 35) located by Goggans et al. (1989) were in logged stands. This supports the findings of the present study, where they were often observed nesting in recent cuts (Tremblay et al., unpublished data). Most of the latter originated from CLMTP that left some large snags suitable for nesting. The study area was characterized by an interspersion of large residual forest blocks, half of which were composed of old coniferous habitat and harvested areas. Given the dominance of old conifer stands in the landscape, the major limiting factor influencing Black-backed Woodpecker home-range establishment may have been the availability of suitable open nesting habitat, rather than the availability of foraging habitat. This factor might explain the observed tendency toward selecting recent cuts within the landscape for home-range establishment.

At the home-range scale, Black-backed Woodpeckers foraged in old coniferous stands and avoided recent cuts. This species is known to preferentially forage on recently decayed coniferous species (Raphael and White 1984, Goggans et al. 1989, Murphy and Lenhausen 1998, Nappi et al. 2003). We found that old coniferous stands offered about 30 $m^3 \cdot ha^{-1}$ of dead wood at the early decay stage. By contrast, this figure dropped to < 9 $m^3 \cdot ha^{-1}$ in recent cuts. In our study area, Black-backed Woodpeckers were regularly observed to nest in recent cuts and travel to nearby old coniferous patches to forage. Among the individuals tracked, only one regularly foraged in a recent cut, but this contained a large number of fallen logs (J.A.T., personal observation). Black-backed Woodpeckers are known to respond opportunistically to insect outbreaks and forest fires (Bent 1939, Blackford 1955, West and Speirs 1959, Baldwin 1968, Bock and Bock 1974, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002), but our results show that they can also obtain sufficient resources in undisturbed stands with relatively high volumes of dead wood to successfully breed in unburned and non-epidemic landscapes.

Dead-Wood Available in Home Range

Pechacek (2004) observed that European Three-toed Woodpeckers adjust home-range size depending on the amount of dead wood available. However, in our study, Black-backed Woodpeckers did not adjust home range size according to the amount of dead wood or dead wood at the early decay stage (mostly available in old coniferous stands). Nevertheless, it was estimated that the home range of breeding Black-backed Woodpeckers contained more than 35 $m^3 \cdot ha^{-1}$ of dead wood, with an average of 42% (15 $m^3 \cdot ha^{-1}$) being at the early decay stage. This is a relatively large share considering that dead wood is at the early decay stage for a much shorter period of time than the older decay stages (i.e., stages 4 and 5: Vanderwel et al. 2006). Vaillancourt et al. (2008) observed that snags present a dome-shaped distribution across the decay class, with a maximum density occurring in decay class 6. Other authors have calculated minimum dead-wood values to determine the presence of woodpeckers in the landscape. For example, in Switzerland Bütler et al. (2004) found a 95% probability of presence of European Three-toed Woodpeckers in forests containing 15 $m^3 \cdot ha^{-1}$ of standing dead wood (snags) over 100 ha. In the same study (Bütler et al. 2004), but for Sweden, this figure dropped to 6 $m^3 \cdot ha^{-1}$. In deciduous forests in Poland, White-backed Woodpeckers (*Dendrocopus leucotus*) were found to require approximately 8 to 17 $m^3 \cdot ha^{-1}$ snags over 100 ha (Roberge et al. 2008). In our study, snags alone represented approximately half the dead-wood volume, so Black-backed Woodpeckers appeared to require a similar volume of standing dead wood as the two abovementioned species. Note that in our study area, Black-backed Woodpeckers were feeding on logs 20% of the time (Tremblay et al., unpublished data), suggesting that dead logs are important resources in addition to snags. Snag and log volume should be combined to adequately present dead-wood requirements of Black-backed Woodpecker in unburned boreal forest.

No relationship was found between Black-backed Woodpecker home-range size and dead-wood volumes, but this does not mean that the volume of dead wood in the landscape did not affect home range. In fact, that home-range size increased with the median distance between the nearest old coniferous patches. Dead wood is patchily distributed, which is reflected by the high variability around the mean value obtained. Foraging individuals were also observed to repeatedly visit the same dead-wood patches, while showing no interest in other apparently similar patches within their home range (J.A.T., personal observation). It is possible that Black-backed Woodpeckers need a threshold dead-wood volume before they will forage in a given patch. When such suitable foraging patches are abundant in the landscape, home-range size would be expected to be smaller than in landscapes where they are scarce—even though the total dead-wood volume available in the two ranges may be the same. This is supported by the fact that individuals were observed to concentrate their foraging activities at specific sites while flying over apparently "uninteresting stands." At the other extreme, when suitable foraging patches are abundant and close to each other, such as following a recent forest fire, home ranges may be as small as 6.9 ha (A. Nappi, personal communication). A better assessment of food availability for each dead-wood decay class would probably provide a more accurate parameter to explain home-range size of this species in unburned forest. However, additional data are required.

CONCLUSION

This study was conducted in a landscape shaped by the first phase of a mosaic harvesting approach under which approximately 50% of the available forest area was harvested, leaving interspersed logged and residual forest blocks. This configuration appears to provide suitable habitat for the two major ecological needs of Black-backed Woodpeckers: foraging and nesting. However, during the second phase of harvesting, the remaining old coniferous stands will be removed as soon as 10 years after the first phase or when the regeneration reaches 3 m if this height is not reached after 10 years (MRNF 2009). Therefore, in the medium-term, such landscapes are likely to be uninteresting for this species of woodpecker due to a reduction in food availability caused by the removal of old coniferous sites and the reduction of nesting sites caused by the rarity of suitable nesting snags in remnant stands. Even if woodpeckers persist in forest remnants (Imbeau and Desrochers 2002a), we would expect densities and breeding success to decrease.

The results of this study show that Black-backed Woodpeckers can successfully forage and breed in unburned forest that comprises a mix of habitat types, including areas managed under mosaic harvesting regime. Under such conditions, we estimate the required home range for a successful breeding pair of Black-backed Woodpeckers to be approximately 150 ha, of which roughly 56 ha must be old coniferous forest (following Fig. 3.3). The lowest dead-wood volume found in a home range with successful breeding was 35 $m^3 \cdot ha^{-1}$, where the average of dead wood at the early decay stage was 15 $m^3 \cdot ha^{-1}$ (42% of the mean dead-wood volume). Although further studies are needed to determine the threshold of dead-wood volume and use relative to prey availability, we suggest that a conservative management approach for Black-backed Woodpecker should target the above values, where about half of the dead-wood volume consists of standing dead wood. We agree with the suggestion of St.-Laurent et al. (2008) concerning the importance of maintaining blocks of mature closed-canopy forest in managed landscapes until regenerating stands have reached a height that reflects the structural attributes of mature forests, or through an entire logging rotation period. Because of the dependence of Black-backed Woodpeckers on recently dead wood, forest management for this species based on the above target values may be expected to benefit other saproxylic species in the boreal forest. Therefore, as suggested by Goggans et al. (1989) for mature and old-growth lodgepole pine stands in Oregon, we propose the use of Black-backed Woodpecker as an indicator species, not only in recently burned stands (Hannon and Drapeau 2005), but also in mature and overmature coniferous stands in northeastern North America.

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Figure 3.1. Habitat configuration, observed home ranges, and study area boundaries located 200 km northwest of Lac Saint-Jean, Quebec, Canada. The study-area boundaries were determined by creating a 4-km buffer zone (1 km playback carrying distance plus 3 km potential bird displacement) on both sides of the roads traveled during capture operations (different in 2005 and 2006).

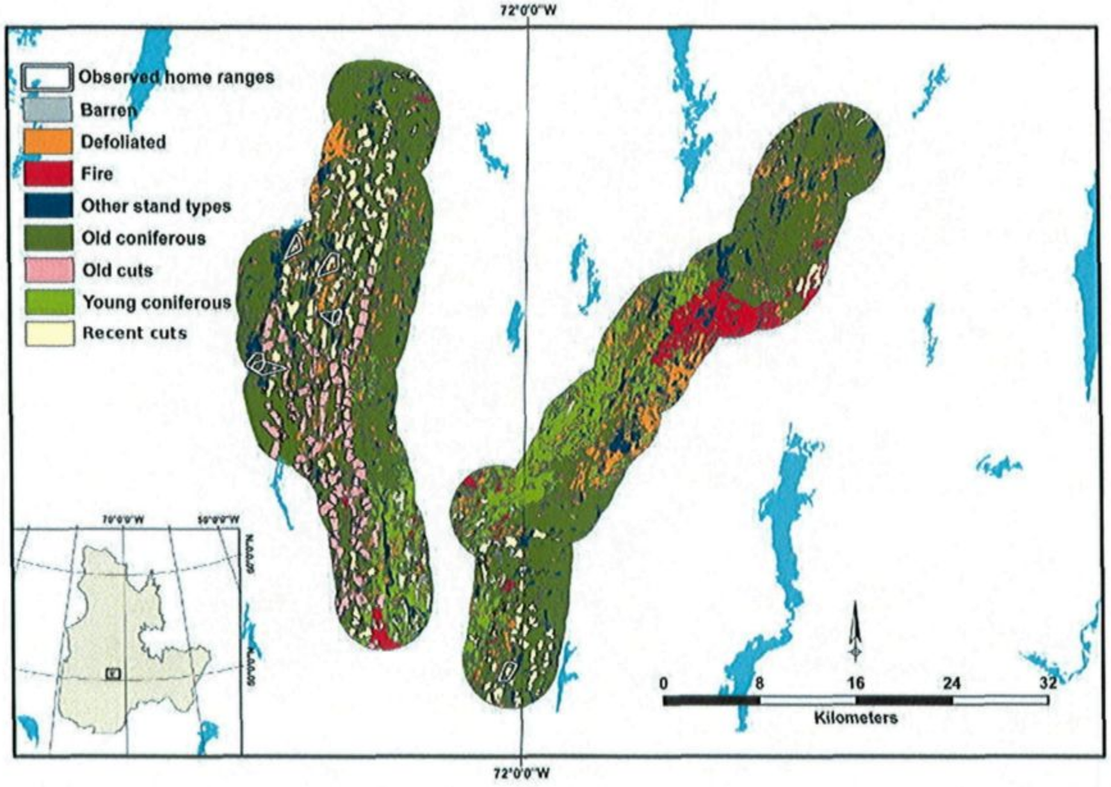

Figure 3.2. Example of interspersed landscape of logged and residual forested blocks after the first pass of the mosaic harvesting regime in the study area.

Table 3.1. Decay classes (1-5) for fallen logs and snags (modified from Tyrrell and Crow, 1994; Bergeron et al., 1997).

Class		Fallen log characteristics			Snag characteristics		
		Leaves	Wood	Shape and form	Leaves	Bark	Top and height
1.	Recent	present	solid	round	present	present	intact
2.	Solid	absent	solid	round	absent	> 50 %	intact
3.	Solid-decayed	absent	solid/punky	round/oval	absent	< 50 %	broken
4.	Decayed	absent	punky	oval, form retained	absent	absent	broken, height > 50%
5.	Very Decayed	absent	punky	± oval, collapsed	absent	absent	< 2 m

Figure 3.3. Habitat composition (mean ± SE) of Black-backed Woodpecker home ranges (gray bars; n = 8) and randomly distributed home ranges (empty bars; n = 8). Habitat types were defined as barren, stands defoliated by windthrows and spruce budworm outbreak, young (<90 years) and old (>90 years) coniferous stands, and young (<5 years) and old (>5 years) cuts.

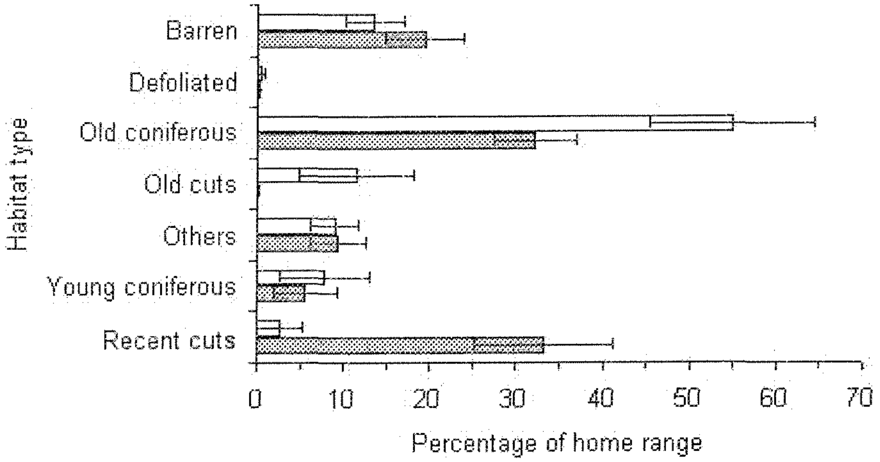

Table 3.2. Logistic regression models predicting Black-backed Woodpecker occurrence (n = 8) according to habitat type at the landscape and home-range scales (AUC = area under the ROC curve, an index of model fit).

	β_j	SE	Odds ratio	Odds ratio CI	AUC*
Landscape scale					
Young cuts	0.1069	0.0562	1.113	0.974-1.271	0.828
Home range scale					
Old coniferous	0.8711	0.2109	2.390	1.343-4.252	0.717
Young cuts	-2.2328	0.5658	0.107	0.035-0.327	

*AUC = area under the ROC curve, an index of model fit.

Figure 3.4. Percentage (mean ± SE) of telemetry locations of foraging Black-backed Woodpeckers (gray bars: n = 128) and random points (empty bars: n = 128) falling in a given habitat type.

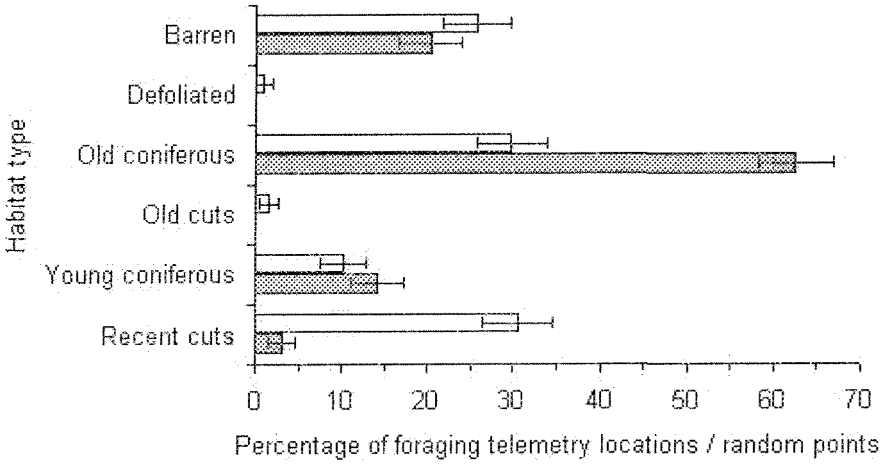

Table 3.3. Mean (SE) dead wood, snags, and fallen log volumes ($m^3 \cdot ha-1$) of total and recently decayed stages (decay classes 1 and 2) by habitat type.

Habitat type	All decayed stages			Recent decayed		
	Dead wood	Snags	Fallen logs	Dead wood	Snags	Fallen logs
Barren	18.1 (4.0)	10.3 (2.5)	7.8 (2.0)	9.8 (2.5)	6.5 (2.0)	3.2 (1.0)
Old coniferous	71.3 (11.2)	39.7 (9.4)	31.6 (3.9)	31.7 (5.7)	16.4 (3.9)	15.3 (2.6)
Young coniferous	49.5 (14.2)	33.8 (11.3)	15.7 (5.2)	26.6 (8.7)	20.0 (6.6)	6.6 (1.7)
Young cut	29.7 (4.4)	2.4 (0.6)	27.2 (4.3)	8.4 (1.1)	0.5 (0.2)	7.8 (1.1)

Table 3.4. Mean (SE) dead wood, snags, and fallen log volumes (m^3 • ha-1) of total and recently decayed stages (decay classes 1 and 2) in asymptotic Black-backed Woodpecker home ranges.

	All			Recent decay		
Home range size (ha)	Dead wood	Snags	Fallen logs	Dead wood	Snags	Fallen logs
100.4	35.6 (4.1)	18.9 (3.8)	16.7 (1.5)	20.0 (2.8)	14.9 (2.9)	5.1 (1.9)
118.5	41.7 (8.0)	16.7 (6.6)	25.0 (3.1)	14.2 (3.4)	5.1 (2.2)	9.1 (2.1)
120.0	42.1 (4.8)	11.6 (4.1)	30.1 (4.5)	17.1 (5.4)	7.6 (4.6)	9.5 (1.9)
132.5	61.7 (30.1)	35.0 (26.3)	26.7 (10.8)	22.8 (10.9)	11.8 (8.4)	11.0 (3.1)
150.9	36.4 (11.1)	17.3 (5.5)	19.2 (6.6)	11.8 (3.4)	4.2 (2.5)	7.6 (3.3)
181.6	41.7 (14.2)	15.9 (7.4)	25.8 (7.6)	21.3 (10.2)	10.1 (5.6)	11.3 (4.7)
256.4	37.5 (9.7)	23.5 (7.4)	14.0 (4.0)	18.9 (5.9)	12.1 (4.8)	6.8 (2.3)
Mean ± SE	42.4 (3.2)	19.8 (2.7)	22.5 (2.1)	18.0 (1.4)	9.4 (1.4)	8.6 (0.8)

CHAPITRE IV

FORAGING ECOLOGY OF BLACK-BACKED WOODPECKER IN UNBURNED EASTERN BOREAL FOREST STANDS

Tremblay, J.A., J. Ibarzabal, and J.P. Savard. Foraging ecology of Black-backed Woodpecker in unburned eastern boreal forest stands. Canadian Journal of Forest Research. Accepté pour publication.

RÉSUMÉ

Les paysages aménagés soumis représentent le type forestier dominant dans l'aire de répartition du pic à dos noir. Cependant, le comportement alimentaire du Pic à dos noir à fine échelle dans ce type de forêts demeure inconnu. Dans cette étude, nous décrivons le comportement alimentaire du Pic à dos noir dans la forêt boréale non brûlée non affectée par une épidémie d'insectes. À cette fin, nous avons mené une étude télémétrique qui porte sur le comportement alimentaire du Pic à dos noir à l'échelle de l'arbre. Vingt-sept individus de Pics à dos noir ont été suivis lors de années (2005-2006) pour un total de 279 observations d'alimentation. Le Pic à dos noir s'alimente sur les arbres vivants, les chicots et les débris ligneux au sol et principalement sur le tronc des chicots récemment morts avec un diamètre à hauteur de poitrine moyen (± erreur-type) de 18.3 ± 0.4 cm. Nos résultats suggèrent que le diamètre et le stade de dégradation des substrats d'alimentation sont des prédicteurs importants des substrats d'alimentation du Pic à dos noir dans les forêts boréales non brûlées étudiées. Nous recommandons que les efforts de conservation pour le pic à dos noir, et les autres espèces dépendantes du bois mort récent, devraient prioriser le maintien de blocs de forêts intacts de vieilles forêts de conifères dans le paysage, ce qui assurerait une production continuelle de bois mort récent en quantité suffisante pour rencontrer les besoins alimentaires du pic à dos noir.

ABSTRACT

Managed coniferous forest dominates much of the Black-backed Woodpecker's breeding range. Despite this, little is known about the fine scale foraging behaviour of this focal species in unburned managed forest stands in the absence of insect outbreaks. To investigate the foraging substrates used in such habitat, we employed radio-telemetry to track a total of 27 Black-backed Woodpeckers. During two successive summers (2005-2006), 279 foraging observations were recorded, most of which were on dying trees, snags and downed woody debris. Individuals frequently foraged by excavation, suggesting that in the absence of insect outbreaks the Black-backed Woodpecker forages mainly by drilling. The majority of foraging events occurred on recently dead snags with a mean (± standard-error) diameter at breast height of 18.3 ± 0.4 cm. Our results suggest that in unburned boreal forest stands, substrate diameter and decay class are important predictors of suitable foraging substrates for Black-backed Woodpeckers. We suggest that conservation efforts aimed at maintaining this dead-wood dependent cavity nesting species within the landscape, should endeavour to maintain 100 ha patches of old-growth coniferous forest. This would ensure the continuous production of a sufficient quantity of recently dead or dying trees to meet the foraging needs of this species.

Keywords : radio-telemetry ; cavity-nesting birds; *Picoides arcticus*; foraging; dead wood; snags

INTRODUCTION

Studies of forest ecosystems continue to highlight the importance of standing dead trees and downed woody debris (hereafter snags and dwd, respectively) for a diverse range of bird and mammal species (e.g., Raphael and White 1984, McComb and Lidenmayer 1999, Martin et al. 2004). Distinct suites of organisms are associated with specific stages of wood decay, with some saproxylic species depending on recently decayed dead wood, and others depending on substrates in a more advanced state of decay (Thomas 1979, Harmon et al. 1986, Grove 2001). As timber harvesting removes mature trees, forestry practices may conflict with the ecological requirements of species associated with recently decayed dead wood (Imbeau et al. 2001, Schmiegelow and Mönkönnen 2002). A recent study (Vaillancourt et al. 2008) showed that although decayed dead wood is present in cutblocks (mainly as logging residues), dying and recently dead trees are scarce in exploited stands. Coupled with this, the 'life-span' of recently decayed dead wood is relatively short. Aakala et al. (2008) observed that in old-growth stands within the northeastern boreal forest, half of all recently decayed black spruce (*Picea mariana*) snags fell within five years. As a result, snag decay classes in the boreal forest show a dome-shaped distribution, with the majority being intermediate decayed snags (Vaillancourt et al. 2008). Thus, in harvested landscapes, species associated with recently decayed dead wood are particularly vulnerable to the loss of vital habitat elements.

Woodpeckers rely on decaying wood for foraging and nesting (Backhouse 2005), and are particularly sensitive to changes in the abundance and distribution of dead wood in the landscape (Pechacek 2004). In northern Europe, intensive forest management has led to the decline, and in some cases the extirpation, of certain woodpecker species (Picidae) (Angelstam and Mikusinski 1994, Mikusinski and Angelstam 1998, Roberge et al. 2008). In North America, results obtained from Breeding Bird Survey (BBS) routes suggest that some woodpecker populations are stable and others are declining (Sauer et al. 2005, Collins and Downes 2009). Because woodpeckers excavate nest cavities, they play a keystone role in forests, providing breeding and roosting sites for secondary cavity users (Martin and Eadie 1999, Martin et al. 2004). In the conifer-dominated boreal forest of eastern Canada, the Black-backed Woodpecker (*Picoides arcticus*) and American Three-toed Woodpecker (*Picoides dorsalis*) are common primary cavity nesters, and rely on recently dead trees for foraging and nesting (Goggans et al. 1989, Nappi 2009). Studies on sympatric American Three-toed and Black-backed Woodpeckers in unburned forest stands have shown that the latter use larger and less decayed trees than the former (Bull et al. 1986, Goggans et al. 1989, Villard 1994, Nappi 2009). Black-backed Woodpeckers appear to be old-growth dependent and more abundant than American Three-toed Woodpeckers in the eastern boreal forest (Thompson et al. 1999, Setterington et al. 2000). Goggans et al. (1989), working in Oregon, recommended that the Black-backed Woodpecker, rather than the American Three-toed Woodpecker, be used as an indicator species for mature and old-growth forests. In the eastern boreal forest, the Black-backed Woodpecker occurs almost exclusively in > 80 year-old forest stands, and requires at least 15 $m^3 \cdot ha^{-1}$ (Tremblay et al. 2009) of recent dead wood during the breeding period. Moreover, this species appears to be sensitive to the removal of dead wood, which is a typical practice in modern forestry (Thompson et al. 1999). In addition, trend estimates for Black-backed Woodpecker populations suggest that the species may be undergoing a widespread decline, and it has been recently added to a number of federal/state agency lists as being of special concern (NatureServe 2009).

While many authors associate the Black-backed Woodpecker with recent post-fire stands (Hutto 1995, Murphy and Lehnhausen 1998, Powell 2000, Hoyt and Hannon 2002), others have shown that unburned forest stands also play an important role in its ecology (Goggans et al. 1989, Bonnot et al. 2008, Tremblay et al. 2009). Tremblay et al. (2009) investigated habitat selection by this species at the landscape and home range scale in unburned landscapes, but habitat selection at the finer scale remains unclear. The few studies that have been done, report that this species forages on recently decayed large-diameter snags (Raphael and White 1984, Bull et al. 1986, Goggans et al. 1989, Villard 1994), but most of these results were obtained from forests in western North America following mountain pine beetle (*Dendroctonus ponderosae* - Coleoptera, Scolitydae) outbreaks (Bull et al. 1986, Goggans et al. 1989). Under such conditions, Black-backed Woodpeckers were mainly observed to forage by pecking and scaling (Bull et al. 1986, Goggans et al. 1989). Although information about foraging and the resilience of Black-backed Woodpeckers in managed boreal forest stands is generally lacking, it is of primary importance in assessing the impact of large-scale forestry on this species, and on secondary cavity users in the eastern boreal forest of Canada. This is especially true given that forestry is now the dominant perturbation in the boreal forest and occurs in most parts of the Black-backed Woodpecker's breeding range.

The objective of this study was to characterize the foraging substrates used by Black-backed Woodpeckers in unburned, managed forest stands in the absence of insect outbreaks. Based on our results, we identified quantitative targets for habitat management of this keystone primary cavity nesting species.

METHODS

Study area

We conducted fieldwork from May to July in two consecutive years (2005 and 2006) at a study site situated 200 km north-west of Lac Saint-Jean (Québec, Canada) (50° 34'N, 72° 10'W; Figure 1), in the black spruce-feathermoss forest of the Canadian boreal forest ecological domain (Saucier et al. 1998). The stands were mainly composed of black spruce (*Picea mariana*), or black spruce mixed with jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*) and, occasionally, tamarack (*Larix laricina*). The topography in the study area is undulating, and forest fire is the major natural forest perturbation, with smaller areas being affected by spruce budworm (*Choristoneura fumiferana*) outbreaks. Commercial timber harvesting at this latitude began in the last decade, and the area was logged using mosaic harvesting, which favours the interspersion of logged and residual forested blocks in the landscape. Even-aged management (cut with regeneration and soil protection, CRSP) was practiced in the southern part of the study area, and uneven-aged management (cut with little merchantable tree protection, CLMTP) in the northern part. Within the study area, Black-backed Woodpecker home ranges typically comprise about one-third mature, one-third post-mature and one-third recently (< 5 years) harvested black spruce (Tremblay et al. 2009).

Trapping and tracking

We conducted roadside surveys from mid-May to June to locate Black-backed Woodpeckers. Playbacks of conspecific calls and drumming (Ibarzabal and Desmeules 2006) were done at stations established at 1 km intervals along major roads. However, we did not sample burned areas or 2-km buffer zones surrounding them. We captured individuals using mist nets and fitted tail-mounted radio-transmitter to the base of the two central rectrices (2.3 g, Model PD-2, Holohil Systems Ltd., Carp, Ontario) of individuals showing signs of breeding (i.e., exhibiting a brood patch). Transmitter batteries lasted from 8 to 10 weeks.

Substrate characteristics

We used the homing method with TRX-2000S radio receivers (Wildlife Materials, Illinois) and three-element Yagi antennas to located birds fitted with radio-transmitters. We tracked individuals on consecutive days, but to reduce any possible bias related to cyclic behaviour, we alternated the time of day (either am or pm) that we recorded locations. Although Black-backed Woodpeckers continue normal foraging activity if observers remain at a distance of >3 m (Tremblay et al. 2009), we only approached birds to within 10 m. We recorded foraging height (the basal-, middle- or top-third of the tree or snag), foraging technique (scaling: surface pecking and prying off layers of bark to get at insects; excavation: digging into the wood to obtain insects; or mixed: combination of scaling and excavating (Bull et al. 1986, Murphy and Lehnhausen 1998)), and foraging site (trunk or branch). When an individual flew from the tree on which it had been foraging (hereafter substrate), we using flagging tape to mark the substrate, and we recorded its location (± 10 m) using a hand-held GPS unit (GPS Legend, Garmin Corp., Olathe, Kansas). When possible, the observer then followed the individual to its next foraging substrate. Once the bird was lost from sight, the observer relocated the substrates that it had been foraging on, and recorded the species, substrate type (i.e., standing or fallen, and live or dead), diameter at breast height (dbh) for standing substrates or diameter at the observation point (dao) for dwd, decay stage (Table 1: modified from Tyrrell and Crow 1994, Bergeron et al. 1997), and the percentage of bark cover (in 10 % increments from 0 = 0 to 10 % to 10 = 91 to 100 %). We matched each substrate with the two nearest substrates of the same type (i.e., live tree, snag or dwd) with a diameter ≥ 5cm to determine variability in the available substrates within the local vicinity. For standing substrates, we measured the distance from base-to-base (Imbeau and Desrochers 2002), but for dwd, the perpendicular distance from the foraging site was used.

Statistical analyses

We used logistic regression for matched case-control pairs (PROC PHREG; SAS Institute 2008) as used by Imbeau and Desrochers (2002), to evaluate which of the different substrate variables most likely determined its potential for use as a foraging substrate. We set woodpecker identity as the STRATA variable, and the COVSANDWITCH option was used to allow the dependence between relocations of the same individual to be considered. We analyzed characteristics for pairs of substrate in the same state (i.e., used live trees vs. nearest available live trees, used snags vs. nearest available snags, and used dwd vs. nearest available dwd). We used a Kruskal-Wallis test to analyse the effects of sex and year on substrate characteristics.

We estimated selection ratios (Manly et al. 2002) for the best predictor characteristics identified using logistic regression. We considered a given category as 'preferred' when the 95 % confidence interval (CI) of its selection ratio was > 1; as 'avoided' when the 95 % CI was < 1; and as used proportionally to its availability when the 95 % CI included 1. For each predictor, we compared selection ratios using Bonferroni-corrected χ^2 tests for multiple comparisons ($\alpha = 0.05$). To respect assumptions of the χ^2 test (Manly et al. 2002), we did not include substrate categories that had observed frequencies < 5. For this reason, we did not estimate selection ratios for live trees because only two woodpeckers presented observed frequencies > 5.

We conducted statistical analyses using SAS version 9.1 (SAS Institute Inc. 2008) and we considered effects with $P \leq 0.05$ as significant. Unless otherwise stated, the figures shown are means ± 1 S.E.

RESULTS

Twenty-seven Black-backed Woodpeckers (12 males and 15 females) provided 279 foraging observations (10.5 ± 2.2 foraging observation per individual) within an area of about 900 km^2 (Figure 1). As sex and year had no effect on substrate characteristics ($P > 0.05$ in all cases; Mann-Whitney test), the data were pooled.

Foraging technique and foraging height

In total, 98.2 % (*n* = 274) of foraging events occurred on snags, live trees or dwd, 1.1 % on female cones of black spruce, and 0.7 % on the ground. All foraging observations on standing substrates (snags and live trees) were on trunks (*n* = 230), and the birds foraged more by excavation (69.5 %; *n* = 158) than by scaling (23.5 %; *n* = 53). Furthermore, the individuals foraged more often on the middle-third of the trunk (63.2 %; *n* = 139) than on the basal- (24.6 %; *n* = 54) or top-third (12.3 %; *n* = 27).

Characteristics of foraging substrates

In total, 67.2 % (*n* = 184) of foraging events were on snags, 16.8 % on live trees, and 16.1 % on dwd. Diameter predicted selection by foraging Black-backed Woodpeckers for all three substrate types, with the mean dbh being 18.9 ± 1.0 cm for live trees (χ^2_{dbh} = 45.28; *n* = 46; $P < 0{,}001$; Table 3) and 18.3 ± 0.4 cm for snags (χ^2_{dbh} = 142.26; *n* = 184; $P < 0{,}001$; Table 4). The mean dao of dwd was 11.9 ± 0.6 cm (χ^2_{dao} = 27.39; *n* = 44; $P < 0{,}001$; Table 5). Black-backed Woodpeckers preferred snags and dwd with a diameter of between 15.1 and 20.0 cm, and avoided substrates with a diameter of between 5.1 and 10.0 cm (Figure 3). Larger diameter classes had high selection ratios, but due to a wide CI that included the threshold value (Figure 3), the results were not significant. The percentage of bark cover was the factor that most strongly predicted the use of live trees ($\chi^2_{\text{bark cover}}$ = 105.91 compared to χ^2_{dbh} = 45.28) (Table 3), with individuals selecting only live substrates with high percentage bark cover (Table 3). Decay class predicted snag use for foraging (χ^2_{decay} = 18,09; *n* = 184; $P < 0{,}001$) (Table 4), with decay class 4 being preferred, and decay classes 6 and 8 being avoided (Figure 4). The tree species was not a good predictor of potential use by foraging Black-backed Woodpeckers, and no tree species was used in a proportion higher than that available (Tables 3, 4 and 5).

DISCUSSION

As a primary cavity nester, the Black-backed Woodpecker is a keystone species in the coniferous boreal forest, and in a conservation management perspective their foraging ecology must be considered as much as their nesting requirements. In the present study area, Black-backed Woodpeckers foraged on live trees, snags and dwd, but the principal substrate used was recently dead snags. The results of the present study suggest that substrate diameter and decay class are important predictors of foraging substrate use by Black-backed Woodpeckers. Furthermore, in our study area, this species foraged more by excavation than by scaling. This suggests that in the absence of bark beetle (Curculionidae, Sub-family Scolytinae) outbreaks, the Black-backed-Woodpecker may be a driller species.

Foraging technique and foraging height

Black-backed Woodpeckers have been reported to forage mainly on tree trunks situated below the crown (Raphael and White 1984, Villard and Beninger 1993, Villard 1994). The present results support these findings, with foraging events occurring exclusively on the trunk, and mainly by excavation on the middle-third of the substrate.

In recently burned forests, Black-backed Woodpeckers feed predominantly on the larvae of large wood-boring beetles (Coleoptera: Buprestidae, Cerambycidae) (Beal 1911, Bent 1939, Apfelbaum and Haney 1981, Harris 1982, Villard and Beninger 1993, Murphy and Lehnhausen 1998, Powell 2000, Nappi et al. 2003), but their diet in unburned forest stands is not well documented. It is reasonable to believe that in the latter, this species may consume lower numbers of wood-boring larvae, because saproxylic insects are at lower densities than in burned forest stands (Saint-Germain et al. 2004a). Some studies have shown that Black-backed Woodpeckers can take advantage of certain insect epidemics, and that in the case of outbreaks of species such as the mountain pine beetle, which lives under the bark, that foraging is mainly by pecking and scaling (Bull et al. 1986, Goggans et al. 1989). However, the fact that Black-backed Woodpeckers in the present study foraged mainly by excavation, suggests that they were feeding on wood-boring insect larvae deep within the substrate. This finding supports Raphael and White's (1984) conclusion that, independent of habitat type, the Black-backed Woodpecker is a driller species in the absence of bark beetle (Scolytinae) outbreaks. Further studies on the diet of Black-backed Woodpeckers in unburned boreal forest stands in the absence of epidemic insect outbreaks are needed.

Characteristics of foraging substrates

In burned forest stands, Black-backed Woodpeckers forage mainly on snags (Villard and Beninger 1993, Murphy and Lehnhausen 1998, Kreisel and Stein 1999, Powell 2000, Nappi et al. 2003), but substrate selection in unburned forest stands seems to be more variable (Raphael and White 1984, Villard 1994). Although individuals in the present study foraged mainly in snags, they also used dying trees and dwd. Raphael and White (1984) observed that Black-backed Woodpeckers are opportunistic in their choice of foraging substrates, preferentially using snags when snag density is high (e.g., in recent burns), and using a variety of substrates when snag density is low (e.g., in mature or post-mature stands). At low snag densities, this species may enlarge its foraging niche to maximise capture success (*sensu* Powell 2000). Villard (1994) reported that Black-backed Woodpeckers in unburned forest stands spent up to 41 % of their time foraging on dwd. In the present study, individuals were only observed foraging on dwd 16.1 % of the time. The dwd used was mainly recently dead trees in post-mature coniferous stands that had been subjected to windthrow; however, large logging residues in cutblocks were also occasionally used (results not shown). In the present study, the proportional use of dwd may have been underestimated because telemetry signals are harder to detect when birds are close to the ground. Furthermore, birds foraging close to the ground may be more difficult to detect visually. Nevertheless, we are not of the opinion that these factors are sufficient to explain the large disparity between the results of the present study and that conducted by Villard (1994). The importance of dwd in unburned forest stands needs to be better quantified.

Substrate diameter was the best predictor of the foraging snags and dwd used by Black-backed Woodpeckers, with individuals preferentially selecting substrates with a greater diameter than generally available. This result is consistent with the results of previous studies (Raphael and White 1984, Villard and Beninger 1993, Villard 1994, Powell 2000, Nappi et al. 2003). Wood-boring insect density increases with bark thickness, which, in turn, increases with tree diameter (Zhang et al. 1993, Saint-Germain et al. 2004b). Foraging Black-backed Woodpeckers selected 15.1 to 20.0 cm (and possibly larger) diameter trees, snags and dwd. Snags with a dbh >20.0 cm represented 37.2 % of all snags used by foraging Black-backed Woodpeckers; however, they constituted only 10.1 % of available snags.

For live trees, the dbh was a good predictor of foraging substrate use, but the present results suggest that bark cover is a better predictor. Generally, wood-boring insects (Coleoptera: Buprestidae, Cerambycidae) lay their eggs on or under bark scales (Holsten et al. 2001). Thicker bark preserves subcortical tissue integrity and provides the moisture conditions required for the development of wood-boring larvae (Gardiner 1957). Although 46 foraging observations were on live trees, only two Black-backed Woodpeckers foraged on these substrates ≥ 5 times, and an additional 12 individuals fed < 5 times on live trees (n=27). While live trees were not a predominant foraging substrate, they may be an important supplementary resource when snags are scarce, or when prey density is higher in live trees following insect outbreaks (Bull et al. 1986, Goggans et al. 1989). In the present study, Black-backed Woodpeckers foraged mainly on dying live trees (decay class 3) (Table 3) that still had a high proportion of bark, and on snags in early decay classes (median decay class of 5). Individuals preferentially selected recently decayed snags (decay class 4), and avoided mid- (decay class 6) and advanced-decay snags (decay class 8). Saproxylic insect density in black spruce is higher in recently decayed snags (Saint-Germain et al. 2007) and recently dwd (Vanderwel et al. 2006). In the study area, these substrates were mainly located in post-mature coniferous stands, which Black-backed Woodpeckers have recently been shown to preferentially select for foraging (Tremblay et al. 2009).

Previous studies have shown that Black-backed Woodpeckers use a wide variety of tree species for foraging (Apfelbaum and Haney 1981, Goggans et al. 1989, Villard and Beninger 1993, Murphy and Lehnhausen 1998, Powell 2000, Nappi et al. 2003). In the present study, Black-backed Woodpeckers showed a high preference for conifers, foraging mainly on black spruce, the predominant species. Powell (2000) observed that trees used for foraging in burned forest stands had consistently higher prey densities than trees selected at random. This pattern may drive substrate selection by foraging Black-backed Woodpeckers in unburned forest stands and explain the selection of dying or recently dead trees.

Management implications

Although the quantity of dead wood in a given area is critical for woodpecker persistence (Angelstam et al. 2003, Bütler et al. 2004, Roberge et al. 2008, Tremblay et al. 2009), current regulations in Canada do not stipulate the quantity that should be left in harvested landscapes. This, in turn, has implications for the survival of a wide range of secondary cavity users (Martin et al. 2004). As cutblocks contain limited amounts of dying or recently dead conifers, and are adjacent to blocks of residual forest that will be harvested as soon as the cutblock reaches 3 m in height or 10 years of age (MRNF 2008), management measures are needed to improve the retention of adequate substrates for dead-wood associated species. If this is not achieved, Black-backed Woodpecker will be limited to intact post-mature coniferous patches (>90 years old) until snag production resumes in cutblocks, which may take up to a century (Imbeau et al. 1999). Maintaining the presence of a sufficient quantity of recently dead or dying trees in the landscape is an essential strategy for the conservation of Black-backed Woodpeckers. In sites where such protection measures are impossible, uneven-aged management practices that leave live and dead coniferous trees ≥18.0 cm should be promoted, especially in black spruce stands, which typically have fewer dead trees than others boreal stands (Vaillancourt et al. 2008). Uneven-aged practices, such as retention harvesting, should favour recruitment of recently decayed coniferous snags and dwd ≥18.0 cm. Recently, Tremblay et al. (2009) showed that Black-backed Woodpeckers can breed successfully in unburned forests with at least 35 $m^3 \cdot ha^{-1}$ of dead wood, of which 42 % (15 $m^3 \cdot ha^{-1}$) was in the early decay stage. As half of the dead wood in this category was standing (Tremblay et al. 2009), Black-backed Woodpeckers may require the presence of over 100 snags/ha with a dbh ≥ 18.0 cm, of which at least 42 are in the early decay stage. No cutblock provides this amount of dead wood, and as recently dead snags have a half-life of less than 10 years in the boreal forest (Aakala et al. 2008), those remaining would disappear rapidly. As snags in cutblocks will probably only persist for the first decade after logging, they cannot ensure the medium- or long-term persistence of Black-backed Woodpeckers in the landscape. Therefore, we suggest that the best conservation strategy for the maintenance of this and other recent dead wood associated species, is to leave recent dead wood in cutblocks, and to preserve 100 ha patches of old-growth coniferous forests that will produce sufficient quantities of recently dead or dying trees in the landscape. The Québec government has recently established an ecosystem-based management approach to be implemented by 2013. This consists of using management strategies and silvicultural treatments that reproduce the main characteristics of the natural forest. Ecosystem-based management aims at minimizing the differences between managed landscapes and the natural forest, and uses the composition of the pre-harvested forest as a reference (Varady-Szabo et al. 2008). In the application of this approach, we recommend the use of the Black-backed Woodpecker as an indicator for species associated with recently decayed dead wood.

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Table 4.1. Characteristics of live and dead tree decay classes (1-8) (modified from Tyrrell and Crow, 1994; Bergeron et al., 1997).

Class	Dwd characteristics			Standing tree characteristics		
	Leaves	Wood	Shape and form	Leaves	Bark	Top and height
Live trees						
1.	≥ 95%	solid	round	≥ 95%	100%	intact
2.	20 < x < 95%	solid	round	20 < x < 95%	> 90	intact
3.	< 20%	solid	round	< 20%	> 75%	intact
Dead trees						
4.	present but dead	solid	round	present but dead	present	intact
5.	absent	solid	round	absent	> 50 %	intact
6.	absent	solid/punky	round/oval	absent	< 50 %	broken
7.	absent	punky	oval, form retained	absent	absent	broken, height > 50%
8.	absent	punky	± oval, collapsed	absent	absent	< 2 m

Table 4.2. Characteristics of the substrates used by Black-backed Woodpeckers and the two nearest similar available substrates in unburned boreal forest stands in Québec (14 individuals used live trees (46 foraging observations), 20 individuals used snags (184 foraging observations), and nine individuals used downed woody debris (44 foraging observations)).

Characteristics	Used substrates		Nearest available substrates		X_2	p
	Mean (median)	SE (range)	Mean (median)	SE (range)		
Lived trees						
Diameter at breast height (cm)	18.9	1.0	8.8	0.6	45.28	< 0.001
Decay class	(3.0)	(1.0-3.0)	(2.0)	(1.0-3.0)	3.14	0.076
Bark cover	(10.0)	(10.0-10.0)	(10.0)	(4.0-10.0)	105.91	< 0.001
Snags						
Diameter at breast height (cm)	18.3	0.4	11.6	0.3	142.26	< 0.001
Decay class	(5.0)	(4.0-8.0)	(6.0)	(4.0-8.0)	18.09	< 0.001
Bark cover	(10.0)	(0.0-10.0)	(8.0)	(0.0-10.0)	1.29	0.256
Downed woody debris						
Diameter at observation (cm)	11.9	0.6	8.5	0.4	27.39	< 0.001
Decay class	(5.0)	(3.0-7.0)	(6.0)	(3.0-8.0)	1.60	0.206
Bark cover	(9.0)	(1.0-10.0)	(7.0)	(0.0-10.0)	1.38	0.241

Figure 4.1. Location of foraging substrates used by 27 Black-backed Woodpeckers in the study area located 200 km northwest of Lac Saint-Jean, Québec, Canada.

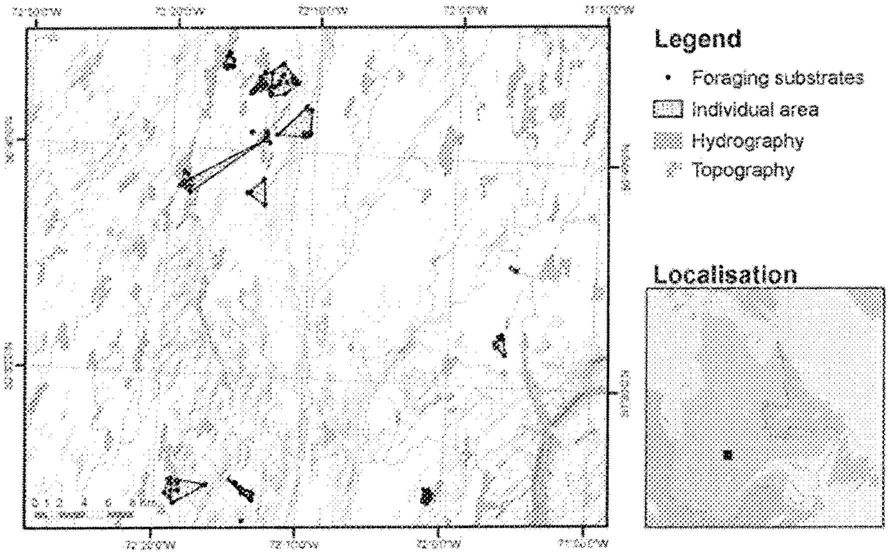


Figure 4.2. Percentage of substrate species used by Black-backed Woodpeckers (empty bars) and the two nearest available substrates (solid bars) in unburned boreal forest stands in Québec (14 individuals used live trees (46 foraging observations), 20 individuals used snags (184 foraging observations), and nine individuals used downed woody debris (44 foraging observations)).

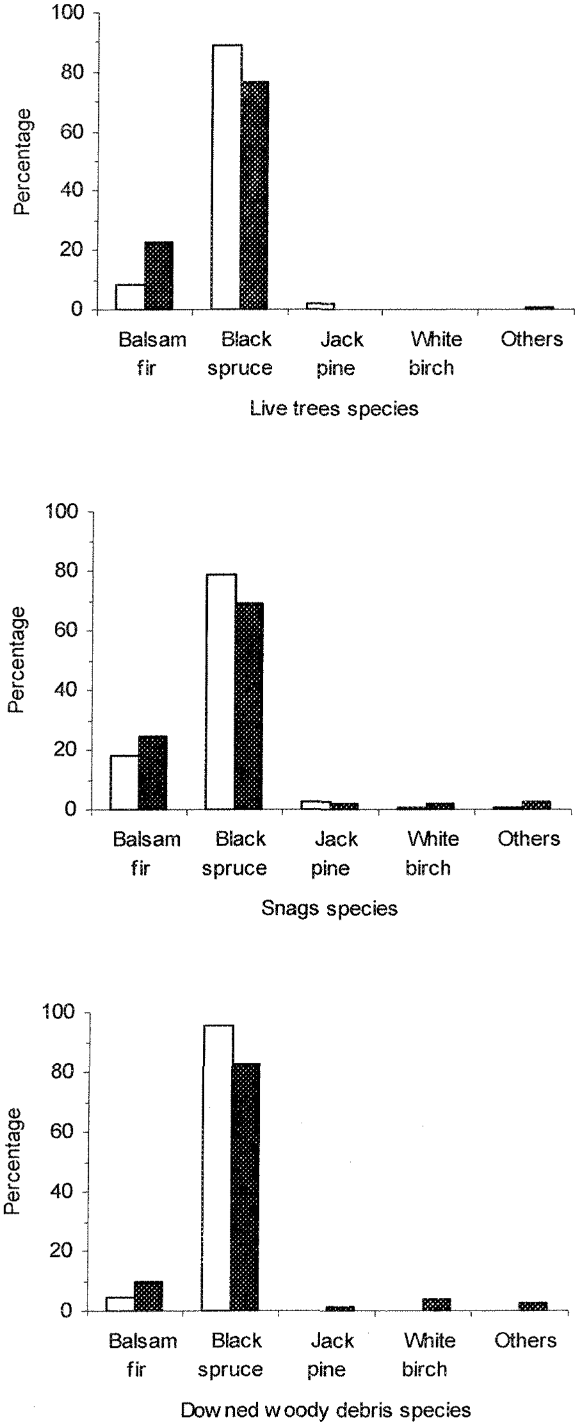


Figure 4.3. Selection ratios and 95% confidence intervals for the diameter at breast height (dbh) of snag classes (A) and for the diameter at observation (dao) of downed woody debris classes (B) used by Black-backed Woodpeckers. Shared letters indicate no significant difference in selection ratios among diameter classes (Bonferroni-corrected χ_2 tests). The dashed line indicates the preference threshold and n_u indicates the number of used substrates in the corresponding category.

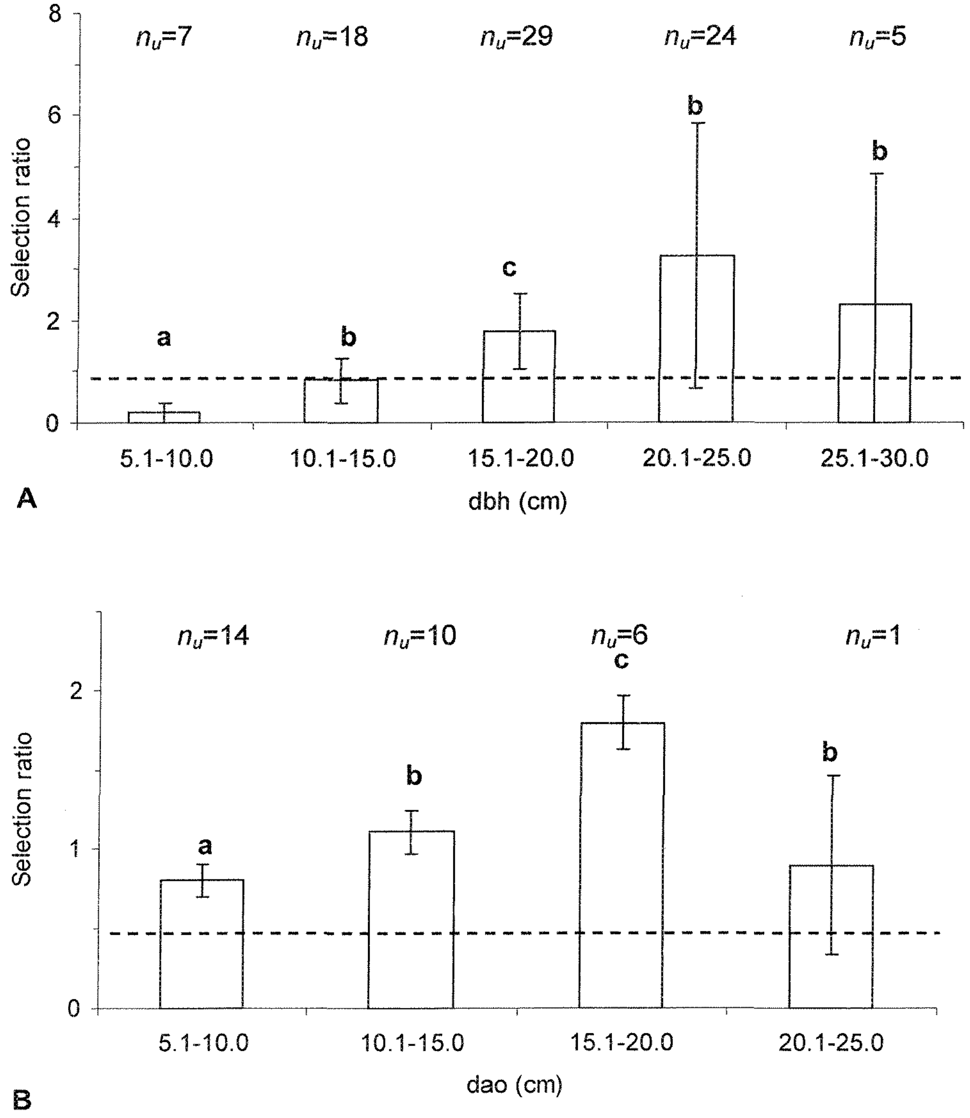
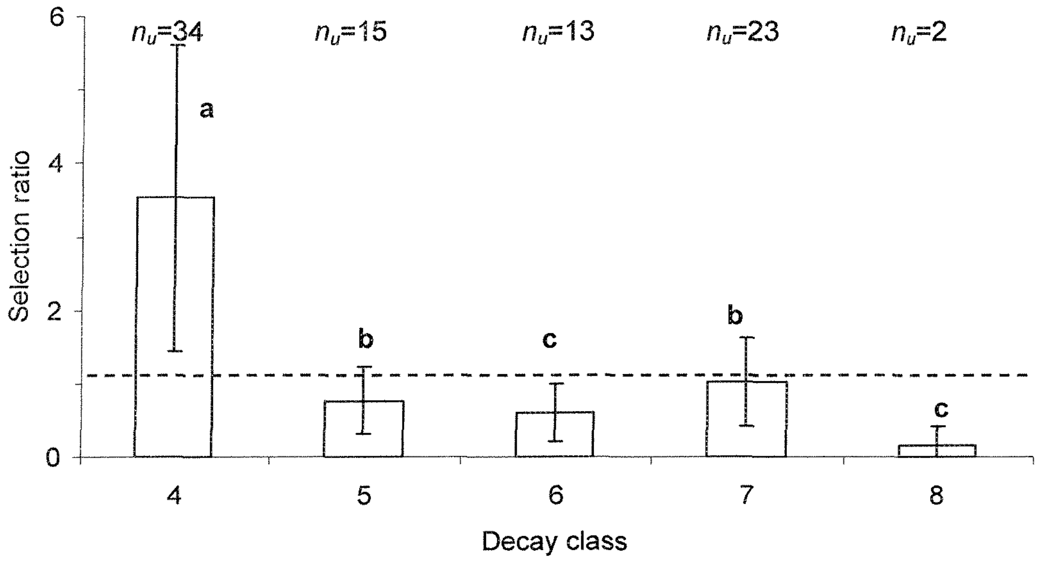


Figure 4.4. Selection ratios and 95% confidence intervals for decay classes of snags used by Black-backed Woodpeckers. Shared letters indicate no significant difference in selection ratios among decay classes (Bonferroni-corrected χ_2 tests). The dashed line indicates the preference threshold and n_u indicates the number of used substrates in the corresponding category.



CHAPITRE V

CONCLUSIONS GÉNÉRALES

Le Pic à dos noir est souvent observé en grande densité dans les forêts récemment brûlées et il a été strictement associé à la présence de forêts brûlées dans l'ensemble de son aire de répartition (Hutto, 1995; Murphy et Lehnhausen, 1998; Hoyt et Hannon, 2002). Cependant, l'espèce est également présente dans les vieilles forêts de conifères et dans les peuplements issus d'une épidémie d'insectes (Raphael et White, 1984; Bull et al., 1986; Goggans et al., 1989 ; Bonnot et al., 2008). Les connaissances sur l'écologie du Pic à dos noir dans les habitats non brûlés demeurent fragmentaires. Cette thèse de doctorat vise à éclaircir le rôle des forêts non brûlées dans l'écologie de nidification et dans la démographie du Pic à dos noir en forêt boréale.

SYNTHÈSE DES RÉSULTATS

Les résultats du Chapitre II montrent que, dans le paysage étudié, certains Pic à dos noirs nichent dans les forêts non brûlés et ce, malgré la présence de forêts récemment brûlées à proximité (< 8 km). Le Pic à dos noir utilise les chicots de conifères, avec une préférence pour le pin gris (*Pinus banksiana*), pour établir sa cavité de nidification. Les substrats de nidification utilisés possèdent un gros diamètre (diamètre moyen (± erreur-type) de 23,8 ± 1,1 cm) par rapport aux tiges disponibles et présentent un stade de dégradation intermédiaire. L'ouverture de la cavité est orientée vers l'est, ce qui confèrerait des avantages thermiques à la cavité en la réchauffant plus rapidement le matin et n'expose pas l'ouverture de la cavité aux vents dominants, venant du nord-ouest. Le succès de nidification, le développement des jeunes et le taux de prédation, bien qu'estimé à partir d'un faible nombre de nids, semblent similaires entre les forêts brûlées et non brûlées. Cependant, les nids des forêts brûlées produisent en moyenne davantage de jeunes par nid achevé. Soumis à différents scénarios de taux de survies des adultes et des juvéniles, les populations des deux habitats réagissent similairement. Ainsi, les populations des deux types habitats présentent un taux d'accroissement semblable, quoique légèrement supérieur dans les forêts récemment brûlées. Contrairement à l'hypothèse de Hutto (1995), les résultats de ce chapitre suggèrent que les forêts non brûlées ne sont pas des habitats puits et que des populations de Pic à dos noir pourraient se maintenir dans cet habitat, sans l'immigration d'individus provenant des forêts brûlées.

Le Chapitre III met en évidence que lors de sa nidification dans les forêts non brûlées, le Pic à dos noir présente un domaine vital moyen de 151,5 ± 18,8 ha qui comporte un volume de bois mort (debout et au sol) supérieur à 35 $m^3 \cdot ha^{-1}$, dont 14 $m^3 \cdot ha^{-1}$ de bois mort récent (stades de dégradation 4 et 5; Chapitre III). Bien que le Pic à dos noir semble nécessiter un seuil minimal de bois mort pour l'établissement de son domaine vital, aucune relation entre le volume de bois mort et la taille du domaine vital n'a été détectée. Cependant, la disposition spatiale des peuplements de vieux conifères semble influencer la taille du domaine vital du Pic à dos noir. Les résultats suggèrent que le domaine vital du Pic à dos noir serait plus grand lorsque la distance médiane entre les blocs de forêts résiduelles est plus élevée. Ainsi, la répartition de la ressource alimentaire du Pic à dos noir dans le paysage semble constituer une caractéristique importante dans la sélection de l'habitat par cette espèce.

Bien que la taille du domaine vital du Pic à dos noir semble être en relation avec les habitats qu'il utilise lors de sa quête alimentaire, la sélection d'habitat du Pic à dos noir présente des sélections opposées qui s'expriment sur deux échelles distinctes : l'espèce recherche des coupes récentes lors de l'établissement de son domaine vital alors que pendant sa quête alimentaire, le Pic à dos noir sélectionne les vieux peuplements de conifères et évite les coupes récentes (Chapitre III). Ces sélections traduisent deux exigences écologiques du Pic à dos noir en forêts non brûlées : 1) des habitats ouverts pour nicher (Chapitre II; Goggans et al., 1989) et, 2) des habitats avec présence de bois mort récent pour s'alimenter (vieux peuplements de conifères; Chapitre III). Ainsi, le paysage issu de la première passe de la coupe en mosaïque permet au Pic à dos noir de satisfaire ces deux exigences écologiques fondamentales par la juxtaposition d'habitats ouverts (particulièrement des coupes récentes) à proximité de vieux peuplements de conifères (Figure 5.1).

Figure 5.1. Juxtaposition de parterres de coupe et de forêts résiduelles qui caractérise la première passe de la coupe en mosaïque dans le centre du Québec.

Les travaux entrepris sur la quête alimentaire du Pic à dos noir au chapitre IV ont révélé qu'il utilise principalement des chicots récents mais également des arbres vivants sénescents et des débris ligneux au sol comme substrats d'alimentation. Le diamètre et le stade de dégradation constituent des caractéristiques prédictives fiables de l'utilisation de ces substrats d'alimentation par le Pic à dos noir en forêts non brûlées. En fait, le Pic à dos noir préfère s'alimenter sur les conifères de plus gros diamètre et spécifiquement sur les gros substrats qui sont peu dégradés et évite les chicots plus dégradés. L'étude montre qu'il s'alimente presque exclusivement sur le tronc des substrats de stades de dégradation récents où il excave principalement pour capturer ses proies. Il s'alimenterait ainsi surtout de larves d'insectes xylophages qui résident essentiellement dans les arbres récemment morts (Saint-Germain et al., 2004). Contrairement à son régime alimentaire rapporté dans les forêts non brûlées issues d'épidémies d'insectes où les scolytes composaient une proportion importante de sa diète (Bull et al., 1986; Goggans et al., 1989), l'alimentation du Pic à dos noir dans les forêts non brûlées sans épidémie d'insectes s'apparenterait davantage à celle observée dans les forêts brûlées, à savoir de larves d'insectes xylophages (Murphy et Lehnhausen, 1998; Powell, 2000; Nappi et al., 2003). Conséquemment, le Pic à dos noir serait dépendant, pour son alimentation, d'un apport plus ou moins continu en bois mort récent lui permettant un approvisionnement adéquat en larves d'insectes xylophages et les vieux peuplements de conifères auraient cette capacité de soutenir un tel apport régulier de bois mort (Drapeau et al., 2002).

LIMITES DE LA THÈSE

Le Pic à dos noir se trouve en faible densité dans les forêts non brûlées de sorte que la détection et la capture des individus nécessitent beaucoup de temps. Heureusement, le Pic à dos noir est fortement territorial et défend son territoire face aux intrusions intraspécifiques, ce qui nous a permis de développer une méthode d'appel qui permet d'attirer le Pic à dos noir à un site de capture sur une distance pouvant atteindre 1 km. Une fois capturé, nous avons utilisé des émetteurs radio afin de suivre les individus par télémétrie et de potentiellement trouver leur site de nidification (c.-à-d. leur cavité). Notre aire d'étude présente un réseau routier limité, une topographie accidentée et deux grandes rivières traversent et morcellent le territoire (la rivière Mistassibi et la rivière Daniel). Nous avons éprouvé de la difficulté à retracer le signal de plusieurs individus car la détectabilité du signal est variable selon la topographie du territoire, la distance maximale de l'émission du signal de l'émetteur radio est d'environ 1,5 km alors que certains Pics à dos noir se sont déplacés sur plus de 3 km de leur site de capture. Malgré ces difficultés, nous avons capturé 38 Pics à dos noir en forêt boréale non brûlée et parmi ceux-ci, 22 ont été pourvu de radio-émetteur. Le signal de 17 oiseaux a été retracé et 4 individus ont perdu leur radio-émetteur pendant l'étude. Nous avons recueillis un nombre suffisant de localisations pour estimer la taille du domaine vital de 8 Pics à dos noir : 7 nicheurs et 1 non nicheur. De plus, nous avons trouvé 17 nids de Pic à dos noir dans la forêt non brûlée. Ces effectifs sont statistiquement peu élevés et, conséquemment, la puissance des analyses statistiques liée à ces paramètres est réduite. Malgré tout, cette thèse présente des données inédites et amène une perspective nouvelle dans la démographie du Pic à dos noir et sur le rôle des forêts non brûlées dans son écologie.

Les recherches portant sur la démographie d'une population nécessite l'estimation de plusieurs paramètres et nous n'avons pu estimer certains d'entres eux en raison d'un manque de données, particulièrement sur la survie annuelle des adultes et des juvéniles. Les estimés de survie annuelle des adultes et des juvéniles nécessitent un suivi étroit de la population et implique la recapture des individus (White et Burnham, 1999). Or, des études récentes sur le Pic à dos noir ont montré que les mâles seraient relativement fidèles à leur territoire alors que les femelles seraient plus enclines à se déplacer sur de grandes distances entre les saisons de nidification (Huot, 2007). Ceci complique considérablement des études portant sur la survie des femelles adultes, qui servent généralement à ces calculs démographiques. Ainsi, des estimés de survie annuelle d'adultes et de juvénile d'espèces voisines au Pic à dos noir ont été utilisés afin d'estimer le taux d'accroissement des populations étudiées (Saab et Vierling, 2001). L'utilisation d'une gamme d'estimés de survie annuelle d'adultes et de juvéniles a permis d'établir divers scénarios démographiques. Nous avons considéré les taux de survie annuelle des adultes et des juvéniles comme étant similaires entre les forêts brûlées et non brûlées. Il pourrait exister des différences dans le taux de survie annuelle entre ces deux habitats et ces différences pourraient avoir des implications importantes sur le taux d'accroissement de ces populations. Cependant lorsque les forêts brûlées et non brûlées sont à proximité, des déplacements d'individus peuvent être possibles entre les habitats et de cette façon, le taux de survie annuelle associé à chacun des habitats pourrait être concordant. Des études sont nécessaires afin d'évaluer si le taux de survie annuelle des adultes et des juvéniles diffèrent entre les forêts brûlées et non brûlées.

CONTRIBUTION DE LA THÈSE ET RECOMMANDATIONS

Cette thèse présente des résultats sur l'écologie de nidification du Pic à dos noir en forêt non brûlée, notamment sur la sélection d'habitat et sur le succès de nidification de l'espèce et offre des éléments de réponse à l'hypothèse de dynamique source-puits. Les résultats suggèrent que les forêts non brûlées ne constitueraient pas l'habitat puits tel que proposé par Hutto (1995), mais plutôt un habitat avec un taux d'accroissement positif (Chapitre II). Ainsi, le taux d'accroissement des populations de Pic à dos noir varierait selon les caractéristiques de l'habitat et les conditions environnementales et présenteraient globalement un bilan positif sur plusieurs décennies. Les forêts brûlées présentent, quant à elles, un taux d'accroissement positif dans les premières années suivants le feu (Saab et al., 2007; Vierling et al., 2008, Chapitre II). Par contre, les forêts brûlées sont favorables au Pic à dos noir seulement sur une courte période de temps, qui varie de trois à sept ans (Hutto, 1995; Murphy et Lehnhausen, 1998; Saab et al., 2007; Vierling et al., 2008) et elles prendront au moins une centaine d'années avant de développer des caractéristiques propices au Pic à dos noir (Imbeau et al., 1999). Par conséquent, les forêts brûlées présenteraient vraisemblablement un bilan négatif à moyen ou long terme. Ainsi, les résultats de cette thèse suggèrent que les forêts brûlées et non brûlées sont bénéfiques au Pic à dos noir mais ils contribueraient différemment à la dynamique des populations de cette espèce. Ainsi, la démographie du Pic à dos noir ne se présenterait donc pas selon une dynamique source-puits. Comme le Pic à dos noir répond de façon opportuniste à l'augmentation de densités d'insectes xylophages produit par les feux de forêts et les épidémies d'insectes (Blackford, 1955; West et Speirs, 1959; Apfelbaum et Haney, 1981; Yunick, 1985), il est essentiel de considérer la sélection de l'habitat du Pic à dos noir dans une perspective de densité d'insectes xylophages (Powell, 2000; Mohren, 2002). Les résultats de cette étude suggèrent que si un habitat présente suffisamment d'opportunités d'alimentation pour la nidification, que cet habitat soit brûlé ou non, le Pic à dos noir le sélectionnera, même si les opportunités d'alimentation sont théoriquement plus densément distribuées dans le peuplement brûlé. D'autre part, les résultats soulignent que, peu importe s'il niche en forêt brûlée sur un petit territoire ou en forêt non brûlée sur un grand territoire, les probabilités de nicher avec succès du Pic à dos noir sont relativement semblables. Cependant, la productivité des nids est supérieure dans les habitats récemment brûlés que non brûlés.

Les impacts de l'exploitation forestière sur les populations de Pic à dos noir se présentent principalement selon deux échelles : 1) la raréfaction des vieux peuplements de conifères dans les paysages aménagés et, 2) la raréfaction du bois mort récent de conifères dans les parterres de coupe. L'aire d'étude présentait un niveau d'exploitation forestière modéré qui était convenable aux besoins de nidification et d'alimentation du Pic à dos noir. Ainsi, la première passe de la coupe en mosaïque ne semble pas nuisible pour le Pic à dos noir mais la seconde passe (non évaluée dans cette thèse), réduira considérablement la proportion de vieux peuplements de conifères dans le territoire, ce qui risquerait de limiter grandement les possibilités d'alimentation et de nidification du Pic à dos noir. Le niveau d'altération du paysage où les effets de la fragmentation et de la perte d'habitat qui affecteraient la persistance des populations de Pic à dos noir sont inconnus, mais nous avons observé que les domaines vitaux du Pic à dos noir comportaient près de 40 % de peuplements de vieux conifères et un volume de bois mort minimal de 35 $m^3 \cdot ha^{-1}$. Quoique des études subséquentes sont nécessaires afin de valider ces valeurs, je suggère qu'une approche préventive pour le maintien du Pic à dos noir en forêt boréale non brûlée doit cibler les valeurs citées précédemment. Ainsi, il pourrait s'avérer nécessaire de maintenir des blocs de plus d'une centaine d'hectares de forêts résiduelles intacts dans les paysages aménagés boréaux, surtout suite à la deuxième passe de la coupe en mosaïque. Ces blocs devraient être conservés jusqu'à ce que les parterres de coupe adjacents aient développé les attributs clés particuliers aux vieilles forêts ou pendant toute la période de révolution. Le maintien de blocs intacts de vieilles forêts offrira, à court, moyen et long termes, des possibilités d'alimentation et de nidification au Pic à dos noir. Dans les secteurs où il est impossible de maintenir une proportion suffisante de vieilles forêts, il est recommandé d'augmenter les possibilités d'alimentation et de nidification du Pic à dos noir dans les parterres de coupe. Ainsi, des arbres vivants et morts de gros diamètre devraient être préservés de la récolte et demeurer sur le parterre de coupe. À cet effet, tel que suggéré par Smith et al. (2008), 10 arbres de qualité/ha devraient être maintenus dans les parterres de coupe ce qui représente, pour le centre du Québec, au moins 10 conifères sénescents ou récemment morts de DHP ≥ 18,0 cm. Cependant, il est important de mentionner que cette mesure offrira au Pic à dos noir des opportunités d'alimentation et de nidification à court et à moyen terme seulement, car l'apport de bois mort récent est limité à une courte période de temps, après la coupe.

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