UNIVERSITÉ DU QUÉBEC À MONTRÉAL

IMPORTANCE DES ARBRES DE GRANDE TAILLE EN FORÊT BORÉALE MIXTE SUR LA DISTRIBUTION DES OISEAUX CAVICOLES AINSI QUE SUR LES PATRONS D'ALIMENTATION DU GRAND PIC (*DRYOCOPUS PILEATUS*)

MÉMOIRE
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AVANT-PROPOS

Ce mémoire comporte deux chapitres rédigés sous forme d'articles. À titre de candidate à la maîtrise, j'ai procédé à la supervision et à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de première auteure. Ces deux articles seront soumis dans des revues scientifiques arbitrées: 1) Habitat use, cavity tree selection, and relationships between primary and secondary cavity nesting birds in boreal mixedwood forests of eastern Canada et 2) Characteristics of foraging patterns and trees selected by Pileated Woodpecker (*Dryocopus pileatus*) in mixedwood forest of eastern Canada. Mon directeur de recherche, Pierre Drapeau, ainsi que mon codirecteur, Louis Imbeau, en sont les coauteurs.

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LISTE DES ABRÉVIATIONS, SIGLES ET ACRONYMES

AIC	Akaike's Information Criterion
AT	Trembling aspen
A. sp.	Aspen species
BAOW	Barred Owl
BBS	Breeding Bird Survey
BOOW	Boreal Owl
BOWO	Boreal woodpeckers
BP	Paper birch
C12	Coniferous mature (> 12 m height) forest
CAAF	Contrat d'approvisionnement et d'aménagement forestier
CT	Closest tree
D	Dead tree
Dbh	Diameter at breast height
Delta AIC	AIC score relative to best score
Dhp	Diamètre à la hauteur de la poitrine
DM12	Deciduous and mixed mature (> 12 m height) forest
DMC12	All mature (> 12 m height) forest
DOWO	Downy Woodpecker
DSI	Disturbance sensitivity indices
FB	Balsam fir
H1	0 to5 m height
H2	5 to 10m
H3	10 to 15 m
H4	More than 15m height
HAWO	Hairy Woodpecker
K	Number of parameters in regression models
LANDM12	Area of mature deciduous and mixed forest combined at landscape scale
LANDMR12	Area of mature forest at landscape scale,
Null	Model with intercept only and no explanatory variable
LANOPN	Area of open areas at landscape scale
LANR12	Area of mature forest of coniferous trees at landscape scale

Li	Living tree
LL	-2Log likelihood
LOCDM12	Area of mature forest combining deciduous-dominated and mixedwood stands within a radius of 250 m at stand scale
NOFL	Northern Flicker
NSWO	Northern Saw-whet Owl
OPN	Open cover types (< 4m height and <40 % cover).
OTH	Others
PCN	Primary cavity nester
PCS	Percentage of co-occurring species
PIWO	Pileated Woodpecker
PJ	Jack pine
R	Degree of ubiquity or median rarity
S	Small excavator
L	Large excavator
SB	Black spruce
SCN	Secondary cavity nester
SD	Standard deviation
SE	Mean standard error mean
SS	Same state (neighboring tree with the same state: live or dead)
Std err	Standard error
STDC12	Area of mature (> 12 m height) coniferous forest at stand scale
STDDMR12	Area of mature (> 12 m height) forest at stand scale
STDOPN	Area of open habitats at stand scale
SW	White spruce
T15	Tree density for DBH ≥ 15 cm
T20	Tree density for DBH ≥ 20 cm
T25	Tree density for DBH ≥ 25 cm
UI	Umbrella index score
USC	Utilisateur secondaire de cavité
WPCN	Weak primary cavity nester
YBSA	Yellow-bellied Sapsucker

RÉSUMÉ

La forêt boréale mixte de l'est du Canada constitue une zone de transition entre la forêt boréale résineuse et la forêt décidue tempérée. Cette zone est composée d'une riche population d'oiseaux cavicoles, incluant sept espèces de pics. Les perturbations humaines (agriculture et industrie forestière) ont beaucoup modifié cet écosystème en réduisant considérablement la quantité et la superficie de forêts matures ainsi que la quantité d'arbres de grand calibre, vivants ou morts, requis pour l'excavation de cavités par les pics. Deux aspects de cette problématique ont été traités dans ce mémoire. Le premier chapitre vise à caractériser les besoins des oiseaux utilisateurs de cavités en déterminant quelles essences d'arbres contribuent à la présence de chicots de grand calibre (dhp $\geq$ 20 cm) et à étudier les caractéristiques de la végétation qui affectent la sélection de l'habitat par les pics à l'échelle locale (rayon de 250 m) et à l'échelle du paysage (rayon de 1 km). Les rôles écologiques (soit espèces clé et/ou parapluie) de ces oiseaux ont également été étudiés. Le deuxième chapitre porte davantage sur les besoins alimentaires du Grand Pic. Les facteurs importants qui distinguent les arbres sélectionnés lors de sa quête alimentaire ainsi que les distributions temporelle et spatiale des marques d'alimentation ont été étudiées. L'aire d'étude se situe en Abitibi, au nord-ouest du Québec, dans la sapinière à bouleaux blancs. Afin de détecter la présence de pics et de hiboux cavicoles, un dispositif de 230 points d'appels a été élaboré le long des routes dans différents milieux forestiers. Dans le but de quantifier les arbres morts et vivants disponibles à l'échelle locale, des transects de végétation ont été effectués (1000m^2). Ces derniers ont aussi permis de caractériser les arbres utilisés pour l'excavation de cavités par les pics ainsi que par le Grand Pic (*Dryocopus pileatus*) lors de son alimentation. Des analyses géomatiques ont été menées pour déterminer les caractéristiques du paysage associées à la présence des pics. Nos résultats indiquent que le Pic flamboyant (*Colaptes auratus*) et le Pic maculé (*Sphyrapicus varius*) sont les deux espèces les plus abondantes dans notre aire d'étude tandis que le Grand Pic, le Pic à dos noir (*Picoides arcticus*) et le Pic à dos rayé (*P. dorsalis*) se font les plus rares. La probabilité d'occurrence pour la majorité des pics est davantage reliée aux attributs de l'échelle locale qu'à ceux de l'échelle du paysage. Le peuplier faux-tremble (*Populus tremuloides*) est l'essence la plus souvent excavée lors de la création de cavités par les pics et elle est aussi l'essence la plus représentée dans la catégorie des arbres de grand calibre. De plus, la majorité des cavités ont été excavées dans des arbres de grand calibre, et ce pour toutes les espèces de pics y compris celles qui creusent de petites cavités. Pour ces raisons, le peuplier faux-tremble est une espèce d'arbre d'intérêt faunique clé en forêt boréale mixte aménagée d'Abitibi. La présence de la Petite Nyctale (*Aegolius acadicus*) est associée de façon significative à la présence du Grand Pic mais pas à celle du Pic flamboyant. Cette association suggère que le Grand Pic serait une espèce clé de voûte (keystone) par la création de grande cavités en forêt boréale mixte. Selon l'indice proposé par Fleishman, la Petite Nyctale représente parmi les espèces cavicoles suivies dans cette étude celle qui est la plus propice à être désignée *espèce parapluie*. Le Grand Pic tend à s'alimenter sur les plus gros arbres disponibles. Il s'alimente majoritairement sur le sapin baumier (*Abies balsamea*) et sur le peuplier faux-tremble. Presque toutes les excavations d'alimentation observées se retrouvent sur la partie inférieure des arbres. Aucune essence ou diamètre d'arbre ne semble être toutefois favorisé lors de la réalimentation année après année.

Mots clés : *excavateurs primaires de cavités, utilisateurs secondaires de cavité, peuplier faux-tremble, Grand Pic, arbres morts*

INTRODUCTION GÉNÉRALE

1.1 Caractéristiques de la forêt boréale mixte de l'est du Canada

La forêt boréale mixte de l'est du Canada constitue une zone de transition entre la forêt boréale coniférienne et la forêt tempérée feuillue. Au Québec, cette zone de transition couvre près de 10% du territoire forestier et correspond à la grande zone de végétation de la sapinière à bouleau blanc (Thibault et al. 1988). Cet écosystème a subi de nombreuses perturbations de nature anthropogénique au cours des dernières décennies. À titre d'exemple, dans le domaine de la sapinière à bouleau blanc en Abitibi, la construction d'un chemin de fer au début du siècle dernier (1912) a permis l'accès au territoire et la colonisation par les premiers agriculteurs et a contribué à l'essouchement des terres à des fins de culture (Villeneuve 2001). À cette époque, le bois était la principale, voire la seule ressource exportée de la région. Encore aujourd'hui, cette région est en grande majorité sous contrats d'approvisionnement et d'aménagement forestier (CAAF). Ces deux activités génèrent des mosaïques forestières constituées de peuplements de plus en plus jeunes qui laissent sur pied peu de forêts matures (Hagan et al. 1997, Drapeau et al. 2000, Harper et al. 2002, Bergeron et al. 2002). De plus, la forêt boréale mixte subit de nombreuses perturbations naturelles telles que les feux (Bergeron 1991, Bergeron et al. 2001) et les épidémies d'insectes. Après de telles perturbations, la récolte d'arbres morts est généralement autorisée, ce qui a pour effet de diminuer la disponibilité d'arbres morts sur pied et donc de modifier considérablement l'accès à cette ressource pour les espèces qui en dépendent (Imbeau et al. 2001, Drapeau et al. 2002, Nappi et al. 2004, Hannon et Drapeau 2005).

Dans la zone boréale canadienne, la majorité de la forêt est sous aménagement, d'où une préoccupation grandissante concernant les effets cumulatifs du rajeunissement des paysages forestiers sur la diversité biologique dans ce biome. Par conséquent, la densité d'arbres de grand calibre vivants ainsi que l'abondance d'arbres morts sur pied de grands calibres sont de plus en plus réduites. En effet, dans une perspective de récolte du bois, la sénescence des arbres représente une perte économique qu'il faut éviter par une récolte avant mortalité. Il n'est pas étonnant que certaines études suggèrent que le nombre d'arbres morts sur pied serait diminué par les coupes forestières et par conséquent les populations des espèces associées à ces arbres auraient aussi diminué (Thomas et al. 1979, Neitro et al. 1985) ou seraient en voie de connaître des déclins (Imbeau et al. 2001, Drapeau et al. 2003).

Par ailleurs, afin de promouvoir un développement durable, les plans d'aménagement doivent dorénavant considérer la biodiversité des forêts. Au Québec, la commission d'étude sur la gestion de la forêt publique québécoise (Coulombe 2004) a identifié l'aménagement écosystémique comme une dimension incontournable du nécessaire virage en vue de rencontrer les objectifs du développement durable. L'aménagement écosystémique a été définit comme suit :

« *Un concept d'aménagement forestier ayant comme objectif de satisfaire un ensemble de valeurs et de besoins humains en s'appuyant sur les processus et les fonctions de l'écosystème et en maintenant son intégrité.* »

Cette définition large de l'aménagement écosystémique incorpore la structure des peuplements, la nécessité de diversifier l'aménagement en fonction de plusieurs ressources (ex. matière ligneuse, chasse, pêche, récréotourisme, biodiversité, etc.), pour maintenir les différents écosystèmes forestiers à l'intérieur de leurs limites naturelles. Dans un tel contexte, le maintien de l'intégrité des écosystèmes forestiers devra aussi considérer le maintien d'attributs essentiels de ces écosystèmes tels les arbres et chicots de grands calibres.

1.2 Importance des arbres morts de grand calibre pour l'avifaune

Les arbres morts et en décomposition sont importants pour le bon fonctionnements des écosystèmes au niveau de la productivité et des cycles géochimiques (Vallauri et al 2002), mais ils sont aussi essentiels pour plusieurs organismes vivants. Au Québec, un peu plus d'une quarantaine d'espèces de vertébrés, dont les oiseaux cavicoles, nécessitent la présence d'arbres vivants et morts sur pied de grand calibre pour s'y abriter et s'y nourrir (Darveau et Desrochers 2001). Dans les forêts du nord de l'Amérique du Nord, les oiseaux cavicoles forment un assemblage important d'oiseaux (Bunnell et al. 1999, Drapeau et al. 2002, Martin et al. 2004). Cette faune est principalement associée avec les vieilles forêts (Imbeau et al 2001, Imbeau et Desrochers 2002, Drapeau et al. 2003) ou avec celles récemment modifiées notamment les brûlis (Drapeau et al. 2002, Saab et al. 2004, Hannon et Drapeau 2005), offrant plusieurs arbres de grands calibres vivants ou morts sur pied.

Les chicots sont utilisés par plusieurs espèces de vertébrés pour se nourrir, se loger, se reproduire, communiquer et s'abriter (Raphael et White 1984). L'importance des arbres morts pour l'alimentation de certaines espèces d'oiseaux cavicoles repose sur le fait qu'ils forment la base de la chaîne alimentaire de certains organismes comme les champignons et les insectes saproxylophages (Vallauri et al. 2002). L'écorce se détachant des arbres morts pourra notamment être utilisée comme abri par plusieurs espèces d'arthropodes.D'autres, comme les fourmis charpentières, profiteront de la structure plus friable du tronc pour y forer leurs galeries (Sanders 1964, 1970). Les arthropodes colonisant les arbres mourants ou récemment morts constituent la base alimentaire de nombreux pics. Par exemple, le Pic à dos noir (*Picoides arcticus)* et le Pic à dos rayé (*P. dorsalis*) s'alimentent principalement d'insectes xylophages tels les scolytes et les longicornes (Murphy et Lehnhausen 1998, Nappi et al. 2003), tandis que le Grand Pic (*Dryocopus pileatus*) s'alimente majoritairement de fourmis charpentières (Bull 1987, Beckwith et Bull 1985, Hoyt 1957).

Le tronc plus friable des arbres morts ou en décomposition encore debout représente un endroit propice à la création de cavités, même si des arbres vivants sont aussi parfois utilisés (Raphael et White 1984). Dans tous les cas, les arbres de faible diamètre (dhp inférieur à 15 cm) sont rarement utilisables en raison du volume minimal nécessaire pour rencontrer les exigences des espèces cavicoles. Ces cavités peuvent être créées de façon naturelle lors de la chute d'une branche ou par l'excavation faite par les excavateurs primaires de cavités (EPC) (Neitro et al. 1985). Certains individus, comme les sitelles (*Sitta sp.*) et la Mésange à tête noire (*Poecile atricapillus*) sont capables d'excaver leur propre cavité, mais ils peuvent aussi utiliser celles déjà excavées. Ces individus sont désignés comme étant de faibles excavateurs primaires de cavités (Martin et al. 2004). D'autres organismes, comme certains oiseaux ou petits mammifères, utilisent aussi des cavités déjà existantes mais sont incapables de les excaver. Ces utilisateurs secondaires de cavités constituent un contingent important de la faune cavicole (USC) (Neitro et al. 1985, Martin et al. 2004).

1.3 Rôles écologiques des pics

Les pics ont des besoins relativement spécifiques et sont étroitement liés à leur environnement, ce qui fait d'eux des espèces spécialistes (Mikusińki et al. 2001). Les picidés sont d'excellents indicateurs de la disponibilité d'arbres morts d'une forêt, puisqu'ils en dépendent pour nicher et s'alimenter (Mannan et al. 1980, Raphael et White 1984, Murphy et Lehnhausen 1998). Pour la plupart, ce sont des espèces résidentes. Tous ces facteurs offrent l'opportunité aux chercheurs de les utiliser comme indicateurs de diversité biologique (Mikusińki et al. 2001). Les pics sont considérés comme étant le groupe le plus exigeant écologiquement en Europe (Mikusińki et al. 2001). Ils ont notamment été utilisés comme groupe indicateur de la diversité ornithologique des Carpates, de l'Est et du Nord-est de la Pologne (Mikusińki et al. 2001). Il a été observé que le nombre d'espèces d'oiseaux se trouvant dans un environnement forestier était directement proportionnel au nombre d'espèces de Picidés s'y retrouvant.

Martin et Eadie (1999) ont récemment proposé que les liens unissant les arbres à cavité, les excavateurs primaires de cavités et les utilisateurs secondaires de cavités soient si bien tissés qu'il soit possible de faire une analogie entre ce système et les réseaux trophiques. Ils ont montré que les oiseaux cavicoles qui sont incapables de créer leur propre cavité sont directement dépendants des pics et que par conséquent, leur présence coïncide positivement avec la présence de ceux-ci. Il a été observé que les populations d'oiseaux utilisateurs secondaires de cavité étaient nettement moindres dans les forêts où les chicots étaient coupés comparativement à lorsqu'ils y étaient laissés sur place (Mannan et al. 1980). Les environnements les plus favorables devraient avoir plus de cavités que ce qu'il est nécessaire pour répondre aux besoins minimaux des utilisateurs secondaires, afin que ces derniers aient, entre autres, la possibilité de faire un autre nid si leur nid est pris par un compétiteur ou un prédateur (Waters et al. 1990). Aussi, ces oiseaux auront l'opportunité d'utiliser un nouveau site si celui qu'ils occupaient les années passées venait à contenir trop de parasites. Il est a noté qu'un même chicot peut contenir plusieurs cavités (Mannan et al. 1980).

Il est important de noter aussi que la grandeur de la cavité aura une grande importance pour les USC: plus une espèce sera de grande taille plus il lui sera difficile de trouver une cavité de la taille appropriée (Bush 1999). Pour cette raison, les grands excavateurs, comme le Grand Pic, sont souvent désignés espèce « clé de voûte » (keystone species) (voir Martin et Eadie 1999, Bonar 2000, 2001, Aubry et Raley 2002). Aussi, les pics ont généralement un grand territoire, ce qui est notamment le cas du Grand Pic, permettant ainsi aux écologistes de les utiliser comme espèces parapluie (Lafleur et Blanchette 1993, Flemmings et al. 1999, Roberge et Angelstam 2004). D'autre part, certaines espèces ont été désignées indicatrices de vieilles forêts. C'est le cas du Pic à dos noir qui se retrouve dans la liste des Critères et Indicateurs proposée par le Conseil canadien des ministres des forêts (Conseil canadien des ministres des forêts 1997).

1.4 Importance de l'étude

La majorité des informations que l'on retrouve sur les pics et leur habitat provient de l'ouest du continent (e.g. Raphael et White 1984, Murphy et Lehnhausen 1998, Bonar 2001), dans des écosystèmes forestiers où les essences présentes atteignent à maturité un diamètre à hauteur de poitrine (dhp) nettement supérieur aux essences que l'on retrouve en forêt boréale mixte de l'Est du Canada (Boucher et al. 2003, Julien et Darveau 2005). Qu'en est-il des pics et de leur utilisation des forêts boréales mixtes quand les arbres n'atteignent pas des tailles aussi considérables que dans les forêts côtières de l'ouest du continent nord-américain? De plus, les études menées dans l'est du continent sont souvent faites dans des régions tempérées où les forêts sont composées d'une plus grande diversité d'essences d'arbres, notamment des essences décidues où on devrait retrouver plus de cavités naturelles que dans des essences résineuses (voir Flemming et al. 1999, Gunn et Hagan III 2000). Ces facteurs font en sorte que les espèces cavicoles sont probablement nettement plus limitées en termes de disponibilité de substrats de grand calibre pour l'alimentation et la nidification en forêt boréale mixte que dans la majorité des autres études actuellement publiées à ce sujet. Mais quelles essences privilégieront les pics en forêt boréale mixte de l'est du Canada pour leur alimentation et leur nidification? Martin et Eadie (1999) ainsi que Martin et al. (2004) ont montré que le peuplier faux-tremble serait une espèce clé en forêt boréale mixte pour l'excavation de cavités et que cette essence est prisée par la majorité des EPC et des USC dans l'ouest du continent. Bien que cette essence soit présente dans l'Est du Canada, peut-on y attribuer un rôle clé aussi prépondérant que dans l'Ouest du continent? Par ailleurs, le peuplier faux-tremble est également une essence de plus en plus convoitée par l'industrie forestière de l'est du Canada (Messier 2002). Une autre question survient alors : si le peuplier faux-tremble est aussi important pour les pics dans l'est du Canada que dans l'ouest, quel est l'avenir des utilisateurs de cavités dans un contexte de prélèvement accru de cette essence?

Les pics ont des besoins particuliers pour leur survie mais ils jouent un rôle clé dans le cycle de vie d'autres espèces par la création de cavités (Martin et Eadie 1999, Bonar 2001, Martin et al. 2004). Leurs rôles écologiques sont nombreux et peuvent varier d'une espèce à l'autre. En comparaison des populations de l'ouest du continent nord-américain, nous disposons toutefois moins de connaissances sur l'utilisation du bois mort et vivant des oiseaux cavicoles à des fins de reproduction et d'alimentation dans la forêt boréale de l'est du Canada. Dans le but de tendre vers un aménagement forestier durable et écosystémique de la forêt boréale, il est capital de prendre en compte les besoins écologiques de ce contingent important de la diversité biologique de la faune vertébrée que sont les pics.

Les populations de Grand Pic, par exemple, ont diminué de façon drastique au début du siècle dernier dans plusieurs régions de leur aire de répartition (Hoyt 1957). La forêt boréale mixte représente la limite nord de la distribution du Grand Pic au Québec et son abondance y est faible (Gauthier et Aubry 1995). Les populations de cette région pourraient se voir menacées une fois de plus avec les coupes extensives qui y sont effectuées et qui éliminent les arbres de grand calibre. Dans le nord-ouest du Québec, la situation est d'autant plus inquiétante que l'industrie exploite depuis peu, et de plus en plus, le peuplier faux-tremble (Messier 2002), l'essence qui produit le plus rapidement les arbres de plus grand calibre et qui est utilisée fortement par le Grand Pic dans l'ouest du Canada (Bunnel et al. 1999, Bonar 2000). Le maintien de cette espèce en forêt boréale ainsi que des espèces associées passe par une meilleure connaissance de son utilisation de l'habitat ainsi que de ses exigences en matière d'arbres de reproduction et d'alimentation. L'alimentation est d'ailleurs peu souvent abordée dans les études sur la faune cavicole et le bois mort, qui mettent davantage l'accent sur les arbres à cavités comme facteur limitant pour les communautés d'animaux cavicoles. Toutefois, les arbres offrant un support d'alimentation adéquat sont également importants pour les excavateurs primaires. Ainsi, même s'il est important de porter attention aux habitats nécessaires pour la quête alimentaire des pics (Conner 1980, Hunter 1990), il est également important d'étudier les arbres d'alimentation pour déterminer la densité de chicots favorisant le maintien les populations d'oiseaux cavicoles (Imbeau et Desrochers 2002, Hutto 2006).

1.5 Objectifs de l'étude

Ce mémoire est divisé en deux volets : le premier porte sur la structure du réseau d'utilisateurs de grandes cavités en forêt boréale mixte et le second touche plus spécifiquement la quête alimentaire du Grand Pic.

De façon plus détaillée, le chapitre 1 a pour objectifs de déterminer 1) les paramètres affectant la sélection d'habitat faite par les pics à 3 échelles spatiales, 2) les caractéristiques des arbres de grand calibre disponibles pour l'excavation de cavités, 3) l'importance des grands excavateurs pour la Petite Nyctale, un utilisateur secondaire de cavité et 4) les espèces pouvant être désignée *espèce parapluie* parmi celles étudiées.

Dans le deuxième chapitre, les objectifs sont de 1) déterminer les facteurs importants qui distinguent les arbres utilisés pour l'alimentation du Grand Pic comparativement aux autres arbres disponibles, 2) déterminer à quelle hauteur le Grand Pic s'alimente sur les arbres et 3) vérifier si cette espèce vient se réalimenter année après année sur certains arbres en fonction de l'essence ou de la taille de ces arbres.

ARTICLE I

HABITAT USE, CAVITY TREE SELECTION, AND RELATIONSHIPS BETWEEN PRIMARY AND SECONDARY CAVITY NESTING BIRDS IN BOREAL MIXEDWOOD FORESTS OF EASTERN CANADA

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Abstract. As a transition zone between deciduous temperate and coniferous boreal forests, the eastern boreal mixedwood forest is characterized by a rich assemblage of cavity nesting birds (including seven woodpecker species). This ecosystem has been considerably disturbed by human disturbances (agriculture and industrial forestry) reducing the amount of older forests that harbour large live and dead trees required by these birds for nesting and foraging. We documented habitat use and cavity-tree selection of cavity nesting birds in a mixedwood landscape of eastern Canada's boreal forest in the Abitibi region, Québec. Presence-Absence and abundance of woodpecker species and cavity nesting owls were assessed using playbacks at 230 sites located along roads. Vegetation transects were conducted at the stand scale to quantify the availability of large trees. Landscape configuration analyses were accomplished to determine the stand and landscape characteristics associated with the presence of woodpeckers. For most woodpecker species, the probability of occurrence was better assessed with stand level habitat characteristics than with variables at the landscape level. Trembling aspen (*Populus tremuloides*) was the tree species that was the most often excavated by all primary cavity nesters (PCN) and we therefore suggest that this tree could be a key species in this ecosystem. Large PCN and secondary cavity nesters (SCN) showed associations whereas the Northern Saw-whet Owl (*Aegolius acadicus*) distribution was significantly correlated to the Pileated Woodpecker (*Dryocopus pileatus*), but not with the Northern Flicker (*Colaptes auratus*). This association suggests that the Pileated Woodpecker could be a keystone species for SCN species. Finally, Fleishman umbrella species index showed that the Northern Saw-whet Owl was the best umbrella species among the PCN and SCN species detected in our study area.

Keywords: multiscale habitat selection, keystone species, primary excavators, nest web, secondatory cavity users, trembling aspen, umbrella species

Introduction

In northern forest ecosystems of North America, cavity-nesting birds make up an important component of bird assemblages (Bunnell et al. 1999, Drapeau et al. 2002, Martin et al. 2004). This fauna is mainly associated with either recently disturbed sites such as burns (Drapeau et al. 2002, Saab et al. 2004, Hannon and Drapeau 2005) or older forests (Imbeau et al 2001, Imbeau and Desrochers 2002, Drapeau et al. 2003) given the availability of large live and standing dead trees (wildlife trees) required by these species to nest and feed. Even-aged forest management systems based on clear-cuts change, however, the age-class distribution of stands, increasing the proportion of young stands at the expanse of a considerable reduction of older forests (Spies et al. 1994, Drapeau et al. 2000, Bergeron et al. 2002), and, hence, reduction in the density of wildlife trees. There are thus raising concerns on the long term viability of populations of these species in managed forest landscapes.

Cavity-nesting birds have usually been divided into primary (PCN), weak primary (WPCN) and secondary nesters (SCN) (*sensu* Martin and Eadie 1999). PCN species (woodpeckers) are able to excavate their own cavities whereas WPCN (nuthatches and chickadees) can either create their cavities or use those produced by PCN. SCN species such as Northern Saw-whet Owl (*Aegolius acadicus)*, Wood Duck (*Aix sponsa)*, Northern Flying squirrel (*Glaucomys sabrinus*) or American Marten (*Martes americana*) cannot excavate their own cavities and thus rely on cavities created by woodpeckers or on natural tree cavities. In eastern Canada, at least 21 species use cavities including four owl and six duck species (Darveau and Desrochers 2001). Even in the northern boreal black spruce forest, where large trees are scarce, cavity nesting birds make up 15 % of the species composition of the avifauna in recently burned and in overmature forest stands (Drapeau et al. 2002).

In recent papers, Martin and Eadie (1999), and Martin et al. (2004) showed the existence of associations between PCN and SCN with regards to the successive use of cavities by these groups of species. In these papers, the authors suggest that these relationships generate a "*nest web*" which is analogous to the concept of food web where the central resource is the cavity instead of food. When natural cavities are rare, many species depend on cavity created by woodpeckers to survive (Bunnell et al. 1999, Aitken and Martin 2004, Martin et al. 2004). Low availability of cavities can increase competition between cavity users, thus constraining breeders' density (Newton 1994). In extreme cases, some species might be absent of a region where cavities are scarce. The more a species has a large body size; the less is its possibility to find a cavity with an appropriate entrance hole or internal volume (Bonar 2000). Hence, large excavators, such as Pileated Woodpecker (*Dryocopus pileatus*), are often designated keystone species since they are responsible for generating large holes required by large secondary cavity users (Bonar 2000, 2001, Aubry et Raley 2002, Martin and Eadie 1999). A keystone species has a disproportionate impact on its environment in comparison with its abundance or biomass (Paine 1969, Mills et al. 1993, Power et al. 1996), and its removal from the community will accelerate the decrease of the species diversity or produce other main transformations in the dynamic or structure of the community (Daily et al. 1993). Besides providing large cavities, Pileated Woodpeckers also have large territories and other specific habitat requirements (Savignac 1996, Bonar 2001). Thus, providing adequate habitat conditions for this species is likely to benefit many other species, whether they are cavity users or not (Lambeck 1997, Simberloff 1998). For this reason the Pileated Woodpecker has also often been designated as an umbrella species (Lafleur et Blanchette 1993, Flemming et al. 1999). An umbrella species may provide targets to select minimal standards for the composition and structure of the smaller possible area protected in reserve network (Roberge and Angelstam 2004). Frequently, conservationists use keystone and/or umbrella species as shortcuts in wildlife management (Simberloff 1998, Lambeck 1997, Roberge and Angelstam 2004). However, these functional statuses are often attributed without empirical validation (Caro and O'Doherty 1999, Andelman and Fagan 2000, Fleishman et al 2001).

Few studies conducted on cavity-nesting birds have investigated relationship between PCN and SCN (but see Martin and Eadie 1999 and Martin et al. 2004) even if knowledge of nest-site selection by PCN is essential to understand SCN cavity use (Kerpez and Smith 1990). In the boreal forest, natural cavities are rare given the fact that stands are dominated by conifers (Courteau et al. 1997) which do not produce natural cavity when a large branch breaks off as it is the case for deciduous trees (Jackson and Jackson 2004). Thus, the association between PCN and SCN is likely to be stronger in boreal forests. In addition, large trees (> 20 cm) in this system are naturally uncommon (Boucher et al. 2003) and by truncating older forest cover types, timber management has further reduced their availability (Bergeron et al. 2002). Thus, PCN populations may be limited by low availability of large nesting trees that may in turn directly affect SCN species. To manage boreal forests adequately with regards to biodiversity, it is thus important to determine how cavity-nesting birds are individually responding to stand structural features and the amount of forest cover at both stand and landscape scales, and how these species are linked to one another with regards to cavity trees availability.

In this paper, we document cavity-nesting birds' distribution patterns in a boreal mixedwood landscape in northwestern Québec, Canada. First, we determine the relationships between individual species and habitat conditions at both stand and landscape scales. We then measure cavity-tree selection by PCN birds as we compare cavity-trees used by small and large excavators with the availability of live trees and snags in the sampled stands. Multi-scale analyses were accomplished to determine which factors, and at which spatial scale, are the most critical for habitat selection patterns by woodpeckers. As large excavators (Pileated Woodpecker and Northern Flicker (*Colaptes auratus*)) may play a crucial role in the boreal forest given the low availability of large trees, we examine their role as potential keystone species for SCN species, which use large cavities to reproduce. For this analysis we used cavity-nesting owls (Northern Saw-whet, Boreal (*Aegolius funereus*) and Barred Owls (*Strix varia*)) because, unlike other SCN such as mammals and ducks, they are easily surveyed with playback methods. Also, a complete examination of the studied guild is done to determine which species is most susceptible of being designated as an umbrella species.

Methods

Study area

The study area is located in the Abitibi -Témiscamingue region, Québec, Canada (47° 46 to 49° 00' N; 79°53' to 78°22' W). This study area covers almost 10 000 km^2 (MRN, 2001) of the bioclimatic balsam fir-white birch domain included in the boreal forest (MRNF, 2006). The land base is characterized by a mixture of deciduous, mixed and coniferous stands composed of either pure or mixtures of trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), and white spruce (*Picea glauca*). Most of the forest is on public lands and is allocated by the Quebec government (MRN, 2001) to the timber industry. Since the region has been colonized in the early 1930's (MRN, 2001), a large proportion of the land base is composed of young stands (30-50 years) (Grenier et al. 1998). The study region is part of a broad physiographic unit known as the clay belt, which extends across northern Quebec and Ontario. The flat topography originates from lacustrine deposits of proglacial lakes Barlow and Ojibway (Vincent et Hardy 1977).

Sampling design

All sampling stations were distributed along the road network of the entire study area. To avoid double counting of individuals, particularly species with large home ranges (Pileated Woodpecker and Northern Saw-whet Owl) and to ensure that landscape metrics measured were completely independent (see multi-scale habitat characterization below), sampling stations were at least 3 km apart from each other. Given the travel distances within the study area we first located a subset of 150 sampling stations in the southern part in 2004, whereas 80 additional sampling stations were located in the northern section in 2005 (Figures 1 and 2). We used a stratified sampling design to cover the range of mature forest cover (both in terms of proportion and stand composition) that characterizes the land base (Table 1). Overall, these 230 sampling stations provided extensive coverage of the study area.

Bird surveys

All bird surveys were conducted from the road by a team of two observers in a similar fashion as to the *Breeding Bird Survey* (BBS) program (Link and Sauer 1998). The owl survey was conducted once between 20 April and 7 May in 2004 and in 2005 using a recording consisting of one minute call sequence, beginning with the smallest owl, separated by pauses of one minute and each playback session was preceded by a one minute pause. Our sampling strictly focuses on cavity-nesting owls: Northern Saw-whet, Boreal and Barred Owls. All owls observed or heard were recorded and their distance was estimated (0-250m, 250-500m, 750-1000m and more than 1000m). During the first nights, observers used triangulation to improve our distance estimates of the birds that were heard. Each sampling station was visited between 30 minutes after sunset and 2:00 in the morning EST. Only one visit could be conducted to cover our study area during the peak of the singing activities of northern saw-whet owls, the species more likely to be found in our area, even if it has recently be convincingly demonstrated that more than one visit is necessary to take into account probability of detection in presence-absence studies (MacKenzie et al. 2006). However, a recent study has shown that detection probability of these three forest owls was unaffected by habitat availability in northern Ontario (Sleep 2005). Overall 178 sampling stations where sampled to detect these owl species over the two years of this study.

Woodpecker censuses were conducted twice at each station between 7 May and 11 June in 2004 and in 2005 using a recording consisting of one minute drumming-call sequence separated by one minute pauses between each species. All woodpecker species known to be present in the region were surveyed: Downy (*Picoides pubescens*), Hairy (*P. villosus*), American Three-toed (*P. dorsalis*), Black-backed (*P. arcticus*) and Pileated Woodpecker, Yellow-bellied Sapsucker (*Sphyrapicus varius*) and Northern Flicker. Each playback session was preceded by a one minute pause. Sampling began at sunrise and ended before 11:00. When a visit was first accomplished at sunrise, the second time, it was done later in the morning. We recorded all woodpeckers detected by sight or sound and estimated their distance in radius categories of 0-50 m, 50-250 m, 250-500 m, 500-750 m and more than 750 m. Woodpeckers and owls calls were broadcasted all around the observers during days with little or no wind and light or no rain. In analyses for bird-cover association and keystone designation, only birds heard inside our stand radius of 250 m were considered to ensure that they were using the habitat characterized at the sampling station.

Live trees, snags and cavity sampling

Live tree and snag availability were measured at each sampling station along line transects of 500 m long x 2 m wide. These transects were oriented perpendicularly from the road, with the bird sampling station as center of each transect. All trees, dead or alive, with a diameter at breast height (dbh) over 10 cm and at least 1.40 m tall were recorded. For each tree, we noted the tree species, the diameter at breast height (dbh) and the decay class. We used a tree decay classification system that ranged from 1–8 for standing trees, with 1 indicating a live tree with no visible signs of decay, 2 indicating a live tree with visible signs of decay, 3 indicating a dying tree with numerous signs of decay, 4-8 dead trees with advancing stages of decay (from Imbeau and Desrochers 2002) and ranged from 9-13 for logs

(Maser et al. 1979). Our classification for remnant tree bark recognized seven classes: (1) tree covered by 100% of bark, (2) >95%, (3) 95%> x >75%, (4) 75%> x >50%, (5) 50%> x > 25%, (6) 25% > x > 1% and (7) no bark present. All tree species with a frequency of occurrence over 5% were retained for analysis (black spruce, balsam fir, jack pine, trembling aspen, white birch) and all remaining species (willows sp. (*salix* sp.), white spruce, balsam poplar (*Populus balsamifera*), tamarack (*Larix laricina*), pin cherry (*Prunus pensylvanica*), coniferous sp., poplar sp. (*Populus* sp.), unknown species, red maple (*Acer rubrum*), eastern white-cedar (*Thuja occidentalis*), spruce sp. (*Picea* sp.), deciduous sp., black ash (*Fraxinus nigra*), maples sp. (*Acer* sp.), eastern white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*)) were pooled in the category *Others*.

Each cavity tree detected from these 230 line transects was also characterized by the same variables. Cavity entrance size was visually estimated and assigned to four possible groups of excavators (i.e. cavities excavated by small (Downy Woodpecker), medium size (Hairy, Black-backed and American Three-toed Woodpeckers and Yellow-bellied Sapsucker), large (Northern Flicker) and very large excavators (Pileated Woodpecker)).

Forest cover characterization at multiple scales

Four major cover types were identified for this study using composition variables derived from digitized provincial forest inventory maps (1:20 000). Three were defined as mature forests (coniferous, deciduous or mixed), which represented trees of >12 m with a canopy cover over 40%. Mature coniferous or deciduous forest cover types, had more than 75% of the basal area composed of coniferous species or deciduous species respectively. The basal area of a mature mixed forest types had between 25 to 75% of coniferous trees. Open habitats were described as stands where trees are small (less than 4 m) and canopy cover was < 25%. Alder stands, wetlands, as well as recently disturbed forests (clear-cuts and young plantations), were classified in this habitat type.

These four cover types were first measured at the stand scale, i.e. within a radius of 250 m centered on our sampling stations. This radius, encompassing an area of approximately 20 ha, corresponds to or is smaller than the mean home ranges of most of the woodpecker species under study. The same measures were compiled at the landscape-scale which corresponds in this study as an area at least three times larger than the mean home range of species. Hence, for species with home range of less than 100 ha, we used a 1 km radius as our landscape analysis area whereas a radius of 1,5 km was used to characterize landscape-scale cover types for species with larger home ranges (Pileated Woodpecker, Northern Flicker and Northern Saw-whet Owl). All multi-scale cover type measures were performed on ArcGIS 9.0 software.

Statistical Analyses

Multi-scale habitat use analysis

In order to determine which factors and at which scales they were most influential in PCN and SCN habitat use, several a priori logistic regression models were compared using Akaike's Information Criterion (AIC). At each spatial scale, specific variables were selected for each species, based on known nesting habitat preference according to the available literature (see Table 2 for selected factors by species). Correlations between parameters were examined: no parameters included within a single model were highly correlated ($r > 0.7$) (Hinkle et al. 1979). When several of those models competed ($\Delta AIC < 2$) or in order to precise which variable within a retained model had a stronger influence, multimodel inference was used to determine weighted average parameter estimates of each variable (Burnham and Anderson 2002).

Live tree and snag availability and their use by woodpeckers

To identify tree species which were over- or under-represented in the different dbh classes sampled in our study area, a Wilcoxon signed ranks test was performed. Trees were divided in four groups: small (dbh 10 cm – 14.9; 15-19.9 cm) and large (dbh ≥ 20-24.9 cm; >25 cm) trees.

To determine if woodpeckers excavated trees randomly or if they selected specific tree species, a compositional analysis was conducted using 1000 iterations (Aebischer et al. 1993). Line transects with three or more cavities were used for this analysis ($n = 29$) and cavity-bearing trees were compared to trees available in transects at the same sampling stations. Since more than 85% of the cavities were excavated in trees with a dbh over 20 cm, suggesting the existence of a minimum threshold for cavity creation occurring approximately at this size, only trees with a dbh >20 cm were considered as available in this analysis.

To point out potential effect of state of the tree (live vs. dead) between selected trees and nearest available trees, a case-control logistic regression analysis was done. Only trees with recently excavated cavities (i.e. cavities with ring of light color and/or where chips on the ground were found) were used for analysis involving state of tree (i.e. live or dead), such characteristics being affected by time since excavation and where also compared with the closer tree of same state (dead tree compared with nearest dead tree and alive tree compared with nearest alive tree). For these analyses, excavators were divided in two categories: small and medium pooled (Downy, Hairy, Three-toed, Black-backed woodpeckers and Yellow-bellied Sapsucker) and large (Pileated Woodpecker and Northern Flicker) excavators. When a cavity-bearing tree had a small and a large cavity, this tree was used twice for analyses: once in small cavity analyses and once in large cavity analyses. To know which characteristics influence cavity tree selection, used dead trees (bearing small cavity n = 144-151[1] and large cavity n= 55) were compared to dead trees available along transect (n = 698) and a standard logistic regression analysis was done. Only transects where cavities were found were used for this analysis.

PCN-SCN relationships

To determine if the large PCN species (Pileated Woodpecker and Northern Flicker) might play a keystone role in the mixedwood boreal forest, we looked at the possible association of their presence with the presence of large SCN species. Chi-square tests were performed to verify this potential relationship. Only Northern Saw-whet Owls could be considered for this analysis since the relative abundance of Barred and Boreal Owls were too low, respectively 1% and <1%. Every birds detected at an unlimited distance were used for those analyses.

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[1] The quantity of cavity bearing trees varies from 144 to 151 because some data are missing.

Identification of umbrella species

To measure the potential of each species (n = 8 species) to be considered as a valuable umbrella species for the studied guild, an umbrella index was calculated for each species according to Fleishman et al. (2000). This index has three criteria: the proportion of co-occurring species, the ubiquity degree and the sensitivity to human disturbance (Fleishman et al. 2000, 2001). Each criterion has a value between 0 and 1 (where 1 is the highest and favoring the species to be an umbrella species). By the summation of these three values, we get an overall value for the umbrella index. The best umbrella species should be those getting a score above the average of all criteria's results added to the standard error of this average. To measure the degree of human sensitivity for each species, data from Hansen and Urban (1992) were used (Table 3). Three conditions are generally recommended to consider species for this index: the species should be abundant without being ubiquitous, it should be sensitive to human disturbance and its occurrence must be over 5% (Fleishman 2000).

Results

Bird species occurrences and habitat use models

The Northern Flicker (74%) and the Yellow-bellied Sapsucker (78%) were the most frequent woodpecker species detected in the 230 sampling sites (Table 4). All woodpecker species occurrences, at the exception of the Downy Woodpecker, were lower the second year. This diminution varied from 1.5% to 19.4%. The two large excavators of this study, Northern Flicker and Pileated Woodpecker, had very different abundances, i.e. respectively 1.34 and 0.15 bird detected by sampling station. In this mixedwood environment, the occurrence of boreal woodpeckers, Black-backed and Three-toed Woodpeckers, were the lowest among the studied guild of woodpecker species. Boreal and Barred owls were almost absent of the study area with a very low occurrence (<1% and 1%).

For most species, stand and landscape variables provided an improvement in the goodness-of-fit of the models over the null models that only considered the species' frequency of occurrence (Table 5). The Pileated Woodpecker was the only species where the null model alone was our best model, followed by a model that included the density of trees with a dbh over 25 cm (T25). This model did not however strongly improve the goodness of fit of the null model. For all woodpeckers habitat use was linked with variables measured at the stand level. Models including either tree density or cover types variables measured within a radius of 250 m ranked high in explaining woodpeckers occurrence in our study area. Northern Flicker, Hairy Woodpecker, and Boreal woodpeckers' best models in the set of candidate models all consisted in stand level variables. Models with landscape variables often had high AIC values but those that showed AIC < 2 where distributed across all categories of cavity users including small (Downy Woodpecker), medium (Yellow-bellied Sapsucker), and large users (Northern Saw-whet Owl). The Yellow-bellied Sapsucker was the only woodpecker species to respond to both stand and landscape level variables whereas the model with the lowest AIC included both sets of explanatory variables. The Northern Saw-whet Owl was the only species to respond to landscape scale variables only (Table 5).

Model averaging of species that were associated with stand level variables indicates that the Hairy Woodpecker was the only species where tree density (T20) increased its probability of occurrence (Table 6). Hence, for most species associated with stand level variables, proportion of habitat types within 250 m measured with digitized forest cover maps was a good predictor of species occurrence. The Yellow-bellied Sapsucker is influenced by the presence of large trees as well as by the mature deciduous and mixed forest present at the landscape scale. All important parameters retained according to this analysis had relationships in agreement from those expected (Table 2).

Tree and snag availability

A total of 16138 trees with DBH $\geq$ 10cm were sampled including 1558 very large trees (DBH $\geq$ 25cm). Trembling aspen and black spruce were the most abundant tree species, with a proportion of 24 and 22% respectively in the sample set (Figure 3). Almost 50% of the large trees were trembling aspen. Trembling aspen was over-represented in the large tree category (i.e. dbh > 25 cm)($Z = -7.3$, $P < 0.05$). Trembling aspen was also over-represented in the 20-25cm dbh category ($Z = -3.85$, $P < 0.05$) accompanied with jack pine ($Z = -3.77$, $P < 0.05$). In the 10-15 cm dbh category, black spruce and balsam fir were over-represented ($Z = -6.98$, $P < 0.05$ and $Z = -7.22$, $P < 0.05$).

Cavity trees

A total of 210 excavated cavities were found in 138 different trees (90% of these trees are snags). When recently excavated trees were compared with the closest available trees, it was clearly found that woodpeckers excavated significantly more in dead trees ($\chi^2 = 9.01$, $P = 0.02$, $n = 22$). The dbh of trees excavated by small woodpeckers ranged from 13 to 65 cm (mean 33.69 ± 1.62 cm) whereas the dbh of excavated trees by large woodpeckers varied from 16 to 78 cm (mean 29.45 ± 0.87 cm; Table 7). Most cavities (87%) were found in trees with DBH $\geq$ 20 cm and 66% of all cavities were in large trees (DBH $\geq$ 25 cm) (Table 8). Among snags, there was a significant difference between cavity-bearing trees and available trees for small and large excavators since both tended to select larger trees than dead trees available inside the transects ($\chi^2 = 233.0$, df = 1, $P < 0.001$, $n = 849$ and $\chi^2 = 144.3$, df = 1, $P < 0.001$, $n = 754$). The percentage of remnant bark of trees was found to influence woodpecker's cavity tree selection: woodpecker excavated cavities in trees with less remnant bark (small PCN: $\chi^2 = 32.4$, $P < 0.001$, df = 1, $n = 842$ and large PCN: $\chi^2 = 29.4$, $P < 0.001$, $n = 753$) than available dead trees inside the transects (Figure 4). Small PCN excavated more on more decayed trees than those available ($\chi^2 = 4.2$, $P = 0.04$, df = 1, $n = 849$) meanwhile no significant selection is observed in the case of large PCN for this parameter ($\chi^2 = 0.06$, $P = 0.8$, df = 1, $n = 754$)

Tree species use by woodpeckers for excavation was not random ($\chi^2 = 76.2$, df = 5, $P = 5.23\text{x}10^{-15}$, $n = 29$). Trembling aspen was the most preferred tree species (Table 9) as 65% of cavities were found in trembling aspen (Table 8) (including 86% of snags). Balsam fir, jack pine and black spruce were the less excavated trees and were used in the same proportion as their availability in our sampled sites (Table 9).

PCN-SCN relationships

Surveys conducted at similar sampling stations for large woodpeckers and owls were conducted in 178 sites. There was no significant association between occupied sites of the Northern Flicker and those occupied by the Northern Saw-whet Owl ($\chi^2 = 1.2$, df = 1, $P = 0.26$). However, a highly significant correlation ($\chi^2 = 7.3$, df = 1, $P = 0.007$) was found between the occupied sites of the Pileated Woodpecker and those occupied by the Northern Saw-whet Owl. Hence, for cavity-nesting birds requiring large cavities, according to our results with the Northern Saw-whet Owl, the Pileated Woodpecker was more likely to be a keystone species than the Northern Flicker.

Umbrella species

For all PCN and SCN species the average of all scores for the Fleishman umbrella index was 1.81 with a standard error of 0.30. The threshold for the identification of umbrella species was therefore 2.11 (Table 10). The Northern Saw-whet Owl was overall the only bird to show a better score than this threshold. The same conclusion can be done even when the two years of this study were analysed separately. Pileated Woodpecker was the most sensitive species to human disturbance (DSI = 1.00) and it tended to cohabit easily with other species (PCS = 0.45). The Northern Saw-whet Owl had the highest degree of ubiquity which was 0.94. Being the most detected species in our surveys, Yellow-bellied Sapsucker had the smallest score with an index value of 1,47.

Discussion

Habitat models

It is well known that habitat selection in birds relies on many spatial scales (Hilden 1965, Hutto 1985, Wiens 1989, Lawler and Edwards 2006). Since the 1990's, ecologists have emphasized the importance of the landscape context in wildlife species habitat use (Freemark et al. 1995, McGarrigal and Mc Comb 1995, Villard et al. 1999). However, stand habitat characteristics remain important variables in the explanation of bird distribution patterns (Drapeau et al. 2000, MacFaden and Capen 2002). MacFaden and Capen (2002) found that the occurrence of larger species such as crows and woodpeckers were, however, more predicted by landscape features. Our results indicate that for the majority of the studied woodpeckers, models with stand level parameters had the highest AIC ranks with the Aikaike model selection approach. The variables that were most often associated with woodpecker's occurrence at the stand scale consisted in amounts of cover types and not fine-grained variables such as stem densities of appropriate nesting or foraging substrates. Hence, a coarse variable such as the amount of mature forest at the stand scale was a better predictor of most woodpecker species occurrence than a more fine-grained variable such as the density of large trees in the sampling station.

As for the importance of landscape level variables in model selection, the Yellow-bellied Sapsucker was the only woodpecker species to have landscape level parameters in its "best" model. The occurrence of our most frequent large secondary cavity-nester, the Northern Saw-whet Owl, also increased with the amount of mature deciduous and mixed forests and with the amount of open habitats at the landscape scale. That most models with landscape variables were not highly ranked does not mean that woodpeckers are not influenced by landscape scale variables in our study area. Indeed, within the set of candidate models, global models (stand + landscape variables) came out has either competing (AIC < 2) or second best models for 4 of the 6 species analyzed. Downy Woodpecker and the Yellow-bellied Sapsucker had global models with AIC < 2. This suggests that these species were influenced by the features at many spatial scales (Bergin 1992, Lawler and Edwards 2006). Hence, even though variables measured at landscape scales were not the main predictors, examination of cavity-nesting birds responses on several spatial scales was necessary to provide a more complete and integrated view of habitat use (sensu Gutzwiller and Anderson 1987) by these species with home-ranges that often encompass a mosaic of stand types in forests ecosystems.

Finally, landscape models for large PCN species (Northern Flicker and Pileated Woodpecker) were not higher ranked in their respective sets of candidate models than those of small PCN species. Northern Flicker selected its habitat in function of the presence of mature forests but it is also the only species which is significantly associated with open areas, according to the model-averaging approach. In fact, this bird feeds in and is often associated with open areas (Burns 1900), can adapt to relatively open conditions (Dennis 1969) and nest near or in openings (Conner and Adkisson 1977, Scott et al. 1977). This association with open habitats explains why it is abundant in timber harvested landscapes in the eastern boreal forest where aggregated cutover areas provide openings (Drapeau et al. 2000, Gagné 2006). At the opposite, the Pileated Woodpecker is more sensitive to the reduction of old forests and to the expansion of agriculture (Scott et al. 1979). In addition, its abundance is generally low (Scott et al. 1979) and it needs large trees to excavate its cavity. The low density of large trees can partly explain its very low abundance in the northern section of the commercial boreal forest. Since our result shown that most of the large trees in our study area were trembling aspen, this tree species likely gets additional importance for the occurrence of this woodpecker species in boreal regions. Indeed, the quantity of stems over 25 cm of dbh was the only variable associated with the presence of the Pileated Woodpecker, even though the null model was still the best model according to AIC values obtained. In our study we suggest that the low occurrence of this species could explain why no other environmental features were found to influence its habitat selection.

Tree and snag availability

The most available tree species in our study area were trembling aspen and black spruce. The black spruce was the most abundant species in terms of stem density. However, most stems of this tree species had a dbh under 20 cm, below a threshold for hole excavation by most PCN birds. In contrast to black spruce, the majority of large trees ≥ 20 cm were trembling aspen in our study area. Our results corroborate Julien and Darveau (2005) analysis of Québec forest inventory data that showed that in boreal mixedwood forests, black spruce with dbh > 20 cm are rare whereas trembling aspen and white birch are the dominant tree species when considering dbh classes over 20 cm in this forest ecosystem. Moreover, trembling aspens reach large size diameters early in the successional stages, i.e., only 65 years after stand initiation (Julien and Darveau 2005). Boucher et al. (2003) have shown with forest inventory data that black spruce forests at the north of our study area support even less large stems (dbh > 20cm). Thus, in the eastern boreal forest, the southern mixedwood fringe represents a sector with a higher potential for providing larger trees.

Cavity trees

Trembling aspen was the most excavated tree species by all woodpecker species regardless of their size and the size of their excavated holes. This preference for trembling aspen was also observed in other forest regions in North America (Dobkin et al. 1995, Martin and Eadie 1999, Martin et al. 2004). Martin et al. (2004) suggest that this preference could be explained by aspen's higher susceptibility to heartwood rot, producing a softer substrate for excavation. Jackson and Jackson (2004) show that living trees experiencing fungal invasion may indeed provide appropriate excavation substrates by isolating the infected rotten portion of the stem and maintaining solid parts around the pocket of decay. Such conditions facilitate excavation while providing external sound wood that provide a more secure environment. While higher susceptibility to fungi invasion may also occur in trembling aspens in our study area, another possible explanation for this obvious preference by all woodpeckers may be that 85% of cavities were excavated in large trees (dbh > 20 cm) whereas trembling aspen make up 52 % of all available large trees in our study sites. This overwhelming selection for trembling aspen may thus reflect the high availability of this species in the large dbh classes. The pattern by which all woodpeckers, including small species, excavate in the largest trees among those available has also been found in aspen woodlands of the northwestern Great Basin where all woodpecker species studied selected trees of a dbh ≥ 24cm (Dobkin et al. 1995). Excavation in larger trees may be linked with a better isolation and protection of cavities against strong winds and predators, and they will stand for a longer period (Raphael and White 1985, Jackson and Jackson 2004). This could explain why small woodpeckers also excavate large trees even though they could use smaller trees as nesting substrates. Furthermore, several woodpecker species also tend to forage on larger trees among those available (Savignac 1996, Gunn and Hagan III 2000, Nappi et al. 2003), highlighting the importance of large trees for all uses by woodpeckers.

For medium size cavity-dwellers our results may not reflect every species' individual preferences since the Yellow-bellied Sapsucker was the most detected species within this group of excavators and it is known to prefer trembling aspen for excavating cavities (Kilham 1971, Peck and James 1983). Thus, because we could not determine the excavator identity for the sampled cavities, our results may not necessarily apply to the other medium size cavity nesters (Black-backed, Three-toed, Hairy and Downy woodpeckers) in our area. Yet, small and large cavities were also preferentially excavated in trembling aspen. Consequently, we suggest that trembling aspen is a critical tree species for cavity-nesting birds in the boreal mixedwood forest of Québec. These results corroborate Bunnell et al. (2002) and Martin et al. (2004) findings for mixed forests of interior British Columbia, highlighting that the key role of aspen for cavity nesters may be found across a significant part of its range within northern boreal mixedwood forests. Such dominant use of a single tree species by different species of cavity-nesting birds has not been observed, however, in other studies and other forest ecosystems. In a study conducted in woodland streamsides of Wyoming, Gutzwiller and Anderson (1987) did not find consistent use of a tree species by cavity-nesting birds in cotton-wood willow stands whereas Raphaël and White (1984) also observed a wide use of different tree species for cavity dwelling species among the community of cavity-nesting birds in Sierra Nevada.

Our results showed that cavity-bearing trees were usually more decayed and had less remnant bark than other available trees. Then, woodpeckers excavated more on dead trees being easier to excavate than living trees. Indeed, trees in advanced decaying stages are usually softer, and therefore do not provide protection against variations in temperature (Wiebe 2001) and other natural risks. The fact that most cavities were found in trembling aspen might partially be explained by the fact that this tree species maintains structural integrity many years after its death (Harestad and Keisker 1989). This selection towards dead and rotten trees is not surprising for the group of small woodpeckers since most of them are weak excavators.

Large PCN-SCN relationships

The presence of woodpeckers in forest ecosystems is often crucial for secondary cavity-nesting bird populations which can become limited by an insufficient amount of cavities (Holt and Martin 1997, Scott 1979, Brawn and Balda 1988). For large SCN species the presence of large PCN, such as Pileated Woodpeckers, may be critical since their cavities often reach the size required by large cavity users. In recent years, several studies have documented the SCN guild using the Pileated Woodpecker's cavities (Martin and Eadie 1999, Bonar 2000, Martin et al. 2004). However, few studies have demonstrated the crucial role of these cavities for large SCN, in addition to the availability of natural cavities. Without detailed data on availability and use of natural and excavated cavities over a long period, or a detailed analysis of cavity selection by large SCN, we suggest that the possible co-occurrence between large PCN and large SCN should be a first possible indication of the keystone role of large PCN. Our results show a significant association between the Northern Saw-whet Owl and the Pileated Woodpecker but not with the Northern Flicker. We therefore suggest that the low occurrence of Pileated Woodpecker and its relationship with the Northern Saw-whet Owl may confer to this large excavator a keystone role in our studied region. However, further investigation, such as cavity availability and use, should be done to grant this status with more confidence to the Pileated Woodpecker. Nevertheless, our association between the presence of Pileated Woodpecker and the Northern Saw-whet Owl could be explained by (1) the low availability of natural large cavities in our region – none being found in this study (2) the site-fidelity of Pileated Woodpecker to its breeding territory year after year, conferring to occupied sites a likely higher availability of old holes than in unoccupied sites. Recently, it has been documented that the Northern Saw-whet Owl seems to prefer nesting in Pileated's cavities than in others cavities on the Canadian west coast (Martin et al. 2004 but see also Johnson and Anderson 2003). This selection for Pileated's cavities over Northern Flicker's cavities probably occurs because larger cavities provide a better isolation, are more durable, reduce competition between chicks, and offer a better heat dispersion and a possibility to raise more chicks per clutch (Aubry and Raley 2002, Aitken and Martin 2004). Many other species, such as the Boreal Owl, also prefer Pileated Woodpecker's cavities for the same reasons (Hayward et al. 1993). In addition, some species cannot fit in smaller cavities, which is the case of large owls, arboreal ducks, and some carnivores (Bonar 2000, Darveau and Desrochers 2001, Aubry and Raley 2002). Since this large excavator is rare, a high demand for Pileated's cavities might occur in our studied area, possibly creating competition among large SCN living in this region.

For smaller secondary cavity nesters, it is likely that other excavators may play a crucial role in our ecosystem, similarly to Martin and Eadie (1999) which found the Red-naped Sapsucker and the Northern Flicker to be the keystone cavity excavators for mixedwood forest of north central British Columbia.

Umbrella species

By protecting an umbrella species, many other species are protected since it shares its vast territory with many other co-occurring species (Simberloff 1998, Roberge and Angelstam 2004). Using Fleishman's criteria (Fleishman et al. 2000, 2001), the Northern Saw-whet Owl came out as the best umbrella species candidate within our studied group of cavity-nesting birds. This result is not surprising since this little owl has a large territory (between 73 and 250 ha in boreal and boreal-ecotone forest) (Milling et al. 1997), with a regional status that makes it a common species without being ubiquitous. It also co-occurs with the Pileated Woodpecker and the Northern Flicker since it can nests in their cavities (Martin et al. 2004). As some broad-scale programs of owl monitoring are currently implemented across Canada, as example the Nocturnal Owl Monitoring in North America

(Takats et al. 2001), our results suggests that they could also give an indirect measure of the status of the primary-excavating woodpecker guild, at least in the surveyed areas within the eastern boreal mixedwood forest. On the other hand, we need to be cautious when using the Northern Saw-whet Owl as an umbrella species, since apart limited nesting opportunities related to cavity availability, its populations could be regulated by the dynamics of small mammal populations (Swengel and Swengel 1997, Cheveau et al. 2004). However, this umbrella status was obtained in both years of our study, despite the fact that small mammal abundance could be fluctuating over a short four year-cycle in our study area (Cheveau et al. 2004).

Conclusions and management implications

Even though an important proportion of the land base in our study area was transformed by agriculture and forest management, the remaining forests had a rich PCN guild where the Northern Flicker and the Yellow-bellied Sapsucker were the most abundant species. This overwhelming use of trembling aspen in our study area is related to its dominance in large dbh classes (> 20 cm) in forest stands. Given that most of the cavities (small and large) detected in the field were in trees larger than 20 cm of dbh, the maintenance of large and old trembling aspens in managed mixedwood forests becomes a key conservation issue for ensuring the maintenance of cavity-nesting birds in this forest ecosystem. A special attention should thus be given to trembling aspen, notably through improved sylviculture practices that favour permanent retention of large live stems and snags, since this species was the largest tree species and the most excavated trees in our study area. Habitat models suggest that mature forest cover was an important predictor of the occurrence of most woodpecker species. This variable came out more often at the stand scale (within most species home range) than at the landscape scale, suggesting that most species can accommodate variable proportions of mature forest cover at the landscape scale if a sufficient amount mature forest is available within most species' home range (our stand scale that covers an area of 20 ha).

Finally, the positive correlation between the Pileated Woodpecker and the Northern Saw-whet Owl provides a first insight on keystone interactions between large PCN and SCN species in our study area. A better understanding of these relationships will require however, further studies that should focus on large cavity searches and monitoring of those cavities over several years to establish the direct links between the keystone excavators for SCN species, in particular the Northern Saw-whet Owl. A special attention should be given to the Pileated Woodpecker since it seems to be a keystone species by creating large cavities used by the Northern Saw-whet Owl which is moreover an umbrella species for this guild of cavity users.

FIGURE LEGENDS

Figure 1. Localization of the study area within the Quebec province (in dark grey and black).

Figure 2. Map of the study area. Green regions represent forests, pink regions represent cultivating lands and blue regions show lakes and rivers.

Figure 3. Available stem density broken by tree species and dbh classes within the 230 sampling stations of an eastern boreal mixedwood forest landscape in Québec, Canada. AT= trembling aspen, BP= paper birch, FB= balsam fir, PJ= jack pine, SB= black spruce.

Figure 4. Cavity-bearing tree characteristics in relation to availability within the vegetation transects of an eastern boreal mixedwood forest landscape in Québec, Canada. Proportion of cavities excavated by large (n = 56) and small (n = 154) excavators and availability of trees along transect (n = 698). (A) decay state: 1= live tree with no visible signs of decay, 2= live tree with visible signs of decay, 3= dying tree with numerous signs of decay, 4-8= dead trees with advancing stages of decay (Imbeau and Desrochers 2002) (B) classes of percentage of remnant bark: (1) tree cover by 100% of bark, (2) >95% of bark, (3) 95%> x >75%, (4) 75%> x >50% of bark, (3) 50%> x > 25%, (2) 25% > x > 1% and (7) no bark present, (C) diameter diameter at breast height (dbh) divided in four categories: 10 to 15 cm, 15 to 20 cm, 20 to 25 cm and > 25 cm.

Figure 1

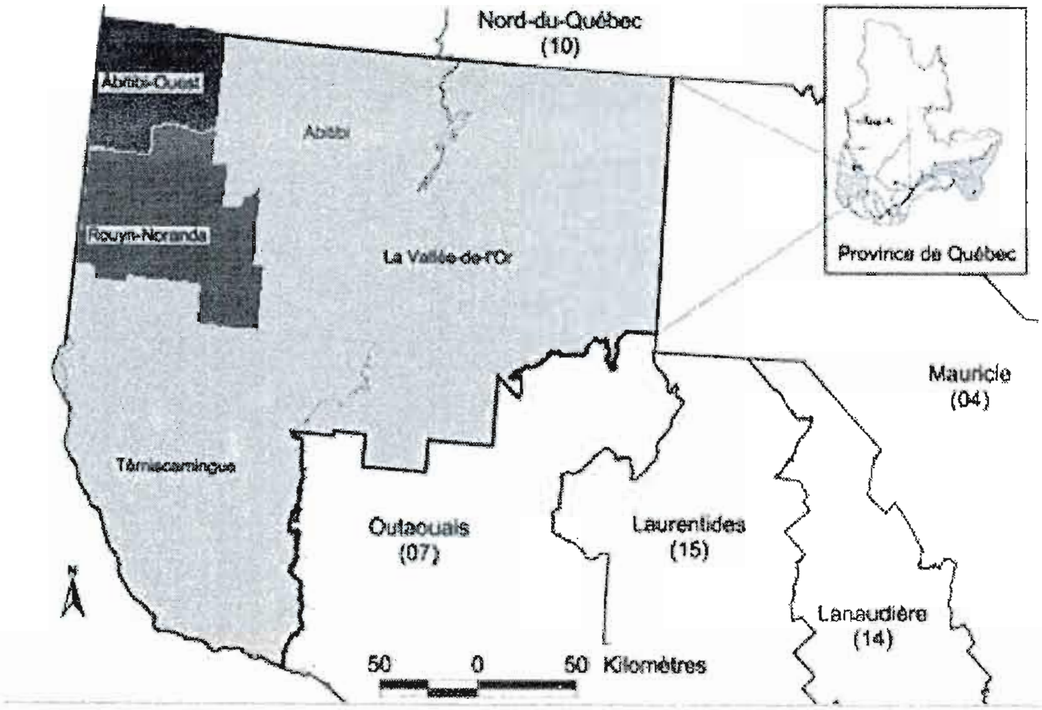

Nord-du-Québec
(10)
Abitibi-Ouest
Abitibi
Rouyn-Noranda
La Vallée-de-l'Or
Témiscamingue
Province de Québec
Mauricie
(04)
Outaouais
(07)
Laurentides
(15)
Lanaudière
(14)
N
50 0 50 Kilomètres

Figure 2

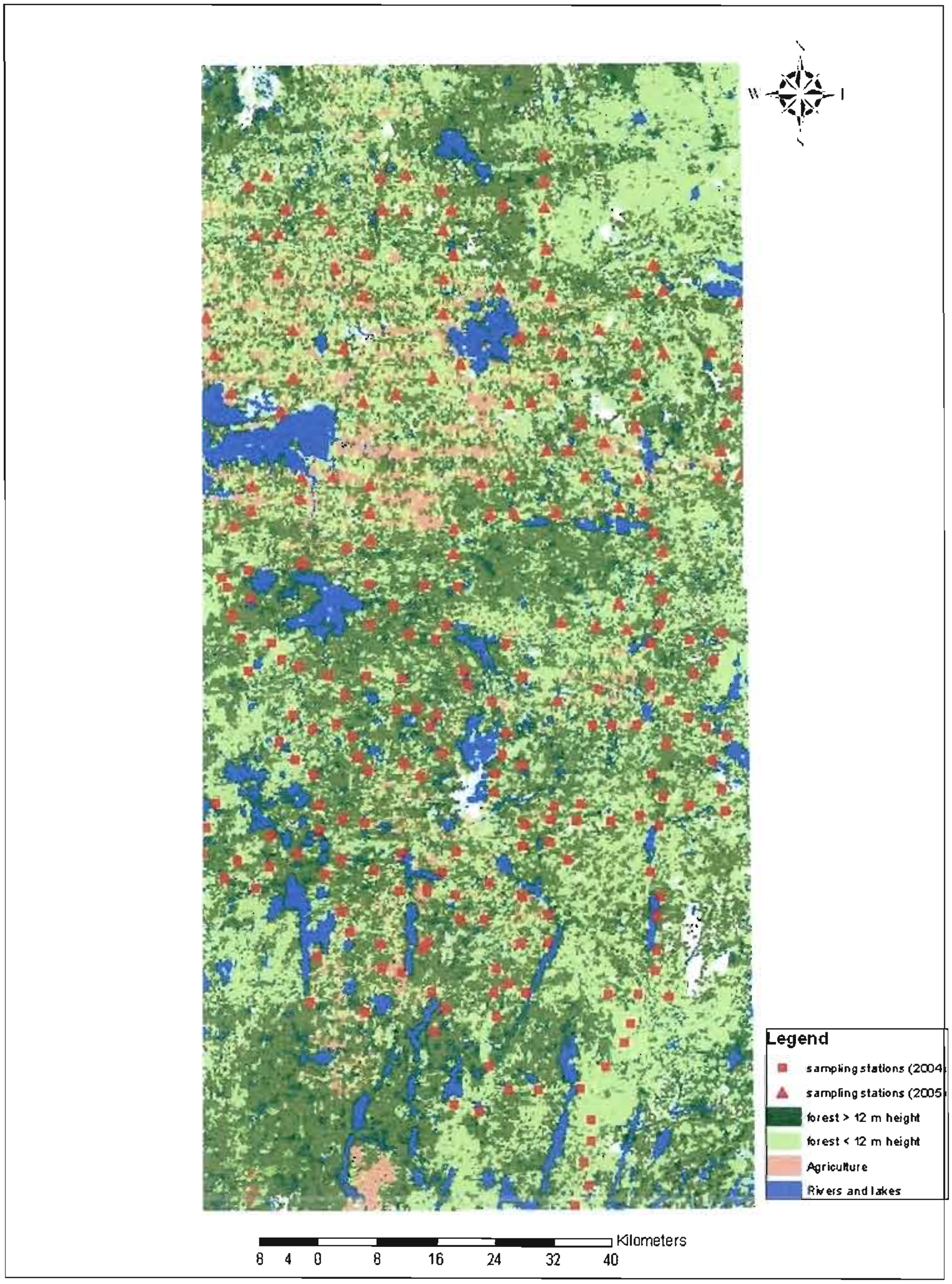

Legend
sampling stations (2004
sampling stations (2005
forest > 12 m height
forest < 12 m height
Agriculture
Rivers and lakes
Kilometers
8 4 0 8 16 24 32 40

Figure 3

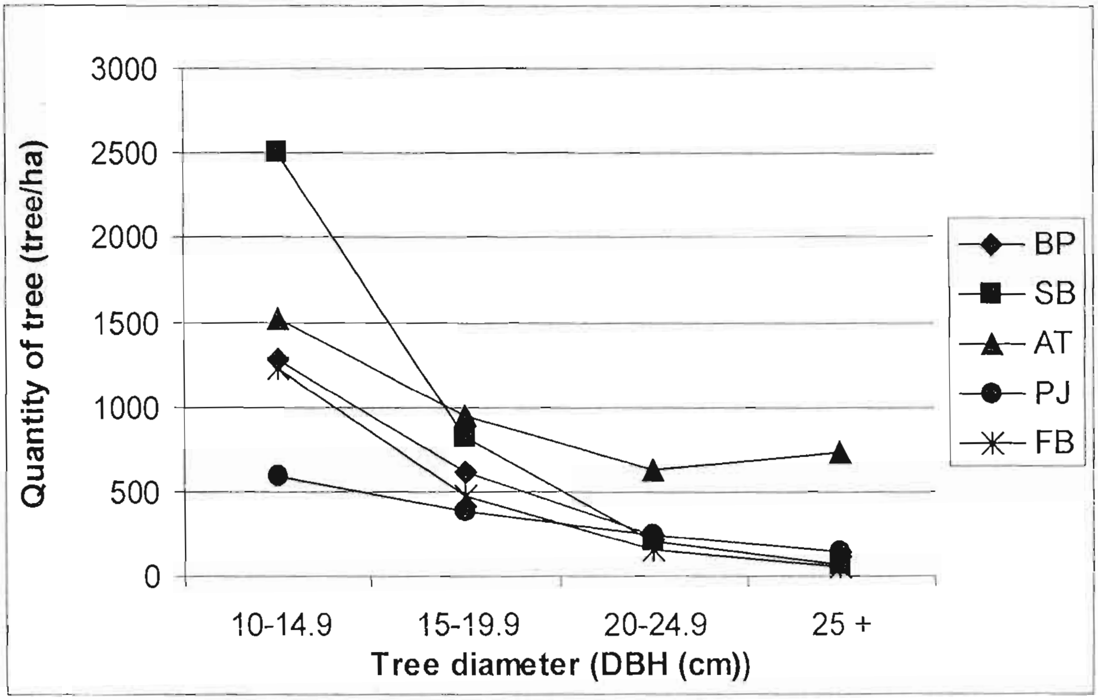
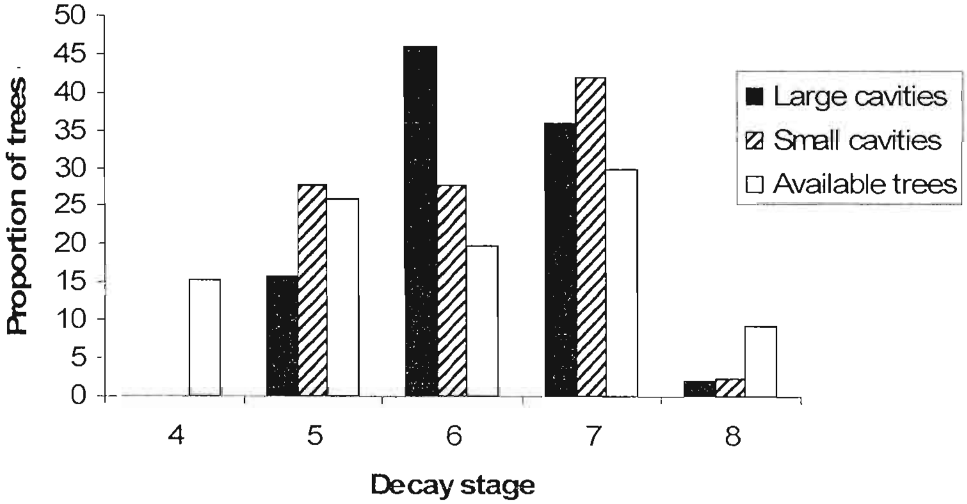
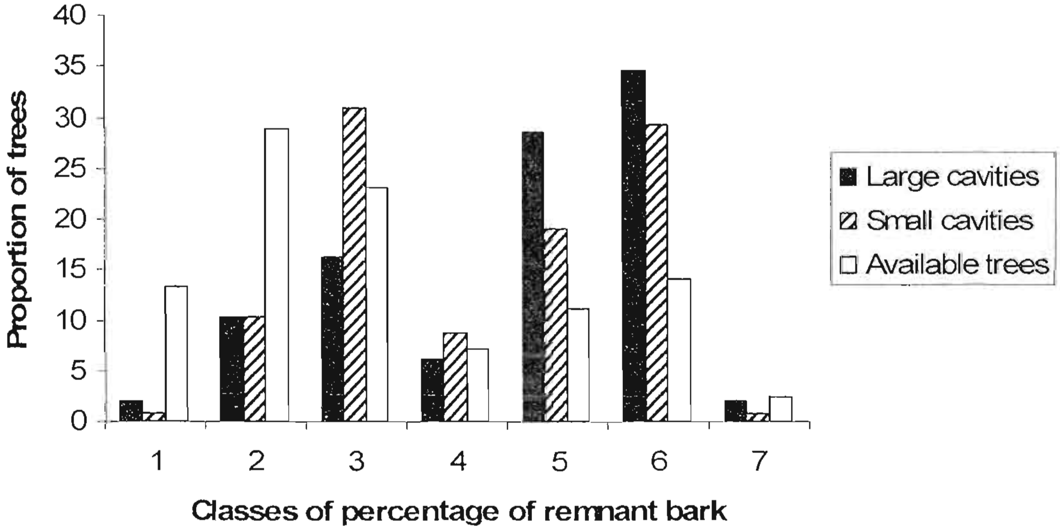

3000
2500
2000
1500
1000
500
0
Quantity of tree (tree/ha)
10-14.9
15-19.9
20-24.9
25 +
Tree diameter (DBH (cm))
BP
SB
AT
PJ
FB

Figure 4

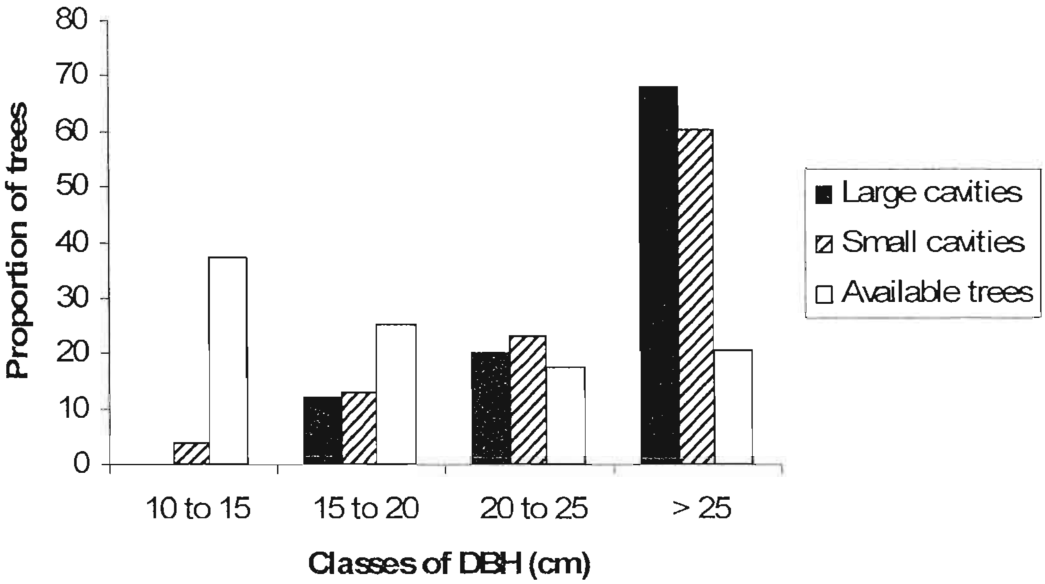
A.


Proportion of trees
50
45
40
35
30
25
20
15
10
5
0
4
5
6
7
8
Decay stage
■ Large cavities
▨ Small cavities
☐ Available trees

B.


Proportion of trees
40
35
30
25
20
15
10
5
0
1
2
3
4
5
6
7
Classes of percentage of remnant bark
■ Large cavities
▨ Small cavities
☐ Available trees

C.



80
70
60
50
40
30
20
10
0
Proportion of trees
10 to 15
15 to 20
20 to 25
> 25
Classes of DBH (cm)
Large cavities
Small cavities
Available trees

Table 1. Composition of stand (250 m radius) and landscape conditions (1000 m radius) in 230 sampling stations located in eastern boreal mixedwood forest in north-western Québec, Canada.

Forest type covert (height ≥ 12m)	Stand				Landscape			
	Mean (%)	SD (%)	Min (%)	Max (%)	Mean (%)	SD (%)	Min (%)	Max (%)
Coniferous	9	18	0	84	9	12	0	62
Mixed	15	20	0	95	16	13	0	68
Deciduous	23	28	0	100	17	16	0	65
Deciduous and mixed	37	31	0	100	33	18	0	84
Open area *	30	29	0	100	31	19	1	98

* Stands where trees are small (less than 4m) and canopy cover was < 25%. Alder stands, wetlands, as well as recently disturbed forests (clear-cuts and young plantations), were classified in this habitat type.

Table 2. Parameters used for the multiscale habitat use models for Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*P. villosus*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Boreal woodpeckers (i.e. American Three-toed Woodpecker (*P. dorsalis*) and Black-backed Woodpecker (*P. arcticus*) pooled), Northern Flicker (*Colaptes auratus*) and Pileated Woodpecker (*Dryocopus pileatus*), Nothern Saw-whet Owl (*Aegolius acadicus*). D= deciduous mature (> 12 m height) forest, M= mixed mature forest, C= coniferous mature forest, OPN= open cover types (< 4m height and < 40% cover).

	Parameters		
Species	Stand scale Tree critical dbh for nesting(cm)	Stand and landscape scales, cover types preferred (+) or avoided (-)	References
Downy Woodpecker	≥ 15	DMC12 (+), OPN (-)	Jackson and Ouellet 2002
Hairy Woodpecker	≥ 20	DM12 (+), OPN (-)	Jackson et al. 2002
Yellow-bellied Sapsucker	≥ 20	DM12 (+), OPN (-)	Waters et al. 2002
Boreal woodpeckers	≥ 20	C12 (+), OPN (-)	Leonard 2001, Dixon and Saab 2000
Northern Flicker	≥ 25	DMC12 (+), OPN (+)	Moore 1995
Pileated Woodpecker	≥ 25	MD12 (+), OPN (-)	Peck and James 1983
Northern Saw-whet Owl	≥ 25	MD12 (+), OPN (-)	Cannings 1993

Table 3. Human sensitivity index, based on different life history criteria, used to evaluate the sensitivity of bird species. In this case, 1 is the least sensitive and 3 is the most sensitive (from Hansen and Urban 1992).

	Sensitivity index		
Variable	**1**	**2**	**3**
Reproduction effort (eggs/year)	> 10	6-10	0-5
Nest form	Hole		Open
Nest height	> 3	1-3	0-1
Territory density (males/km^2)	>100	15-100	< 15
Migration	Resident	Short	Long
Edge sensitivity	Generalist, no data		Interior, edge
Area sensitivity	Generalist, no data		Positive, negative

Table 4. Cavity-nesting birds' frequency of occurrence and mean abundance for the two years of the study, †using all detections (unlimited distance) and ‡using detection inside a 250m radius, n* = total sampling stations for PCN, n** = total sampling stations for SCN, DOWO = Downy Woodpecker, HAWO= Hairy Woodpecker, YBSA= Yellow-bellied Sapsucker, BOWO= boreal woodpecker, NOFL= Northern Flicker, PIWO= Pileated Woodpecker, NSWO= Northern Saw-whet Owl, BOOW= Boreal Owl (*Aegolius funereus*), BAOW = Barred Owl (*Strix varia*).

Species	Occurrence of birds (%)†			Mean Abundance	Occurrence of birds (%)‡ (<250m)
	2004 (n*=150) (n**=98)	2005 (n*=80) (n**=80)	2004-2005	(ind./station)	2004-2005
Primary Cavity nesters					
DOWO	45	50	48	0,617	48
HAWO	25	24	25	0,317	25
YBSA	81	74	78	1,730	65
BOWO	10	5	8	0,096	7
NOFL	81	61	74	1,343	64
PIWO	15	10	13	0,152	10
Secondary cavity nesters					
NSOW	53	40	47	0,419	7
BOOW	0	1	< 1	0,004	< 1
BAOW	1	1	1	0,009	0

Table 5. AIC of the logistic regression models results of habitat use by each species of the studied guild. Models with a delta AIC < 2, suggesting substantial evidence for the model, are in bold. Species: DOWO: Downy Woodpecker, HAWO: Hairy Woodpecker, YBSA: Yellow-bellied Sapsucker, BOWO: includes Black-backed Woodpecker and Three-toed Woopecker, NOFL: Northern Flicker, PIWO: Pileated Woodpecker and Northern-Saw-whet Owl. Variables: T25: Tree density for DBH ≥25 cm, T20: Tree density for DBH ≥ 20 cm, T15: Tree density for DBH ≥ 15 cm, LOCDM12: Area of mature forest combining deciduous-dominated and mixedwood stands within a radius of 250 m at stand scale, STDOPN: Area of open habitats at stand scale, STDC12: Area of mature coniferous forest at stand scale, STDDMR12: Area of mature forest (coniferous,decidous, mixed combined) at stand scale, LANDM12: Area of mature deciduous and mixed forest combined at landscape scale, LANOPN: Area of open areas at landscape scale, LANR12: Area of mature forest of coniferous trees at landscape scale, LANDMR12: Area of mature forest at landscape scale, NULL: model with intercept only and no explanatory variable. LL: -2Log likelihood, K: number of parameters, AIC: Akaike's Information Criterion score, Delta AIC: AIC score relative to best score, Aikake weight: model weight.

Species	**Models**	**LL**	**K**	**AIC**	**Delta AIC**	**Akaike weight**
PIWO	**T25**	**153,527**	**2**	**157,580**	**1,678**	**0,237**
	LOCDM12+LOCOPN	153,411	3	159,517	3,615	0,090
	LANOPN+LANDM12	152,910	3	159,016	3,114	0,116

	T25+LOCDM12+LOCOPN+LANDM12+LANOPN	151,896	6	164,272	8,370	0,008
	NULL	**153,885**	**1**	**155,902**	**0,000**	**0,549**
NOFL	T25	299,920	2	303,973	16,295	0,000
	LOCDMR12+LOCOPN	**281,572**	**3**	**287,678**	**0,000**	**0,920**
	LANOPN+LANRDM12	289,982	3	296,088	8,410	0,014
	T25+LOCDMR12+LOCOPN+LANDMR12+LANOPN	280,597	6	292,974	5,295	0,065
	NULL	300,802	1	302,819	15,141	0,000
BOWO	T20	110,714	2	114,767	9,612	0,006
	LOCR12+LOCOPN	**99,049**	**3**	**105,155**	**0,000**	**0,781**
	LANR12+LANOPN	104,502	3	110,608	5,453	0,051
	T20+LOCR12+LOCOPN12+LANR12+LANOPN	96,147	6	108,524	3,368	0,145
	NULL	110,901	1	112,918	7,763	0,016
YBSA	T20	268,599	2	272,652	37,004	0,000

	LOCDM12+LOCOPN	247,619	3	253,725	18,078	0,000
	LANDM12+LANOPN	237,625	3	243,732	8,084	0,017
	T20+LOCDM12+LOCOPN+LANDM12+LANOPN	**223,271**	**6**	**235,647**	**0,000**	**0,983**
	NULL	297,202	1	299,219	63,572	0,000
HAWO	**T20**	**256,543**	**2**	**260,596**	**0,000**	**0,640**
	LOCDM12+LOCOPN	**256,372**	**3**	**262,478**	**1,882**	**0,250**
	LANOPN+LANDM12	260,278	3	266,385	5,789	0,035
	T20+LOCDM12+LOCOPN+LANDM12+LANOPN	254,173	6	266,549	5,954	0,033
	NULL	264,024	1	266,041	5,446	0,042
DOWO	T15	297,613	2	301,666	14,965	0,000
	LOCDMR12+LOCOPN	**280,595**	**3**	**286,701**	**0,000**	**0,577**
	LANDMR12+LANOPN	290,561	3	296,667	9,966	0,004
	T15+LOCDMR12+LOCOPN+LANDMR12+LANOPN	**274,969**	**6**	**287,345**	**0,644**	**0,418**
	NULL	314,716	1	316,733	30,032	0,000

NSOW	T25	93,052	2	97,105	6,574	0,022
	LOCDM12+LOCOPN	87,091	3	93,197	2,667	0,158
	LANDM12+LANOPN	**84,424**	**3**	**90,530**	**0,000**	**0,600**
	T25+LOCDM12+LOCOPN+LANDM12+LANOPN	80,826	6	93,203	2,672	0,158
	NULL	93,064	1	95,082	4,551	0,062

Table 6. Multimodel inference results; parameter estimates, standard errors, upper and lower 95% confidence intervals. Parameters with the confidence interval excluding 0 are in bold.

Species	Parameters	Estimate	Std err	Upper 95%	Lower 95%
PIWO	**T25**	**0,050470**	**0,0326314**	**0,1493911**	**0,0484512**
	NULL	**-2.1498**	**-.2157**	**-1.727**	**-2.573**
NOFL	**LOCOPN**	**0,0000146**	**0,0000037**	**0,0000219**	**0,0000074**
	LOCRMD12	**0,0000068**	**0,0000031**	**0,0000129**	**0,0000007**
BOWO	LOCOPN	0,0000077	0,0000063	0,0000200	-0,0000047
	LOCR12	**0,0000202**	**0,0000063**	**0,0000326**	**0,0000079**
YBSA	**T20**	**0,0651117**	**0,0244009**	**0,1129375**	**0,0172858**
	LOCOPN	0,0000043	0,0000053	0,0000148	-0,0000061
	LOCDM12	0,0000069	0,0000042	0,0000151	-0,0000013
	LANOPN	0,0000008	0,0000005	0,0000018	-0,0000003
	LANDM12	**0,0000021**	**0,0000006**	**0,0000032**	**0,0000009**
HAWO	**T20**	**0,0400152**	**0,0163594**	**0,0720796**	**0,0079508**
	LOCOPN	-0,0000010	0,0000036	0,0000062	-0,0000081
	LOCDM12	0,0000062	0,0000032	0,0000124	-0,0000001
DOWO	T15	0,0152778	0,0112942	0,0374144	-0,0068588
	LOCOPN	-0,0000012	0,0000056	0,0000097	-0,0000122
	LOCRMD12	**0,0000119**	**0,0000036**	**0,0000189**	**0,0000048**
	LANOPN	-0,0000009	0,0000005	0,0000001	-0,0000020
	LANRMD	-0,0000004	0,0000004	0,0000005	-0,0000012
NSWO	LANOPN	0,0000003	0,0000005	0,0000012	-0,0000007
	LANDM12	**0,0000009**	**0,0000003**	**0,0000015**	**0,0000002**

Table 7. Characteristics of excavated trees. Small excavators regroup Downy Woodpecker, Hairy Woodpecker, Yellow-belied Sapsucker, Three-toed Woodpecker, Black-backed Woodpecker. Large excavators are Northern Flicker and Pileated Woodpecker. Min = minimal DBH of tree excavated, Max = maximal DBH of tree excavated, Range = range between the smallest and the largest tree excavated, SE mean = standard error of the mean, SD= standard deviation, *n* = number of cavity-bearing trees.

Excavators	*n*	Tree size				SE mean	SD
		Min (cm)	Max (cm)	Range	Mean (cm)		
Small	154	13	65	52	29.45	0.87	10.80
Large	56	16	78	63	33.09	1.62	12.09
All	210	13	78	65	30.42	0.78	11.25

Tableau 8. Number of cavities in different tree species by DBH classes according to the size of the excavators. BP= paper birch, SB= black spruce, AT= trembling aspen, PJ= jack pine, FB= balsam fir, OTH= others, S=small excavators (Downy, Hairy, boreal woodpeckers and Yellow-bellied Sapsucker), L= large excavators (Northern Flicker and Pileated Woodpecker), Li: living tree, D= dead tree.

Species	Tree diameter (cm)								Percentage of living and dead trees (%)	
	10-14,9		15-19,9		20-24,9		25+			
	S	L	S	L	S	L	S	L	Li	D
BP	-	-	-	-	1	1	3	4	0	100
SB	-	-	-	1	-	-	-	-	-	100
AT	5	-	7	2	23	7	39	12	14	86
PJ	-	-	-	-	-	-	1	-	0	100
FB	-	-	1	1	2	1	1	1	0	100
OTH	-	-	2	-	1	-	11	7	5	95
Total	5	0	10	4	27	9	55	24		

Table 9. Ranking matrix for cavity-bearing trees based on comparing proportional tree excavated with proportions of total available trees, based on a compositional analysis (Aebischer et al. 1993). Each sign is based on mean element; a triple sign represent significant deviation from random at $P < 0.05$. Rank 1 is the less selected and rank 5 is the most selected. AT= trembling aspen, BP= paper birch, FB= balsam fir, OTH= others, PJ= jack pine, SB= black spruce.

	BP	**SB**	**OTH**	**AT**	**PJ**	**FB**	**Rank**
BP		+	-	---	+	+	**3**
SB	-		-	---	+	-	**1**
OTH	+	+		-	+	+	**4**
AT	+++	+++	+		+++	+++	**5**
PJ	-	-	-	---		+	**1**
FB	-	+	-	---	-		**1**

Table 10. Umbrella index score with the scores of each parameter. PCS: percentage of co-occuring species, R: degree of ubiquity or median rarity, DSI: disturbance sensitivity indices, UI: umbrella index score. DOWO = Downy Woodpecker, HAWO= Hairy Woodpecker, YBSA= Yellow-bellied Sapsucker, BOWO= boreal woodpecker, NOFL= Northern Flicker, PIWO= Pileated Woodpecker, NSOW= Northern Saw-whet Owl. All the maximal value obtained for each parameter is in bold.

Species	PCS	R	DSI	UI	UI (2004)	UI (2005)
DOWO	0,45	0,92	0,67	2,04	1,99	2,01
HAWO	0,52	0,55	0,89	1,97	1,96	1,84
YBSA	0,38	0,43	0,67	1,48	1,38	1,53
BOWO	0,50	0,16	0,89	1,55	1,53	1,42
NOFL	0,39	0,55	0,61	1,55	1,34	1,72
PIWO	**0,57**	0,28	**1,00**	1,85	1,82	1,68
NSOW	0,45	**0,94**	0,89	**2,28**	**2,24**	**2,07**
Average	0,47	0,55	0,80	1,82	1,75	1,75

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ARTICLE II

CHARACTERISTICS OF FORAGING PATTERNS AND TREES SELECTED BY PILEATED WOODPECKER (DRYOCOPUS PILEATUS) IN MIXEDWOOD FOREST OF EASTERN CANADA

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Abstract. Studies on cavity users are often focusing primarily on the factors affecting cavity tree selection, despite the fact that several hole excavators are also limited by the availability of suitable foraging trees. Considering the importance of food availability and the abundance of foraging substrates in bird territory selection, we documented the foraging habits of Pileated Woodpecker (*Dryocopus pileatus*), the largest cavity excavator in North America, at the northern limit of its distribution where its abundance is low. The objectives of the present study were to determine 1) the foraging tree characteristics (i.e. species, dbh, percentage of bark remnant, decay class and state of tree (live or dead)) as compared to available trees, 2) the parts of trees more excavated and 3) the tree species or sizes mostly susceptible to be reused year after years. A total of 230 sampling stations were distributed to cover extensively the study area located in the eastern Canada's boreal mixedwood forest. Transects were conducted to quantify and characterize available and foraging trees. Only trees with obvious Pileated Woodpecker's marks of excavations were used as foraging trees for analysis. Our results showed that Pileated Woodpecker tended to excavate in the largest available trees. It mostly selected balsam fir (*Abies. balsamea*) and trembling aspen (*Populus tremuloides*) to forage. Pileated Woodpecker seemed to forage unequally on the surface of the trees and it foraged mostly near the ground. Some trees were reused for many years regardless of the tree species or its dbh. Larger trees (dbh over 15 cm) are more likely to be used more than once over a year than smaller trees, independently of their tree species.

Keywords: Pileated Woodpecker, foraging pattern, foraging tree characteristics

Introduction

The Pileated Woodpecker (*Dryocopus pileatus*) is the largest excavator in North America (Bull and Jackson 1995). It is considered a biological indicator of older forests (McClelland 1977, Bull and Holthausen 1993) and an umbrella species since it has a very large territory (Lafleur and Blanchette 1993). By creating large cavities used by large secondary cavity users, Pileated Woodpecker is also often designated as a keystone species (Hoyt 1957, Bull and Holthausen 1993, Bonar 2000, 2001, Maisonneuve and al. 2002, Aubry et Raley 2002, 2003, see also chapter 1). Of the seven species of woodpeckers that nest in boreal mixedwood forests, the Pileated Woodpecker is the only species that requires large trees for both nesting and foraging (Nappi, personal communication). As with other studies on primary excavators (Conner 1980, Hunter 1990, Imbeau and Desrochers 2002), those studies on Pileated's ecology have often dealt with nesting requirements (Bonar 2001, Aubry et al. 2002, 2003), assuming that snags used for nesting may be the limiting factor for these populations. However, it has recently been recognized that some woodpeckers are more likely to be limited by the availability of foraging trees instead of nesting trees (Imbeau and Desrochers 2002, Hutto 2006). In the boreal forest the overall amount of large trees is less than in temperate forests or hemiboreal forests (Boucher et al. 2003). Moreover, human disturbances such as timber harvesting and agriculture generate forest landscapes with a low proportion of older forests (Drapeau et al. 2000, Harper et al. 2002) and thus further reduce the availability of large live and dead trees that is generally concentrated in such forest cover types. In such environments, Pileated Woodpeckers could be limited by both nesting and foraging habitat attributes. It is thus important to improve our knowledge not only on nesting but also on foraging ecology requirements of this species.

Pileated Woodpecker sometimes feeds on logs but mainly forages on dead or live standing trees (Bull et al. 1986, Bull and Holthausen 1993). Food availability and the abundance of food resources will influence its territory selection (Raphael and White 1984, Renken and Wiggers 1989, Loose and Anderson 1995, Gunn and Hagan III 2000). Pileated's diet varies with season and it is composed of fruits, bark beetle larvae, nuts, and mainly of carpenter ants which can make up 95% of its diet (Bull 1987, Beckwith et Bull 1985, Hoyt 1957). Indeed, even if it can scale the bark off trees and peck on the surface of the bark, it mainly excavates deep into the interior wood of the trees to reach carpenter ant galleries (Conner 1981, Bull 1987, Flemming et al. 1999, Hartwig 1999). By excavating deeply into the trees, Pileated Woodpecker opens the access to the central chamber of the tree, which is often empty (Aubry and Raley 2002). These foraging excavations are used by other animals. Different birds and small mammals can then roost and nest inside those foraging excavations. Moreover, weak excavators can get access to the foraging resource too (Aubry and Raley 2002, Bull and Jackson 1995). Finally, Pileated accelerates wood decomposition by breaking wood apart which facilitates fungal infection.

Many large trees are required to provide enough food for Pileated Woodpecker (Mannan et al. 1980, Conner et al. 1994, Bull and Jackson 1995). Renken and Wiggers (1989) suggest that large trees have a higher potential to harbour large colonies of ants than do smaller trees. Hence, if resource availability (i.e. carpenter ants biomass) is low more trees are needed for foraging by this large insectivore., To our knowledge, no study has been conducted on the relationship between Pileated Woodpeckers, carpenter ants distribution patterns and foraging trees availability in the eastern boreal mixedwood forest of Canada. Pileated Woodpecker relationships with foraging trees have however been well documented in western North America (Mannan et al. 1980, Bull 1987, Bull and Holthausen 1993, Bonar 2001). In the northeastern part of North America, studies conducted in the last decade have increased our knowledge on Pileated Woodpecker's foraging ecology. Four studies have been conducted on the foraging habits of this species: in Québec (Savignac 1996, 2000), in New-Brunswick (Flemming et al. 1999, Lemaître and Villard 2005) and in Maine (Gunn and Hagan III 2000). These studies were conducted in different forest ecosystems across the distribution range of the species but consistently showed that Pileated Woodpeckers feed on larger trees. However, preferred tree species vary from one region to another. Hence, tree species which were the most excavated in some regions may be avoided in other areas. This is the case with the balsam fir (*Abies balsamea*) that is avoided in Maine (Gunn and Hagan III 2000) but it is significantly selected in New Brunswick (Flemming et al. 1999).

This chapter documents foraging tree characteristics that influence the Pileated Woodpecker habitat selection in a boreal mixedwood forest landscape in eastern Canada which is at the northern limit of the Pileated Woodpecker's distribution (Gauthier and Aubry 1995). We determine which tree species were mainly excavated by Pileated Woodpecker and how the selected trees vary with regards to stage of decay, percentage of remaining bark, diameter at breast height (DBH), type (deciduous or coniferous) and state (dead or alive) of trees. Trees with foraging excavations were compared to non-excavated available trees. On foraging trees we also assessed if there were foraging preferences for any given height along the trunk and if trees were reused by Pileated Woodpeckers year after year.

Methods

Study area

The study area is located in the Abitibi -Témiscamingue region, Québec, Canada (47° 46 to 49° 00' N; 79°53' to 78°22' W). It covers almost 10 000 km^2 (MRN, 2001) of the bioclimatic balsam fir-white birch domain included in the boreal forest (MRNF, 2006). The land base is characterised by a mixture of deciduous, mixed and coniferous stands composed of either pure or mixtures of trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam fir, and white spruce (*Picea glauca*). Most of the forest is on public lands and is allocated by the Quebec government (MRN, 2001) to timber industry. Since the region has been colonised in the early 1930's (MRN, 2001), a large proportion of the land base has been converted to young stands (30-50 years) (Grenier et al. 1998). The study region is part of a broad physiographic unit known as the clay belt, which extends across northern Quebec and Ontario. The flat topography originates from lacustrine deposits of proglacial lakes Barlow and Objibway (Vincent et Hardy 1977).

Sampling design

All sampling stations were distributed along the road network of the entire study area (Figures 1 and 2). Since Pileated Woodpecker has a large home range, sampling stations were at least 3 km apart from each other, to ensure that, stations with foraging marks could be considered independent. We used a stratified sampling design to cover the range of forest cover (both in terms of proportion and stand composition) that characterizes the land base (Table 1). Given the travel distances within the study area, we first located a subset of 150 sampling stations in the southern part in 2004, whereas 80 additional sampling stations were located in the northern section in 2005. Overall, these 230 sampling stations provided extensive coverage of the study area. Also, in 2005, 21 other sampling stations were visited to find more excavated trees in areas likely to be occupied by Pileated Woodpeckers.

Available live trees, snags, and used foraging trees sampling

Live tree and snag availability were measured perpendicularly from the road along two line transects of 250 m long x 2 m wide at each sampling station. All trees, dead or alive, with a diameter at breast height (dbh) over 10 cm and at least 1.40 m tall were recorded. For each tree, we noted the tree species, percentage of remnant bark, the diameter at breast height (dbh) and the decay class. Following Imbeau and Desrochers (2002), we used a tree decay classification system that ranged from 1–8 for standing trees, with 1 indicating a live tree with no visible signs of decay, 2 indicating a live tree with visible signs of decay, 3 indicating a dying tree with numerous signs of decay and 4-8 dead trees with advancing stages of decay. Our classification for tree bark remnant recognized seven classes: (1) tree cover by 100% of bark, (2) >95% of bark, (3) 95%> x >75%, (4) 75%> x >50%, (5) 50%> x > 25%, (6) 25% > x > 1% and (7) no bark present. Tree height was estimated in one of the four following categories: less than 5 m, 5 -10 m, 10-15 m, > 15 m.

Foraging trees used by Pileated Woodpeckers were found using evidence of excavations by this species, which are clearly recognizable from other woodpeckers by their size and shape (Lemaître and Villard 2005). Only foraging excavations were considered since they are easier to detect by their form, they do not require any focal contact with the animal as opposed to foraging techniques such as pecking or scaling (Lemaître and Villard 2005). These foraging excavations are often linked with carpenter ants colonies which are considered a primary food resource for the Pileated Woodpecker (Bent 1939, Hoyt 1957, Beckwith and Bull 1985, Bull et al. 1992). Each tree showing visible excavations detected from these line transects was characterized by the same variables as those used to characterize available trees. The height of each foraging excavation was also recorded in four classes, similar to the ones used to estimate tree height, i.e., < 5 m, 5-10 m, 10-15 m and > 15 m. Each foraging excavation was categorized as recent, old, or very old according to its coloration and the presence of wood chips. Foraging excavations were considered recent (i.e. during the past year) when their color was brightest and wood chips were observed at the litter surface; old excavations still had a bright color but chips were not found at the litter surface; very old excavations were further characterized by the loss of their brightness, showing no contrast with the unexcavated part of the stem.

Stastical analyses

Foraging tree characteristics

To identify potential differences between selected trees and nearest available trees, tree characteristics (dbh, decay stage, percentage of remnant bark, type (deciduous or coniferous) and state (dead or alive)) were used in case-control logistic regression analysis. For analysis involving percentage of remnant bark, state and decay stage, only recently excavated trees were used, because these characteristics are affected by time since excavation. Foraging trees were compared with the closest available trees and also with the closest trees in the same state (dead trees compared with dead trees and live trees compared with live trees).

Foraging height

To determine if Pileated Woodpeckers foraged on trees randomly or if they selected some specific part of the stem, a compositional analysis on foraging excavations was conducted using 1000 iterations (Aebischer et al. 1993). Used trees were divided in four sections of 5 m each (1= 0 to 5 m above the ground, 2= 5 to 10 m, 3= 10 to 15 m and 4= more than 15 m). Only trees taller than 15 m were used for this analysis (n = 43) to ensure that all height categories were represented. Each variable (used parts vs available parts of trees) are represented as proportions and were compared with Compos Analysis 5.1 standard (Smith 2003).

Reutilisation of the same tree

To point out if some tree species or large trees were more likely to be used several times for more than a year by Pileated Woodpecker year after year, chi-square tests were performed. Excavation marks were analysed for three different categories measured in the field, i.e.: recent, old, very old.

All excavated tree species with a frequency of occurrence over 5% were retained for analysis (balsam fir, trembling aspen, jack pine, white spruce and aspen sp.) and all remaining species (coniferous sp., black spruce, eastern white-cedar (*Thuja occidentalis*), eastern white pine (*Pinus strobus*), spruce sp. (*Picea* sp.), paper birch, balsam poplar (*Populus balsamifera*), red pine (*Pinus resinosa*), unknown species, pine sp. (*Pinus sp.*), deciduous sp., willows sp. (*Salix* sp.), tamarack (*Larix laricina*)) were pooled in the category *Others* (Figure 3). Chi-sqare tests were performed (1) to determine some tree species were more likely to be used several times for more than a year than others, and (2) to assess if large trees were more reutilized than small trees, with four categories of dbh: 10-15 cm, 15-20 cm, 20-25 cm and over 25 cm.

Results

Foraging tree characteristics

A total of 570 foraging trees were found in 157 different stations. Among those, 192 trees were recently excavated in 79 different stations and 78% of them where excavated in snags. The diameter at breast height of the excavated trees ranged from 10 cm to 57.8 cm (mean 25.3 ± 8.6 cm). The two most excavated tree species were the balsam fir and the trembling aspen (Figure 3).

When used trees were compared with the closest available tree, a significant difference was observed: Pileated Woodpecker tended to forage on trees larger than those available ($\chi^2 = 24.54$, $P < 0.05$, $n = 140$) (Figure 4A). Dead trees were more selected then live trees ($\chi^2 = 38.39$, $P < 0.05$, $n = 64$). There were no significant selection towards deciduous or coniferous trees ($\chi^2 = 0.046$, $P = 0.831$, $n = 140$).

Analyses were performed with the closest available tree of the same state (live or dead) for recently excavated trees. Dead (snags) and live trees were analysed separately (i.e. used vs available pooled according to their state). Pileated Woodpecker foraged on larger trees independently of the state (dead: $\chi^2 = 48.34$, $P < 0.05$, n= 143, live: $\chi^2 = 17.67$, $P = 0.003$, n= 43) (Figure 4A). Pileated foraged on snags that were less decayed ($\chi^2 = 13.97$, $P < 0.05$, n= 144) with less remnant bark ($\chi^2 = 10.78$, $P = 0.002$, $n = 144$) (Figure 4B-C). However no significant difference was observed between used and available live trees for the decay stage ($\chi^2 = 3.59$, $P = 0.17$, $n = 43$) and for the percentage of remnant bark ($\chi^2 = 0.46$,

$P = 0.52$, $n = 43$) (Figure 4B-C). Pileated Woodpecker significantly selected more live coniferous than live deciduous ($\chi^2 = 13.44$, $P = 0.01$, $n = 43$) but no significant preference was observed in the snag group for deciduous neither for coniferous ($\chi^2 = 0.03$, $P = 0.85$, $n = 139$).

Foraging height

A total of 2115 marks were observed: 1877 marks were found in the lower part of trees, 232 marks in the second height classes (5 to 10m) and only two (2) and three (3) excavation marks were observed in the third and fourth height classes of the tree. Pileated Woodpecker did not forage equally on all the surface of the trees ($\chi^2 = 117.70$, $P < 0.05$, df= 3, n= 43) (Table 2). It foraged significantly more often near the ground, on the lower part of the tree (0 to 5m) (Table 3). The 10-15 m height class was the less excavated of all height classes.

Reutilisation of the same tree

The majority of trees showing foraging excavations were utilized only once (67%). However, each tree species seemed to be excavated in the same proportions over years (balsam fir: $\chi^2 = 2.2$, $P = 0.329$, df = 2, $n = 222$, jack pine: $\chi^2 = 0.06$, $P = 0.972$, df = 2, $n = 37$, trembling aspen: $\chi^2 = 4.4$, $P = 0.110$, df = 2, $n = 145$, aspen sp.: $\chi^2 = 2.5$, $P = 0.288$, df = 2, $n = 26$, others: $\chi^2 = 0.7$, $P = 0.693$, df = 2, $n = 114$) except for the white spruce, which is more often reused over years than other species ($\chi^2 = 6.5$, $P = 0.038$, df = 2, $n = 25$) (Figure 5a). A significant difference was observed between tree of different size: trees with 10-15 cm of dhb where less excavated ($\chi^2 = 12.0$, $P = 0.002$, df = 2, $n = 43$) while trees white > 25 cm where more reused than other trees species ($\chi^2 = 9.4$, $P = 0.009$, df = 2, $n = 236$) (Figure 5b).

Discussion

Foraging tree characteristics

Our results corroborate other studies that found that Pileated Woodpeckers tend to forage in the largest available trees (Savignac 1996, Flemming et al. 1999, Bonar 2001). It, indeed, has been shown that the tree dbh is a good predictor of the foraging substrate used by the Pileated Woodpecker (Lemaître and Villard 2005). This preference for foraging on large diameter trees is not without potential links with the fact that *Camponotus* and *Formica* ants also use the largest trees available (Torgensen and Bull 1995). In northwestern Ontario, wood ants prefer dead trees over 30 cm dbh and live trees over 20 cm dbh (Sanders 1970). In New-Brunswick, *Camponotus* attacks only trees over 18cm dbh (Sanders 1964). Renken and Wiggers (1989) suggested that larger trees contain more carpenter ants, and then for woodpeckers the effort of excavation is improved when large trees are choosen. In Quebec, the average dbh of excavated trees by Pileated Woodpeckers found by Savignac (1996) (i.e. > 30 cm) was coherent with the average (25.3 ± 8.6 cm) found in our study area. Trees with larger dbh can offer an additional solidity to decayed trees (Renken and Wiggers 1989). Most of the excavated trees were dead but excavated snags were less decayed than other dead trees. Also, the percentage of bark remaining on stems was less on excavated trees than on other snags, suggesting that the Pileated Woodpecker selected decayed deadwood for foraging. These results are consistent with those obtained in other parts of its range (Bull 1987, Bull and Holthausen 1993, Fleeming et al. 1999, Bonar 2001). Like Pileated Woodpecker, wood ants attack decayed trees (Sanders 1964). However, wood ants colonize a very large range of decayed stems, including live trees, snags, logs, stumps (Sanders 1964). Consequently, if Pileated Woodpeckers closely track carpenter ants they should leave foraging marks on trees with these different stages of decay, including downed wood. In our study, however, few foraging excavations were found on downed wood. This marginal use of downed woody debris could be partly explained by the sampling technique, which was based on observation of foraging signs rather than on direct visual observations of birds foraging on trees (see Flemming et al. 1999). It is thus possible that we missed foraging excavations near the ground hidden by vegetation or trees. Moreover, low temperatures in winter considerably reduce the amount of insects, as a result less insects are available on tree surfaces and then Pileated Woodpecker needs to excavate deeper in trees to find them (Conner 1981). Also, in other cold regions, as downed woody debris are covered by snow in the winter, they possibly show a lower amount of foraging signs than standing trees that can be used throughout the year (Conner 1981, Bonar 2001).

Among live trees, coniferous trees are mostly preferred to deciduous trees. Nevertheless, this observation is not significant among snags, probably because coniferous trees are softer than deciduous. In our study area, trembling aspen and balsam fir were the two most excavated tree species by Pileated Woodpeckers. Lemaître and Villard (2005) found that tree species is a significant predictor of this species foraging substrate in New Brunswick's hemiboreal forests. However, it is not surprising that preferred tree species for foraging substrate will also differ since Pileated Woodpecker has a wide distributional range and forest composition and structure are likely to differ. In our region, balsam fir was not the most abundant species but it was the most used by Pileated Woodpecker to forage. In southeastern New Brunswick, balsam fir was also a preferred species along with red spruce (*Picea rubens*) (Flemming et al 1999). In Maine, Gunn and Hagan III (2000) found that balsam fir was avoided by the Pileated Woodpecker, whereas American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) were preferred. In northwestern New Brunswick, American beech was the main species used by Pileated Woodpecker to forage (Lemaître and Villard 2005). Tree species used by Pileated Woodpeckers for foraging thus differed across regions but can also differ throughout the year as the seasons change. In Alberta, Bonar (2001) observed a change in types of foraging substrate over seasons: Pileated Woodpecker tended to forage more on coniferous during winter and the proportion of deciduous used increased in summer. A similar study, including focal observations of foraging individuals should be conducted across seasons to determine if such behavior occurs in mixedwood forest in our study area.

Even though Pileated Woodpeckers foraged on deciduous and coniferous tree species, they preferred coniferous species to others available when comparing foraged trees with the random closest trees. These results corroborate observations made in other studies (Flemming et al. 1999, Bonar 2001, Lemaître and Villard 2005). In northeastern parts of North America, carpenters ants seem to mainly attack coniferous species as well (Sanders 1964).

Pileated Woodpeckers' large diameter foraging trees could be linked to ant habitat selection. In northeastern Oregon, Pileated Woodpeckers seemed to avoid the same tree species than carpenter ants (Torgensen and Bull 1995). In south New Brunswick, carpenters were mostly found in balsam firs and in white cedars (*Thuja occidentalis*) (Sanders 1964). Unpublished data available in Sanders' article showed that the most attacked tree species by ants for New Brunswick, New England and New-York were balsam fir and spruces. This author suggested that a wide growth annual ring of rapidly growing trees could be easier to excavate by ants. Since, trembling aspen is one of the tree species with the fastest growth rate among tree species, this tree species could be favoured by carpenter ants.

Foraging height

Most foraging excavations were found at the base of trees where heart rot fungi infections frequently occur (Jackson and Jackson 2004). Conner (1981) found that Pileated Woodpecker mainly forage deep within the lower portions of tree trunks to find carpenter ants during winter. The higher parts were almost completely avoided. One possible explanation for such foraging pattern may be that carpenter ants colonize the base of the trees, usually the first 5-7 meters from the ground (Sanders 1964).

Reutilisation of the same tree

Overall, the proportion of trees that showed foraging excavation marks from different time periods was lower than the number of foraging trees characterized by marks from one time period. A strong dynamic in foraging tree use by the Pileated Woodpecker thus seems to occur in our study area. Larger trees were reused more often than were smaller trees. This suggests that food resources are more likely to persist in large trees. For instance, the availability of carpenter ants may extend over a longer term in these large snags (Torgensen and Bull 1995). This could in turn, explain why Pileated Woodpeckers are more likely to reuse such foraging trees. Our results are based, however, on a crude measure of reutilization. Separating foraging marks in the three broad classes used in this study does not allow determining exactly when and how long foraging trees have been used in our system. Long-term research on foraging ecology of woodpeckers in permanent study sites could provide such fine-grained information on the exact time-frame for which snags are used by Pileated Woodpeckers.

Our results show a significant preference for white spruce by Pileated Woodpecker. Most of the white spruce bearing foraging marks were not dead (75%) and had a DBH superior to 25 cm (96%). Those observations suggest that white spruce can be attacked by ants while it is still alive and it can shelter large colonies of ants due to its size. Thus, this species may play a key role for the Pileated Woodpecker's foraging behaviour. However, no significant difference was observed between patterns of reutilization among the other tree species, suggesting that deciduous and coniferous snags are as likely to be reused as foraging substrate over time. However, the broad categories of our foraging excavations classification system can mask a dynamic of reutilization that may be different between conifers and deciduous trees at specific time periods. For example, in the very old excavation category, foraging excavations of 20 years old may be in the same group as foraging excavations of 6 years old. However, long-term monitoring of permanent plots could show that conifers are more used by woodpeckers earlier in the decay process (5-10 years old) whereas aspen become more utilized later on (10-20 years).

Conclusions and management implications

The importance of the Pileated Woodpecker as a key species for many other large cavity users has been shown in numerous regions, including our studied area (Martin and Eadie 1999, Bonar 2000, 2001, Aubry et Raley 2002). Thus, within a biodiversity conservation standpoint, it seems critical to consider its foraging requirements in forestry planning. Pileated Woodpecker prefers to forage on large diameter trees, particularly trembling aspen and balsam fir. Moreover, Pileated Woodpecker finds most of its food in snags. Concurrently, timber harvesting focuses on large trees and in recent years trembling aspen has become an important commercial timber species throughout Canada's boreal forest. Pileated Woodpecker main foraging substrate may thus become limited in the near future. Live and standing deadwood retention strategies that incorporate trembling aspen is likely to be critical in the near future. Special attention should also be paid to white spruce, since large colonies of ants can be found at the base of the trunk of this tree species, particularly large trees on which Pileated Woodpecker feeds year after year.

FIGURES LEGEND

Figure 1. Localization of the study area within the Quebec province (in dark grey and black).

Figure 2. Map of the study area. Green regions represent forests, pink regions represent cultivating lands and blue regions show lakes and rivers.

Figure 3. Proportion of tree species used by Pileated Woodpecker for foraging. FB = Balsam fir, AT= trembling aspen, A.sp.= Aspen species, SW= white spruce, PJ= jack pine, OTH= others species.

Figure 4. Proportion of used trees, closest tree (CT) and tree of same state (SS) in function of (A) diameter at breast height (dbh) divided in four categories: 10 to 15 cm, 15 to 20 cm, 20 to 25 cm and > 25 cm, (B) decay state: 1= live tree with no visible signs of decay, 2= live tree with visible signs of decay, 3= dying tree with numerous signs of decay, 4-8= dead trees with advancing stages of decay (Imbeau and Desrochers 2002), (C) classes of percentage of remnant bark: (1) tree cover by 100% of bark, (2) >95% of bark, (3) 95%> x >75%, (4) 75%> x >50% of bark, (3) 50%> x > 25%, (2) 25% > x > 1% and (7) no bark present.

Figure 5. Representation of the quantity of excavations according to the number of uses over time. Where 1- marks of the same age on the same tree, 2- marks of two different periods of time on the same tree and 3- marks of three different periods of time on the same tree, and divided by A) tree species and B) dbh classes. FB = balsam fir, AT= trembling aspen, A.sp.= Aspen sp., SW= white spruce, PJ= jack pine, OTH= others species.

Figure 1

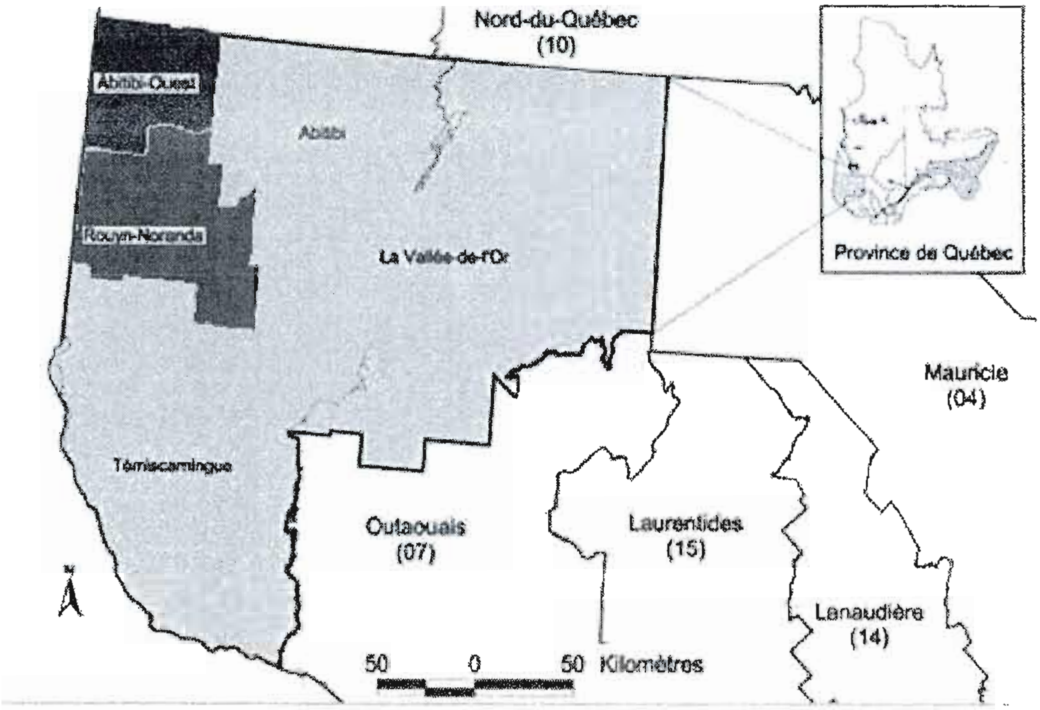

Nord-du-Québec
(10)
Abitibi-Ouest
Abitibi
Rouyn-Noranda
La Vallée-de-l'Or
Témiscamingue
Province de Québec
Mauricie
(04)
Outaouais
(07)
Laurentides
(15)
Lanaudière
(14)
N
50
0
50
Kilomètres

Figure 2

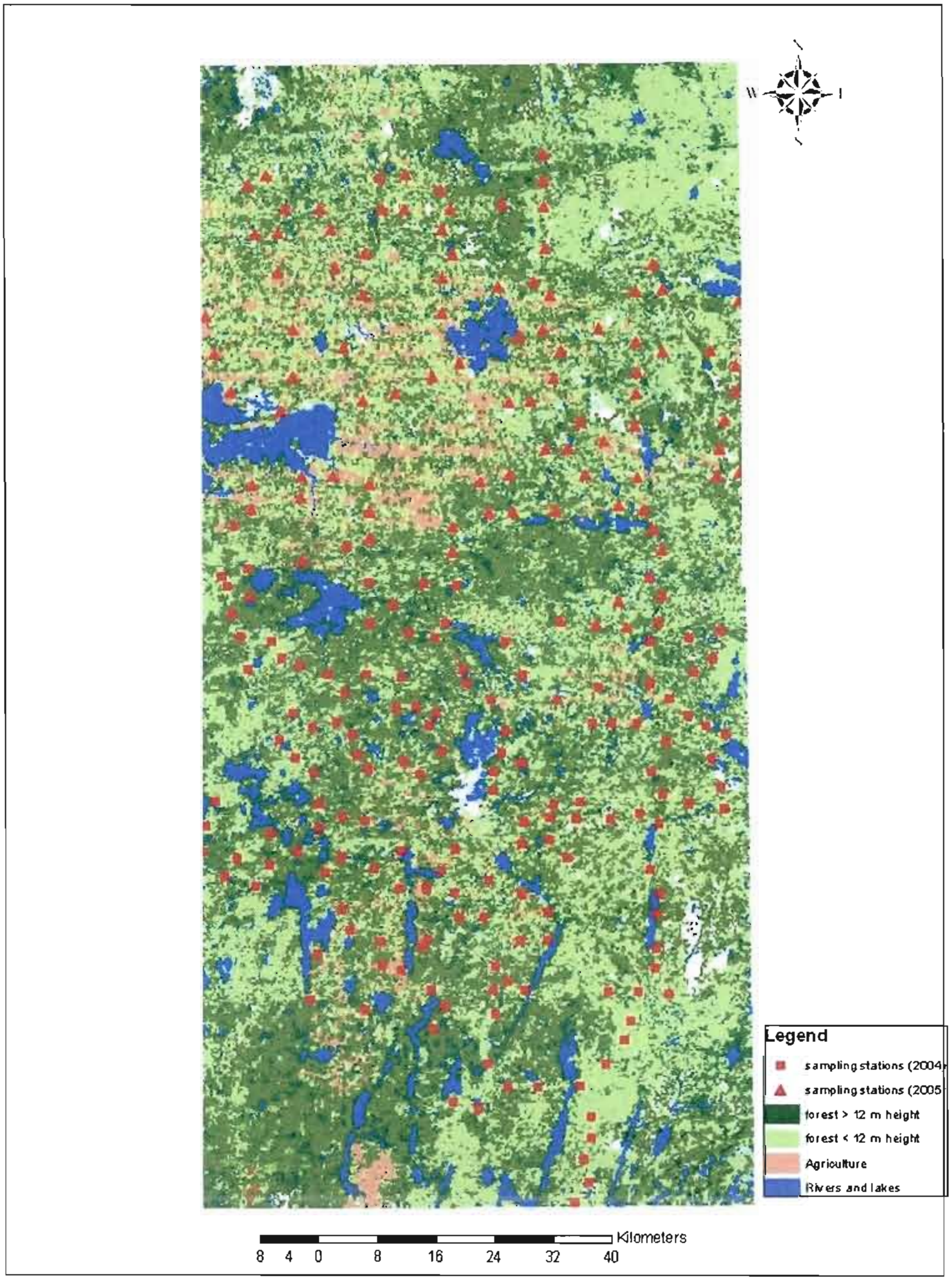

Legend
sampling stations (2004
sampling stations (2005
forest > 12 m height
forest < 12 m height
Agriculture
Rivers and lakes
Kilometers
8
4
0
8
16
24
32
40

Figure 3

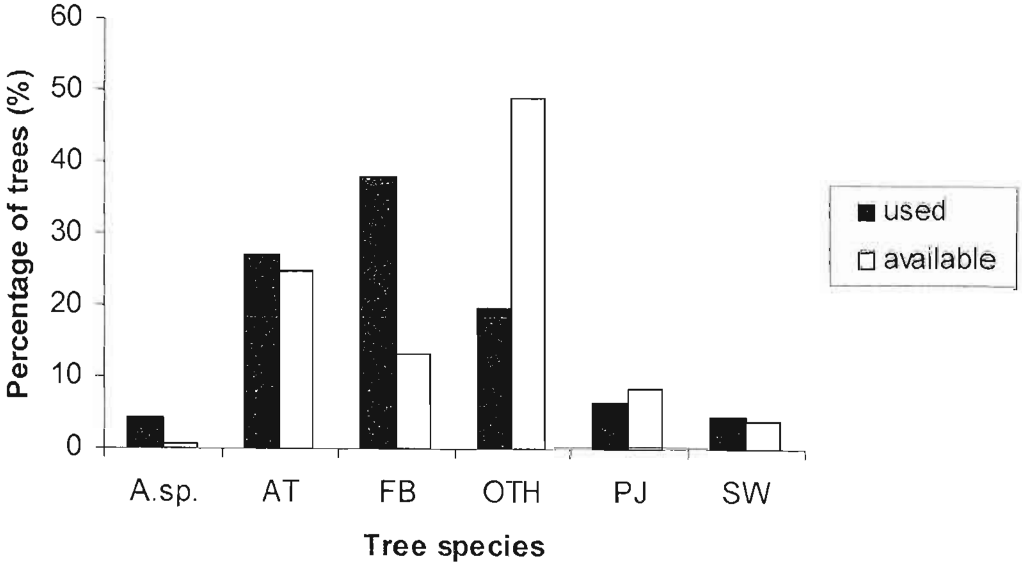
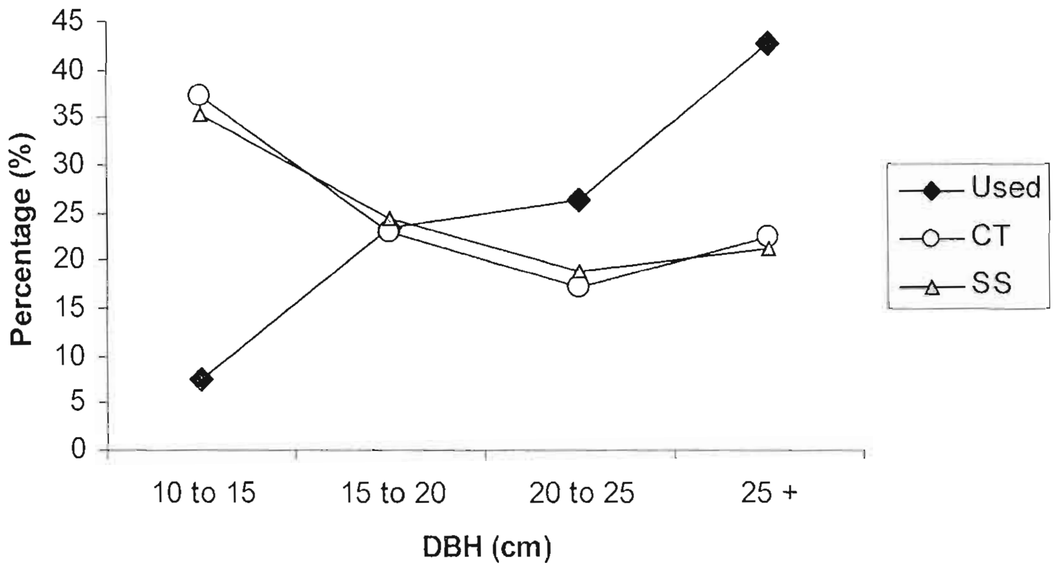
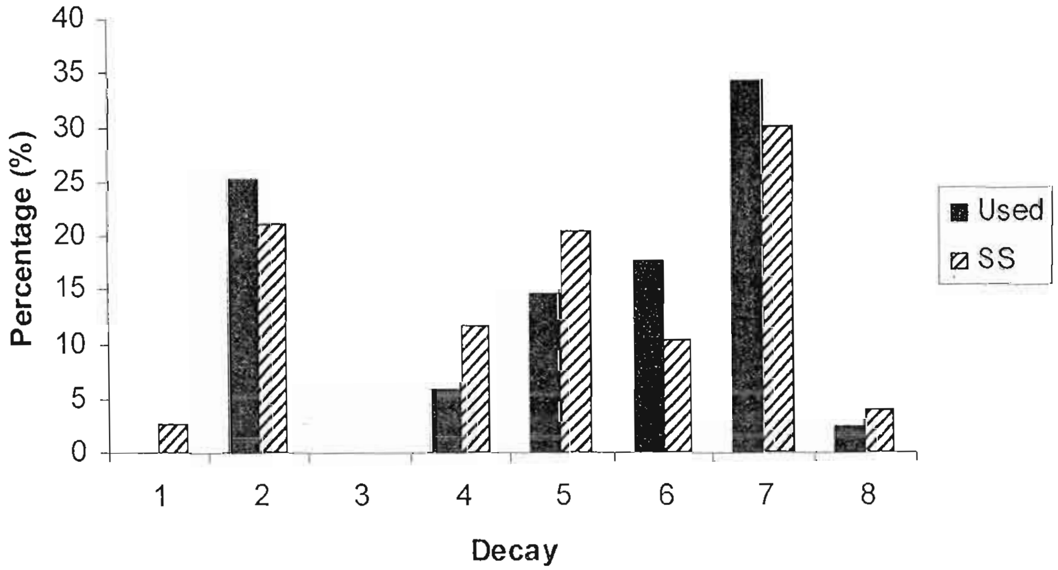

60
50
40
30
20
10
0
Percentage of trees (%)
A.sp.
AT
FB
OTH
PJ
SW
Tree species
■ used
□ available

Figure 4

A.


45
40
35
30
25
20
15
10
5
0
Percentage (%)
10 to 15
15 to 20
20 to 25
25 +
DBH (cm)
Used
CT
SS

B.


40
35
30
25
20
15
10
5
0
Percentage (%)
1
2
3
4
5
6
7
8
Decay
Used
SS

C.

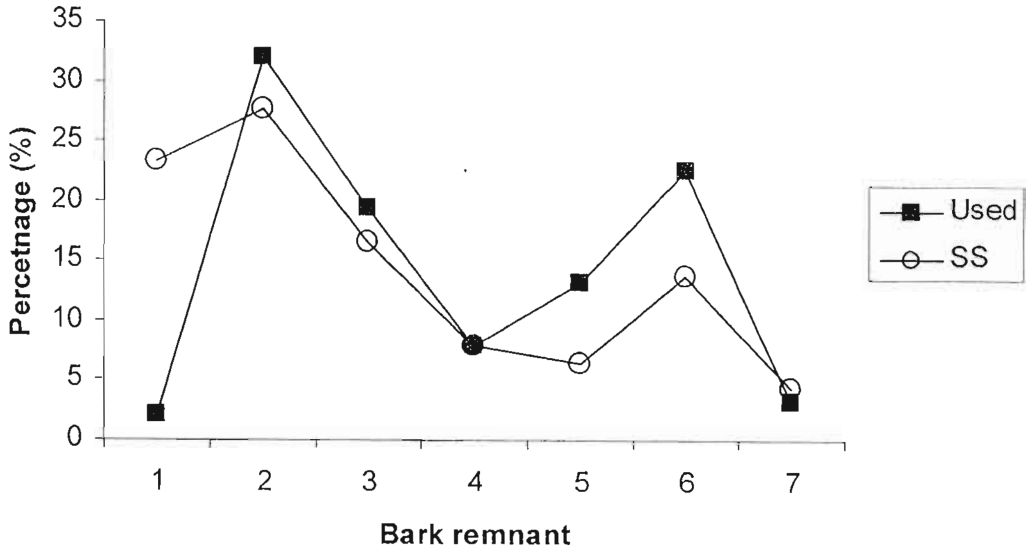
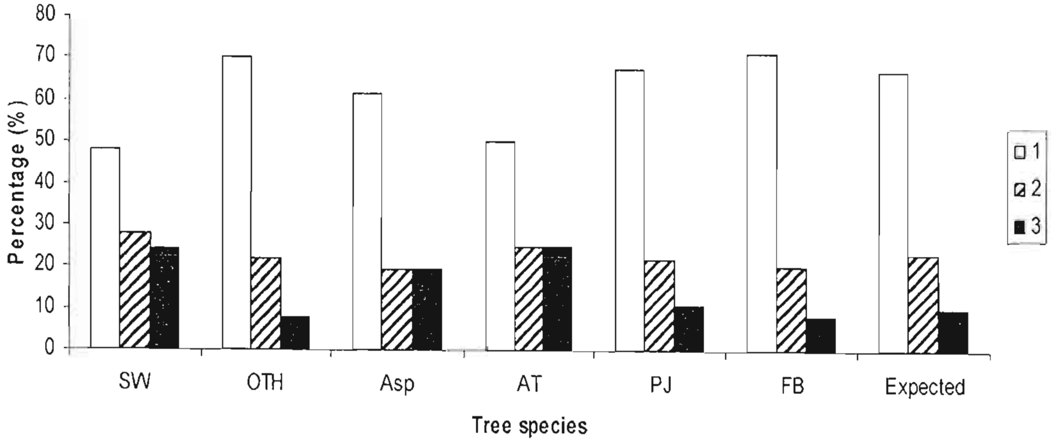


Figure 5

A.


80
70
60
50
40
30
20
10
0
Percentage (%)
SW
OTH
Asp
AT
PJ
FB
Expected
Tree species
1
2
3

B.

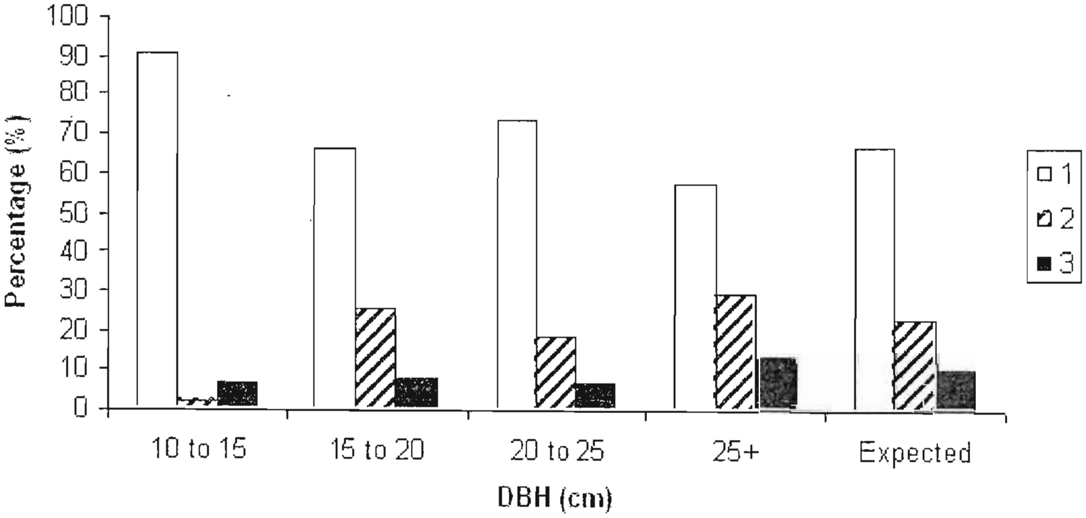

100
90
80
70
60
50
40
30
20
10
0
Percentage (%)
10 to 15
15 to 20
20 to 25
25+
Expected
DBH (cm)
1
2
3

Table 11. Composition of stand (250 m radius) and landscape conditions (1000 m radius) in 251 sampling stations located in eastern boreal mixedwood forest in north-western Québec, Canada.

Forest type covert (height ≥ 12m)	Stand				Landscape			
	Mean (%)	SD (%)	Min (%)	Max (%)	Mean (%)	SD (%)	Min (%)	Max (%)
Coniferous	9	18	0	84	9	12	0	62
Mixed	15	20	0	95	16	13	0	68
Deciduous	23	28	0	100	17	16	0	65
Deciduous and mixed	37	31	0	100	33	18	0	84
Open area *	30	29	0	100	31	19	1	98

* Stands where trees are small (less than 4m) and canopy cover was < 25%. Alder stands, wetlands, as well as recently disturbed forests (clear-cuts and young plantations), were classified in this habitat type.

Table 12. Proportion of marks, in percentage, for each section of tree grouped by tree species. n = 2115.

Tree species	Height of excavations (m)			
	0 to 5	5 to 10	10 to 15	> 15
Aspen sp.	3.07	0.61	0.00	0.00
Trembling aspen	19.81	5.91	0.09	0.14
Balsam fir	35.51	1.94	0.00	0.05
Others	17.45	1.89	0.00	0.00
Jack pine	6.57	0.61	0.00	0.00
White spruce	6.34	0.00	0.00	0.00
Total	88.75	10.97	0.09	0.19

Table 13. Ranking matrix for heights of foraging excavations on trees based on comparing proportional section of tree excavated with proportions of total section available, based on a compositional analysis (Aebischer et al. 1993). Each sign is based on mean element; a triple sign (+++ or ---) represent significant deviation from random at $P < 0.05$. Rank 1 is the less selected and rank 3 is the most selected. H1= 0 to5 m height, H2= 5 to 10m, H3= 10 to 15 m and H4= more than 15m height.

	H1	H2	H3	H4	Rank
H1		+++	+++	+++	3
H2	---		+	+	2
H3	---	-		-	0
H4	---	-	+		1

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CONCLUSION GÉNÉRALE

2.1 Distribution des pics et des arbres d'intérêt pour l'excavation

Notre étude montre que le Pic flamboyant et le Pic maculé sont les deux espèces les plus abondantes dans la région. Les pics boréaux (i.e. le Pic à dos noir et le Pic à dos rayé) et le Grand Pic, quant à eux, sont les espèces ayant eu la plus faible probabilité d'occurrence. Contrairement à plusieurs études effectuées ces dernières années (Gutzwiller and Anderson 1987, Freemark et al. 1995, McGarrigal and McComb 1995, Villard et al. 1999), nos travaux indiquent que la plupart des pics sont davantage influencés par les attributs de la forêt à l'échelle locale que par la composition ou la configuration des habitats au pourtour des forêts échantillonnées. Seul le Pic flamboyant semble influencé par la présence de milieux ouverts, mais cette espèce a une très grande capacité d'adaptation face à l'ouverture du couvert forestier et à l'augmentation de l'ouverture du territoire par l'agriculture ou la récolte forestière contrairement aux autres pics.

Les deux essences d'arbres les plus abondantes dans la région étudiée sont l'épinette noire et le peuplier faux-tremble. Cependant, la majorité des arbres de grand calibre (≥ 20 cm) sont des peupliers faux-tremble. La majorité des cavités de nidification ont été retrouvées dans des peupliers faux-tremble, et ce pour l'ensemble des espèces de pics. Toutes les espèces de pics, incluant les pics qui creusent de petites cavités, ont majoritairement fait leurs cavités dans les arbres ayant le plus grand diamètre (>20 cm). Nos résultats, tout comme ceux de Martin et al (2004) obtenus dans l'ouest canadien, tendent à confirmer que le peuplier faux-tremble serait une essence d'arbre clé pour l'excavation de cavités, et ce notamment parce qu'elle est fortement représentée dans les classes de diamètre de grande taille (> 20 cm).

2.2 Rôles écologiques de certaines espèces

Les excavateurs primaires de cavités, les pics, permettent à divers organismes de pouvoir réaliser leur cycle vital grâce à leur rôle de création de cavités. La Petite Nyctale fut le seul hibou cavicole ayant une occurrence suffisamment élevée pour pouvoir être analysée comme utilisateur secondaire de cavités dans nos analyses. Bien que ce petit hibou puisse utiliser les cavités excavées par le Pic flamboyant et le Grand Pic, son occurrence fut principalement corrélée à celle du Grand Pic. Donc, malgré sa très faible occurrence régionale, le Grand Pic pourrait être une espèce clé de voûte comme cela a pu être suggéré dans d'autres parties de son aire de distribution (Aubry et Raley 2002, 2003, Bonar 2000, 2001, Hoyt 1957, Bull and Holthausen 1993, Maisonneuve et al. 2002). De plus, en se basant sur les critères de Fleishman et al. (2000, 2001) pour les espèces parapluie, la Petite Nyctale pourrait sûrement être désignée espèce « parapluie » pour les oiseaux cavicoles étudiés. Cette espèce répond à toutes les exigences en co-habitant avec plusieurs autres espèces cavicoles, n'étant ni omni-présente ni rare et tout en étant sensible aux perturbations humaines.

2.3 Alimentation du Grand Pic

La présence d'arbres de grand calibre est importante pour la création de grandes cavités, mais elle l'est aussi pour l'alimentation des pics, notamment le Grand Pic. Nos résultats, en forêt boréale mixte, montrent que le Grand Pic s'alimente majoritairement sur les chicots de plus grand calibre qu'il peut trouver. Ces arbres de grand calibre représentent de bons substrats pour ce dernier, puisqu'ils peuvent abriter de plus grandes colonies de fourmis charpentières que les arbres de moins grand calibre (Bull 1987, Beckwith et Bull 1985, Hoyt 1957). D'ailleurs, plusieurs caractéristiques des arbres excavés par le Grand Pic sont souvent aussi retrouvées sur les arbres attaqués par les fourmis charpentières (Torgensen and Bull 1995). Le fait que les fourmis attaquent généralement les arbres à la base explique probablement pourquoi la plupart des excavations retrouvées se situent à la base des arbres (Sanders 1964). Le Grand Pic s'alimente significativement plus sur les sapins baumiers ou les peupliers faux-tremble. Cela met encore en évidence l'importance globale du peuplier faux-tremble comme espèce d'arbre clé pour les pics. Le fait que le Grand Pic s'alimente sur les trembles de grand calibre vient de façon indirecte appuyer le rôle d'espèce clé pour le peuplier faux-tremble car les arbres d'intérêt pour son alimentation (chicots de grand calibre ayant un stade de dégradation avancé) peuvent dans leurs premiers stades de dégradation être utilisés par toute la guilde des pics. Ainsi, une planification de rétention d'arbres de grand calibre pour l'alimentation du Grand Pic peut permettre de mieux rencontrer la conservation des besoins d'arbres de nidification pour les autres pics. Enfin, le Grand Pic peut aussi retourner s'alimenter sur le même arbre à plusieurs reprises année après année. Cependant, dans ce cas, il ne semble pas préférer une essence particulière bien que les arbres de plus faible diamètre aient moins de probabilité d'être réutilisées que ceux ayant un grand calibre.

2.4 Projets futurs

Notre étude a permis de déterminer que le Peuplier faux-tremble est une essence clé pour les pics, (tant lors de la sélection d'arbres à cavités que pour l'alimentation). Puisque les pics choisissent davantage les arbres de grand calibre pour excaver leurs cavités et que plusieurs espèces dépendent de ces cavités pour se loger et se reproduire, il serait intéressant de vérifier si la pose de nichoirs artificiels entraînerait une augmentation d'utilisateurs secondaires de cavité, notamment pour les utilisateurs de grandes cavités (ex. Chouette rayée, Grand Polatouche, etc.).

Afin de vérifier le statut d'espèce clé de voûte du Grand Pic pour la Petite Nyctale, il serait pertinent de faire un suivi des cavités de Grand Pics et de Pics flamboyant (espèce qui a aussi le potentiel d'être une espèce clé par l'excavation de grandes cavités). De plus, cela permettrait de connaître quelles sont les autres espèces qui occupent ces grandes cavités en forêt boréale mixte.

Nos résultats nous donnent des informations sur la présence des arbres d'alimentation utilisés par le Grand Pic, mais nous n'avons pas évalué si le contexte du paysage joue dans la disponibilité de ces arbres d'alimentation. Il serait intéressant de savoir si la sélection des arbres est influencée par d'autres échelles spatiale que l'échelle locale. Enfin, d'autres études ont relevé le fait que les excavations faites par le Grand Pic lors de son alimentation peuvent être fort utiles pour d'autres organismes (ex. offrir un abri, offrir l'accessibilité à la ressource alimentaire, etc.). A l'instar du suivi des cavités de nidification, un suivi plus ciblé des excavations d'alimentation pourrait accroître nos connaissances sur les relations fonctionnelles entre le Grand Pic et une autre suite d'espèces associés à ces excavations.

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