SILVA FENNICA
Silva Fennica 45(1) research articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Snag Characteristics and Cavity-Nesting Birds in the Unmanaged Post-Fire Northeastern Canadian Boreal Forest

Jeovanna Lowe, David Pothier, Jean-Pierre L. Savard, Ghislain Rompré and Mathieu Bouchard

Lowe, J., Pothier, D., Savard, J.-P.L., Rompré, G. & Bouchard, M. 2011. Snag characteristics and cavity-nesting birds in the unmanaged post-fire northeastern Canadian boreal forest. Silva Fennica 45(1): 55–67.

We studied the availability and characteristics of snags and their use by cavity-nesting birds in the northeastern part of the Canadian boreal forest. We built up two long-term (>200 years) chronosequences following time since the last fire in the unmanaged boreal forest of northeastern Québec, one in the balsam fir-white birch domain (southern region) and one in the spruce-mosses domain (northern region). We then sampled and characterized snags and live trees in 30 stands from each of these two chronosequences. We also looked for nest cavities on all sampled snags, performed bird inventories by point counts, and calculated tree mortality rate from permanent sample plots. Results show that mortality rates follow a U-shaped pattern, with more snags of large diameter (>20 cm DBH) in young (<50 years) and in old (>200 years) forests. In the latter, we also found more nest cavities than in any other age classes. Although abundance of primary cavity nesters (excavating species) did not vary among age classes, secondary cavity nesters (using cavities already available) tend to be more numerous in older forests. Our results highlight the capacity for young and old-growth forests to provide quality habitat for species that are dependent on large snags. Proper forest management should maintain a mosaic of different age forest stands, including snags, to promote biodiversity and provide important resources for resident bird species.

Keywords snags, cavity nesting birds, boreal forests, old-growth, long term chronosequence, time since fire, mortality rate, basal area

Addresses *Lowe* and *Pothier*, Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, Québec, G1V 0A6, Canada; *Savard*, Wildlife Research, Science and Technology, Québec Region, 1141 Route de l'Église, P.O. Box 10100, Québec, Québec, G1V 4H5, Canada; *Rompré*, Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, Québec, G1V 0A6, Canada & Department of Biology and Health Sciences, 84 West South Street, Wilkes University, PA 18766, USA; *Bouchard*, Ministère des Ressources naturelles et de la Faune, Direction de l'Environnement et de la Protection des Forêts, 880 Chemin Ste-Foy, Quebec, Québec, G1S 4X4, Canada
E-mail jeovannalowe@gmail.com

Received 2 August 2010 **Revised** 7 December 2010 **Accepted** 4 January 2011
Available at http://www.metla.fi/silvafennica/full/sf45/sf451055.pdf

1 Introduction

In boreal forest ecosystems, snags (dead standing trees or dying trees) contribute to many biological functions and provide valuable habitats for the conservation or enhancement of wildlife (e.g. black-backed woodpecker; Bate et al. 1999, Drapeau et al. 2002, Saint-Germain et al. 2004, Hutto 2006). They are used by a wealth of invertebrate, vertebrate, and plant species. Furthermore, organisms such as fungi and insects that are found in dead trees greatly enhance the value of snags for other wildlife. For example, decomposers invade dead or dying trees, and weaken and soften them, facilitating their use by primary cavity-nesters (i.e. woodpeckers and nuthatches) and secondary cavity-nesters (species that use cavities excavated by primary cavity nesters or natural cavities created by decay; Thomas et al. 1979, Bull 1983, Drapeau et al. 2002).

In the eastern part of the Québec boreal forest, the humid climate lengthens the fire cycle up to 500 years (Bouchard et al. 2008), resulting in a multi-aged mosaic with old-growth stands covering 60–65 % of the unmanaged forest territory (Boucher et al. 2003, Côté et al. 2010). In earlier studies, snag abundance has been observed to follow a well-defined U-shaped pattern over stand age. This pattern is characterized by high volume of snags in stands recently disturbed by fire, few snags in actively growing stands, and an increasing snag abundance in ageing stands as canopy trees become progressively senescent (e.g., Harmon et al. 1986, Spies and Franklin 1988, Tyrrell and Crow 1994, Clark et al. 1998). In the course of this long-term stand development, other forest attributes may change, including species composition and tree size distribution. In the northeastern Canadian boreal forest, balsam fir (*Abies balsamea* (L.) Mill.) generally increases in abundance, while tree diameter distribution becomes increasingly irregular, as black spruce (*Picea mariana* (Mill.) BSP) dominated forests get older (Pham et al. 2004, Bouchard et al. 2008, Côté et al. 2010). In turn, this could affect snag production since balsam fir is more vulnerable than black spruce to wood decay and spruce budworm (*Choristoneura fumiferana* (Clem.)), an important defoliation insect causing much mortality in boreal forests of eastern Canada (Whitney 1995, Hennigar et al. 2008).

Some studies on bird abundance, species richness, and diversity have compared succession changes originating from fire and logging (Imbeau et al. 1999, Le Blanc et al. 2010), but few have investigated changes in bird communities along a long-term gradient in unmanaged forests. Fire has an immediate positive impact on woodpecker breeding and foraging because of the high number of snags produced (Nappi et al. 2003), confirming the importance of early post-fire disturbance forests for wildlife (Dixon and Saab 2000). In old-growth boreal forests, however, results from the western part of the Quebec province indicate relative low snag abundance (Drapeau et al. 2002), while studies of other boreal regions in Canada suggest the high potential for old-growth forests for cavity nesting birds due to high abundance of snags (Schieck et al. 1995). If snag abundance varies from early post-fire years to old-growth, we should expect use of snags to change as well. In addition, little is known about the capacity of old-growth forests to provide adequate habitat for bird species associated with large snags. By exploring these issues, we might be able to provide better recommendations and rationales to manage and harvest forest landscape considering habitat protection for cavity-nesting birds in the boreal forests of eastern Canada.

The general objective of this study was to determine if there is variation in snag availability for cavity-nesting birds along two long term chronosequences after fire, and to relate any variation to avian species richness and abundance. First, we quantified snag abundance (basal area) and characteristics (e.g. size classes) as well as tree mortality rate coming from permanent sample plots along chronosequences following fire. Second, we evaluated the effect of tree size and wood degradation levels on the number of bird cavities. Finally, we estimated species richness and bird abundance of cavity nesting birds according to time since fire.

2 Materials and Methods

2.1 Study Area

Our study was conducted in the North Shore region of Québec, in the northeastern part of the

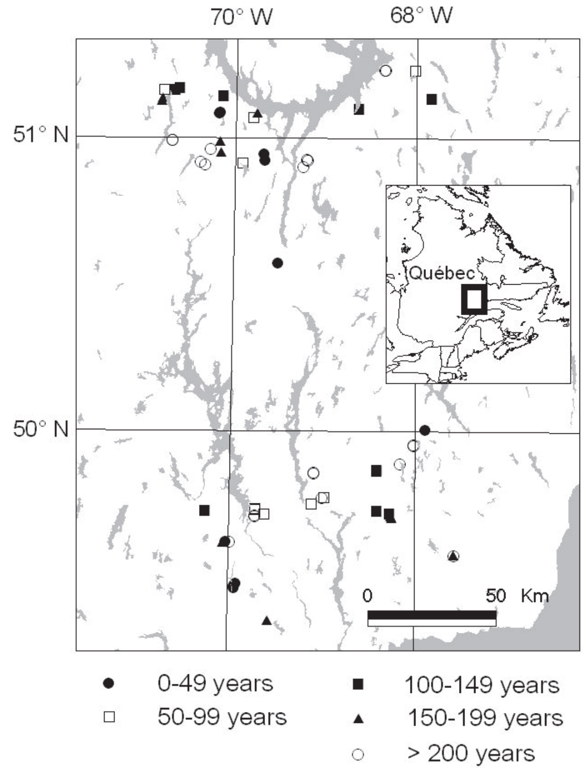

Fig. 1. Location of the study area and fires mapped for the period 1800–2000. Fire dates are shown only for fires >200 km^2.

Canadian boreal forest. The topography is characterized by hills and moderate slopes (16–30%), with a maximum recorded altitude of 700 m and a cold maritime climate (Robitaille and Saucier 1998). The climate is boreal humid and is characterized by average annual temperatures between –2.5 and 0.0 °C and annual precipitation ranging from 1000 to 1400 mm (Garet et al. 2009).

Surveys were carried out in two regions of the study area: the southern region (49°42´N, 68°51´W) located a few km north of Baie-Comeau, and the northern region (50°57´N, 68°50´W) located south of the Manic 5 reservoir (Fig. 1). These regions overlap two bioclimatic sub-domains of the boreal zone: the balsam fir - white birch domain (southern region) and the spruce-mosses domain (northern region). Balsam fir characterizes the former, with black spruce dominating stands in poorer sites (MNRF 2003). As latitude increases (shifting to the northern sub-domain), forest stands are increasingly dominated by black spruce. Dominant species found in the region include balsam fir and black spruce, with minor components of white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb), white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.). With time since the last fire, the size structure of live trees becomes more irregular, which is generally accompanied by a gradual increase in balsam fir abundance (De Grandpré et al. 2000, Côté et al. 2010). The region is known for outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens)), especially in the southern part of the study area (near Baie-Comeau) between 1975 and 1990 (Bouchard and Pothier 2010). However, in the northern part of the study area, these outbreaks resulted in very little tree mortality (Bouchard and Pothier 2010). Although the southern part was also used for logging, numerous fragments of unmanaged forests still remain today (Bouchard et al. 2008) and were used in this study.

Fire history has been reconstructed over the area by Bouchard et al. (2008) who mapped burned stands larger than 10 hectares and up to 200 years since last fire. In each of the two regions, 30 stands were identified to form a chronosequence after fire (Fig. 1). For each chronosequence, five independent stands were selected in each of the following age classes: from 0 to 50 years since last fire (class 1), 51 to 100 years (class 2), 101 to 150 years (class 3) and 151 to 200 (class 4). We also selected ten old-growth stands for which the time since fire (from here on TSF) was not determined, but was greater than 200 years (class 5). Overall, we sampled 60 stands (2 chronosequences of 30 stands per chronosequence) that were then inventoried.

2.2 Standard Inventory Plots

In each selected stand, we established standard inventory plots during summer 2007 to characterize stand composition and diameter distribution. In each of these circular, 400-m^2 plots, all snags and live trees were identified, along with their diameter at breast height (DBH) for trees larger than 9.1 cm. The state of decomposition of each snag was categorized following Hunter's classification (decay stages, 2 declining to 7 decomposed; Fig. 10.1 in Hunter 1990).

2.3 Dead Standing Tree Plots

To quantify snag decomposition, we established one 50 x 20 m plot adjacent to the standard inventory plots in each of the 60 stands selected from the two chronosequences. In each plot, we tallied all snags to increase sample size because standard inventory plots (400 m^2) were too small to accurately determine the number of snags available to birds.

For each snag, we determined height (+0.1 m), DBH (+1 cm), and the state of decomposition. For the purpose of this study, only snags with DBH >9.1 cm and a minimum height of 1.3 m were considered. These characteristics are considered minimal conditions for nesting or foraging birds (Thomas et al. 1979).

2.4 Permanent Sample Plots

To estimate the snag production rate at different stand ages in the studied territory, we used a network of permanent sample plots (PSPs) established in 1970 by the Ministère des Ressources Naturelles et de la Faune du Québec (MRNFQ). We overlapped these georeferenced PSPs to the fire map of Bouchard et al. (2008), to determine the time since the last fire for each of the 460 PSPs corresponding to the territory covered by the fire map. Each of these PSPs was inventoried two to four times (depending on the year of establishment) during the snow-free periods between 1970 and 2007 for a total of 1107 plot measurements. The inventory taken in each 400 m^2 circular PSP consisted of measuring the DBH (1.3 m, DBH ± 1 mm) of each tree (live and dead) larger than 9.0 cm. Also, the age and height (± 0.1 m) of at least three live dominant tree species were recorded (Pothier and Mailly 2006). Periodic measurements of each PSP allowed us to quantify the rate of mortality in terms of basal area and to relate this rate of mortality to time since fire as well as to stand characteristics. The average time period between two successive measurements of the PSPs was 10 years, but the mortality rates were calculated on an annual basis. Although the size of these PSPs (400 m^2) is rather small to evaluate snag abundance, we believe that the quite long time period covered by these numerous PSPs compensates for this disadvantage.

2.5 Bird Nest Cavity

We considered a cavity nest to be a hollowed-out opening in the trunk of a tree, either found naturally in snags or purposely made by birds such as woodpeckers (as long as they were occupied cavities; excluded were the natural holes not used by birds or foraging cavities). Other examples of cavity-nesting birds include chickadees, nuthatches, and creepers (Hunter 1999). We also included brown creepers' nests, built between the trunk and a loose piece of bark, since they

Table 1. List of cavity-nesting bird species found in the study area.

Species name (English)	Scientific name
Brown creeper	*Certhia americana*
Tree swallow	*Tachycineta bicolor*
Boreal chickadee	*Parus hudsonicus*
Hairy woodpecker	*Picoides villosus*
Black-backed woodpecker	*Picoides arcticus*
Northern flicker	*Colaptes auratus*
Yellow-bellied sapsucker	*Sphyrapicus varius*
Three-toed woodpecker	*Picoides tridactylus*
Red-breasted nuthatch	*Sitta canadensis*

are found mostly on dead or dying trees (Hejl et al. 2002). A list of the cavity-nesting species found in the study area is presented in Table 1. From mid-May to July 2007, in addition to dead tree inventories, all 60 stands were surveyed for the presence of cavities in each snag located in the 50 x 20 m plots.

2.6 Point Counts

To estimate species richness and bird abundance of cavity nesting birds, we used the point count method (Reynolds et al. 1980, Hutto et al. 1986). One point was located at the center of each standard inventory plot established in the 60 stands from the two chronosequences. All these stands were independent, but in some few cases, one stand was close to another. In these cases, we applied a minimal distance of 200 m between two points while all points were at least 100 m from the edge of a burned site. Therefore, we avoided repetitions in bird detection which could have produced spatial autocorrelation.

Two visits were conducted at each point during the breeding period (late May to late June 2007), to allow detection of a maximal number of species during their peak of singing activity. Observers recorded the number of individuals of each bird species detected by sight or sound for each of the following distance classes from the center of the point: 0–30 m, 30–50 m, 50–75 m, and 75–100 m. In this study, we used the number of species detected in both visits of each point count to a maximum radius of 100 m.

Observers were familiar with bird vocalizations. However, if identification was doubtful, they recorded the bird song using a digital tape recorder with a directional microphone. The two visits to each stand were made by a different person to minimize observer bias. Similarly, we varied the time we visited each point count (e.g.: early vs. later in the morning) to maximize detection probabilities of each species present. At each visit, birds seen or heard were recorded at 10-min intervals for a 20-min period. This is the standard time procedure for boreal forest bird communities when one wants to relate bird richness and abundance with the vegetation characteristics of the area around the point (Drapeau et al. 2000, 2002).

2.7 Statistical Analyses

An analysis of variance (ANOVA) was used to compare mean snag basal area and rate of tree mortality between the two chronosequences and among TSF classes. We weighted the number of snags per plot so that each plot contributed to only one degree of freedom in the model (Desrochers 1992). This technique allows the use of all observations while avoiding pseudo-replication (Machlis et al. 1985). We used TSF as a classification variable rather than as a continuous variable in the statistical analyses, because we were not able to determine the exact value for plots with TSF >200 years (class 5) from the available fire map (Bouchard et al. 2008). When the ANOVA detected a significant difference for one of the factors, we compared the means of this factor using a Waller-Duncan comparison test. In addition, when the ANOVA detected a significant difference for the interaction between two factors, we compared the means of each level of the interaction using the same comparison test. For all analyses of point count data, we used the maximum number of individuals for each species recorded (resident vs. migrants, primary vs. secondary cavity nesters) at each plot after merging together the observations of the two visits.

3 Results

3.1 Snag Basal Area and Tree Mortality Rate

A total of 1740 snags were measured from 60 stands (30 per chronosequence) covering five TSF classes. Significant differences in snag basal area were observed between the two chronosequences, with a higher value observed in the southern chronosequence (Fig. 2). Snag availability changed significantly among TSF classes (F=3.33, df = 9, P = 0.003). These differences were more structured in the northern than southern chronosequence, showing a defined U-shaped pattern of abundance. Snag basal area was larger in TSF classes 0–50 and > 200 years because of a higher presence of large sized trees.

Tree mortality rate, calculated on a basal area basis using the repeated measurements of the permanent sample plots, differed among TSF classes (F=5.92, df = 4, P = 0.0001) and tended to increase with TSF (Fig. 3). The average annual mortality rate was twice as large in the two oldest plots (> 150 years, rate ≈ 0.40%) compared to the two younger ones (< 100 years, ≈ 0.18%). For

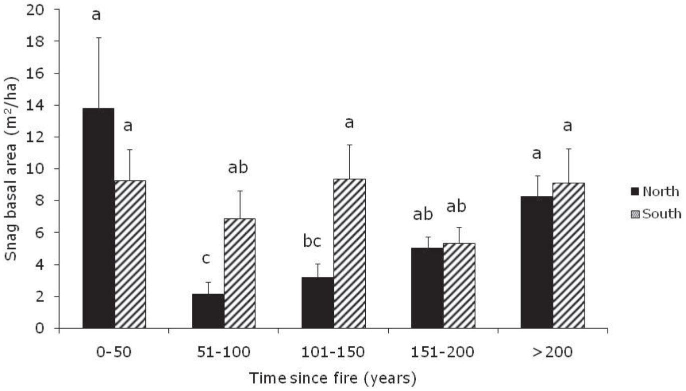

Fig. 2. Snag basal area according to the time since last fire. Significant differences (P < 0.05) for means values (± S.E; n = 30 per chronosequence) among years are indicated by different letters.

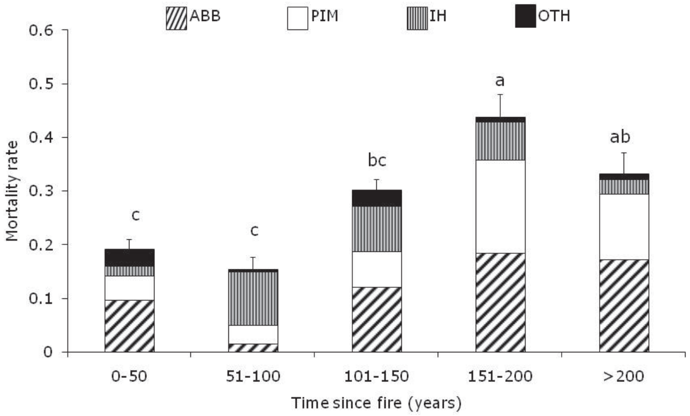

Fig. 3. Annual tree mortality rates (%) calculated on a basal area basis for each time since fire (TSF) classes and for four tree species groups. Species groups are balsam fir (ABB), black spruce (PIM), intolerant hardwoods (IH) and the other remaining species (OTH).

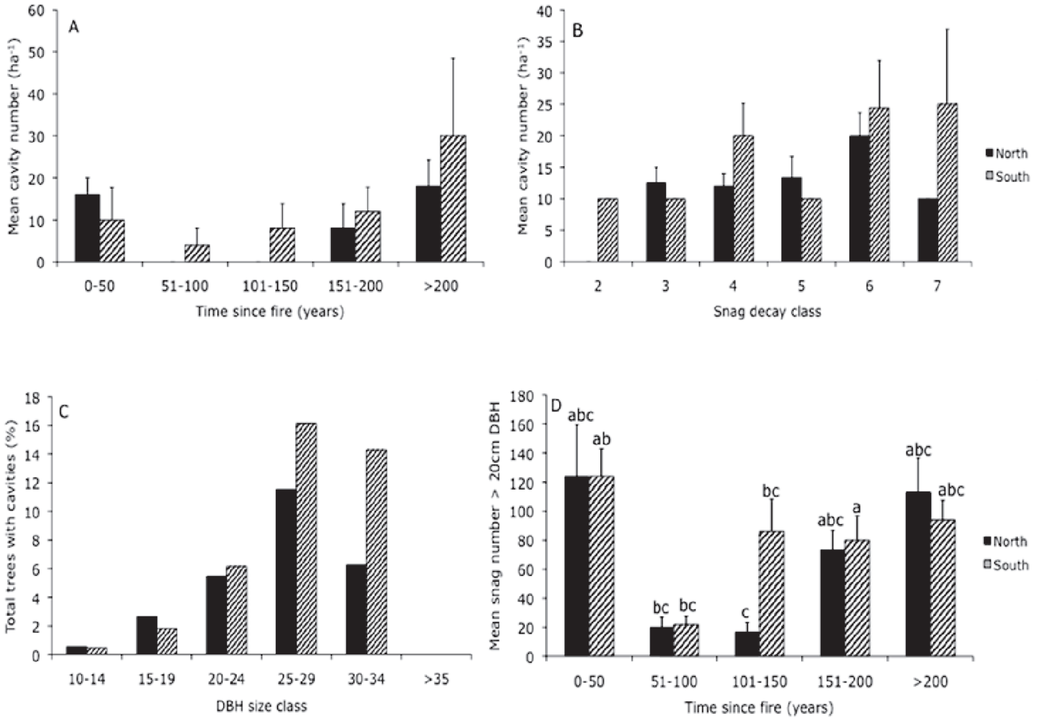

Fig. 4. Snag availability and cavity numbers following the two chronosequences. The four diagrams show (A) average number of cavities according to the time since fire; (B) average number of cavities by state of snag decomposition; (C) proportion of trees holding cavities by DBH class; and (D) average number of snags >20 cm DBH per ha according to time since fire.

TSF over 200 years, however, the mortality rate tended to decrease.

Annual tree mortality rates also differed among TSF classes and tree species groups (Fig. 3). For instance, mortality rates of black spruce increased with TSF, while those of intolerant hardwoods (mostly composed of white birch, and trembling aspen) were highest in TSF classes between 51 and 200 years. Mortality rates of balsam fir remained relatively constant versus TSF except in the 51–100 class, within which mortality rates were low. No difference in mortality rates were observed in the other species groups dominated by white spruce, and jack pine.

3.2 Cavity Abundance

A total of 71 cavities were found in 50 snags, representing 2.87% of all snags tallied in this study (1740). The number of cavities per hectare did not differ significantly among chronosequences and TSF classes, but young stands (0–50 years) and those older than 200 years tended to contain more cavities (Fig. 4a). When snags were in a more advanced stage of decomposition, they seemed to support more cavities (Fig. 4b). Also, a greater proportion of trees with cavities were observed in snags larger than 20 cm DBH compared to smaller snags (8.2% and 1.2% respectively) (Fig. 4c). The number of cavities present in snags larger than 30 cm DBH seemed to be relatively low because such trees were rare on our study sites. The mean number of large snags (>20 cm) per hectare was significantly different among TSF classes (F=2.83, df=9, P=0.0031; Fig. 4d). Snags >20 cm DBH were generally more abundant in young (0–50 years) and old (>200 years) stands, compared to those of intermediate ages.

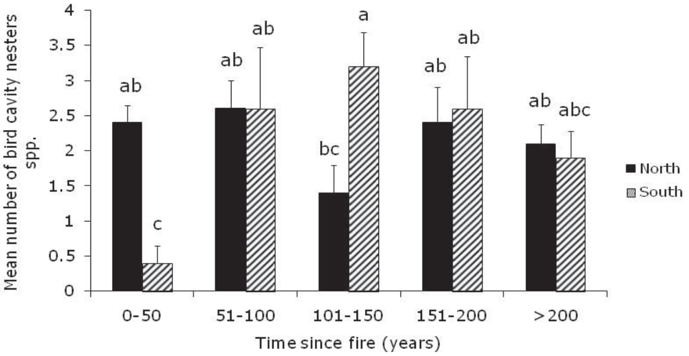

Fig. 5. Average number of bird species using cavities per plot according to the time since last fire (TSF). Significant differences (P<0.05) among mean values (±S.E; n=30 per chronosequence) of TSF classes are indicated by different letters.

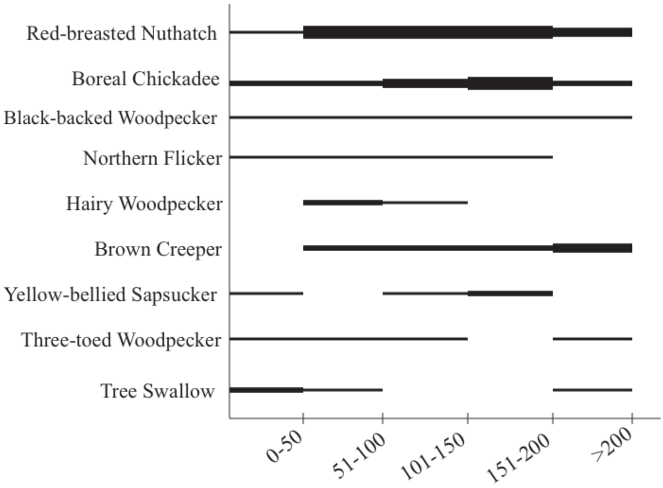

Fig. 6. Presence of cavity-nesters according to time since fire. For each species, line width corresponds to the relative abundance of these birds during point counts (see Methods). Within each TSF class, no line means 0 birds per point count, the thinner black line represents a density of ≤0.2 bird/point count whereas the thickest black line corresponds to a density of ≥0.8 bird/point count. Scientific names for the species listed can be found in Table 1.

3.3 Cavity Nesting Birds

Although cavity nesting bird species were all present in both chronosequences (no differences in cavity nesting bird species composition), we found a significant interaction between TSF and chronosequence that influenced the species richness (F=2.39, df=9, P=0.0246). Young forests (age class: 0–50 years) were associated with fewer cavity nesters than other TSF classes in the southern chronosequence but not in the northern one (Fig. 5). Apart from these young stands, no other significant differences were observed between cavity nesters and TSF.

Relative abundance (averaged for all point counts) of primary cavity nesters did not vary among age classes. However, secondary nesters seemed to be more abundant in older forests (>100 years). These included the boreal chickadee and brown creeper (Fig. 6).

4 Discussion

4.1 Snag Characteristics

Snag availability changed with time since the last fire in the two chronosequences (Fig. 2). In general, our results for the northern chronosequence agree with the typical snag abundance for unmanaged boreal forests, characterized by the U-shaped pattern that represents an early, high level of snags followed by a subsequent transition phase with few snags, and then, a later increase in snag abundance once a forest matures (Harmon et al. 1986, Peet and Christensen 1987, Clark et al. 1998). In the southern chronosequence, this pattern was not observed: rather, during the 101–150 year period, we found an increase in the overall mean basal area for dead trees. Since we inventoried the two chronosequences in 2007, it is possible that the presence of some dead trees in these stands was caused by the late defoliation years of the last spruce budworm outbreak that ended during the early 1990s (Aakala et al. 2007) and that mainly affected the southern area of the studied territory (Bouchard and Pothier 2010). This might also be related to a severe ice storm that occurred during the 2004–2005 winter and that top-killed many dominant trees in stands of the southern chronosequence. These damages on the top of the trees were not observed in the northern chronosequence, likely because the colder temperature resulted in precipitation falling as snow instead of as rain.

According to yield curves for black spruce stands of the study area (Garet et al. 2009), total tree mortality rates (all species) were proportional to the temporal pattern of change of living tree volume as previously observed by Aakala et al. (2008). At the species level, even though balsam fir is thought to be more susceptible to mortality agents than black spruce (Burns and Honkala 1990, Aakala et al. 2007), the increasing snag availability with TSF seems unrelated to the increasing occurrence of balsam fir in old-growth stands (Fig. 3). Indeed, balsam fir and black spruce mortality rates in stands of varying ages seem proportional to their respective abundance that changes with TSF in agreement with the pattern of tree succession observed after fire in the study area (Bouchard et al. 2008, Gauthier et al. 2010). However, species-specific mortality rates are also influenced by the longevity of each species and by secondary disturbances such as spruce budworm defoliation.

It is now widely accepted that early post-fire forests are key habitats for snag recruitment (Fig. 2) because trees killed by fire are a major source of new snags (Wein and MacLean 1983, Gauthier et al. 2001). At the other end of the chronosequence spectrum, though, old-growth forests also provide a large number of snags, mostly with large DBH, at varying stages of decomposition (this study; Bergeron 2000, Bergeron and Harper 2009). These large-diameter snags are more valuable for wildlife than smaller ones because they persist longer (lower falling rate, see Saab and Dudley 1998) and they are suitable for small as well as large cavity-nesting birds (Vaillancourt et al. 2008). Indeed, large diameter snags resulted in an increased number of cavities, and cavity nesters such as woodpeckers are known to prefer these trees (Mannan et al. 1980, Swallow et al. 1986, Drapeau et al. 2002, Nappi et al. 2003, Smith et al. 2008). The number of cavities per unit area also tends to increase in stands composed of numerous highly decayed trees (Fig. 4b). This result is likely related to the residence times of these trees which promote their use by a large variety of cavity-nesting birds, from woodpeckers in lightly decayed snags (at the beginning of the residence time) to weak excavators in highly decayed snags (at the end of the residence time) (Vaillancourt et al. 2008). In our study area, the residence times of dead standing trees is less than five years in the early stage of tree decomposition, but can reach as much as 40 years in the last stage (Aakala et al. 2008). For comparison, the residence times of dead standing Scots pine (*Pinus sylvestris* L.) trees in drier sites of Finland averaged 81 years whereas some dead trees remained standing as long as 200 years (Rouvinen et al. 2002).

4.2 Cavity Nester Abundance

In this study, we used point counts to quantify the occurrence patterns of cavity-nesting birds. We believe that bird abundance should reflect differences observed in their habitat even though this relationship might be better with more detailed data on demography (see Van Horne 2002). Previous studies of the occurrence of primary and secondary cavity nesters have found that some species are more common in recently-burned forests and old-growth stands (Drapeau et al. 2002). In our study, black-backed woodpeckers were not necessarily more numerous in the recently-burned or old-growth forests, but rather were found in all TSF classes. Due to our low number of sample plots per age class for point count purposes, and consequently, low detection of these species, it is difficult to provide abundance estimates by TSF class. Most studies have shown that high productivity in terms of burn use by this woodpecker occurs only 1 to 3 years following a burn (Dixon and Saab 2000, Nappi et al. 2003), but our 1–50 year TSF class included only one such recent fire. This explains why the woodpecker population may not dominate as much as it does in other studies that may have included the period right after fire. Indeed, the present study did not specifically focused on the early years post-fire, it rather focused on the overall long term chronosequences. Meanwhile, in the southern chronosequence, dead tree abundance was not found only in young and old TSF classes, but also in the 101–150 years (Fig. 2). This might explain why black-backed or American three-toed woodpeckers were not necessarily more abundant in any age class (Fig. 6). Nevertheless, similar to the findings of Drapeau et al. (2000, 2002) in the boreal forests of western Québec, cavity nesters such as the red-breasted nuthatch, boreal chickadee and brown creeper were all more abundant in mature and old-growth forests than in younger stands. The high quantity of live and dead trees >20 cm DBH might explain their abundance in these forests as they provide higher opportunities for nesting and for foraging.

4.3 Implications for Management

The boreal forest of eastern Québec is characterized by long fire-return intervals (Bouchard et al. 2008) that lead to the dominance of old-growth forest stands. These stands are characterized by, among other factors, a high level of deadwood, which has a significant ecological function in the ecosystem (Hunter 1999, Imbeau et al. 2001, Bergeron et al. 2006). Our study shows the importance of conserving this forest age structure at the landscape scale and of applying silvicultural practices, such as the irregular shelterwood system (Ruel et al. 2007, Raymond et al. 2009), in exploited old-growth forests (>150 year). These management methods should help retain structural elements essential to the maintenance of biological diversity, such as snags throughout the regeneration cycle. This would maintain nesting and foraging opportunities for cavity nesters, whereas secondary nesters will also benefit from such management. Our results therefore highlight the strong capacity for old-growth forests to provide quality habitat for species dependent on large snags. Likewise, since non-salvaged post-fire stands were also characterized by numerous large-diameter snags, clear-cutting with snag retention should help preserve important features of cavity-nesting bird habitats.

Acknowledgments

This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) – Université Laval Industrial Research Chair in Silviculture and Wildlife and by the Fonds québécois de la recherche sur la nature et les technologies (FQRNT). We would like to thank the field crew, Herman Frouin and Gabriel Fortin, for data collection. Jean-Gabriel Elie provided valuable help with logistics and useful advice about data analyses. Thanks also to the industrial partners who facilitated the fieldwork and provided access to the different forest management areas: Abitibi-Bowater, Kruger and Arbec. Finally, thanks to the reviewers for their helpful comments on the manuscript.

References

Aakala, T., Kuuluvainen, T., De Grandpré, L. & Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Canadian Journal of Forest Research 37: 50–61.

— , Kuuluvainen, T., Gauthier, S. & De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255: 410–420.

Bate, L., Garton, E. & Wisdom, M. 1999. Estimating snag and large tree densities and distributions on landscape for wildlife management. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-425. 76 p.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81: 1500–1516.

— & Harper, K.A. 2009. Old-growth forests in the Canadian Boreal: the exception rather than the rule? In: Wirth, C., Gleixner, G. & Heimann, M. (eds.). Old-growth forests. Springer-Verlag, Berlin– Heidelberg. p. 285–300.

— , Cyr, D., Drever, C., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Le Goff, H. & Lesieur, D. 2006. Past, current and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Canadian Journal of Forest Research 36: 2737–2744.

Bouchard, M. & Pothier, D. 2010. Spatio-temporal variability in tree and stand mortality caused by spruce budworm outbreaks in eastern Québec. Canadian Journal of Forest Research 40: 86–94.

— , Pothier, D. & Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Canadian Journal of Forest Research 38: 1621–1633.

Boucher, D., De Grandpré, L. & Gauthier, S. 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. Forestry Chronicle 79: 318–328.

Bull, E. 1983. Snag habitat management. General Technical Report RM-99. USDA, Fort Collins, CO.

Burns, R.M. & Honkala, B.H. 1990. Silvics of North America. U.S. Department of Agriculture, Forest Service, Washington, DC. Agriculture Handbook 654. 877 p.

Clark, D.F., Kneeshaw, D.D., Burton, P.J. & Antos, J.A. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Canadian Journal of Forest Research 28: 284–290.

Côté, G., Bouchard, M., Pothier, D. & Gauthier, S. 2010. Linking stand attributes to cartographic information for ecosystem management purposes in the boreal forest of eastern Québec. Forestry Chronicle. (In press).

De Grandpré, L., Morissette, J.L. & Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. Journal of Vegetation Science 11: 791–800.

Desrochers, A. 1992. Age and foraging success in european blackbirds – variaton between and within individuals. Animal Behaviour 43: 885–894.

Dixon, R.D. & Saab, V.A. 2000. Black-backed woodpecker (Picoides arcticus). In: Poole, A. (ed.). The birds of North America online. Cornell Lab of Ornithology, Ithaca. [Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/509doi:10.2173/bna.509].

Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P.L., Bergeron, Y. & Vickery, W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecological Monographs 70: 423–444.

— , Nappi, A., Giroux, J.-F., Leduc, A. & Savard, J.-P.L. 2002. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. USDA Forest Service, General Technical Report PSW-GTR-181: 193–205.

Garet, J., Pothier, D. & Bouchard, M. 2009. Predicting the long-term yield trajectory of black spruce stands using time since fire. Forest Ecology and Management 257: 2189–2197.

Gauthier, S., Leduc, A., Harvey, B., Bergeron, Y. & Drapeau, P. 2001. Les perturbations naturelles et la diversité écosystémique. Naturaliste canadien 125: 10–17.

— , Boucher, D., Morissette, J. & De Grandpré, L. 2010. Fifty-seven years of composition change in the eastern boreal forest of Canada. Journal of Vegetation Science 21: 772–785.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. & Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Hejl, S.J., Newlon, K.R., Mcfadzen, M.E., Young, J.S. & Ghalambor, C.K. 2002. Brown creeper (Certhia americana). In: Poole, A. (ed.). The birds of North America online. Cornell Lab of Ornithology, Ithaca. [Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/669].

Hennigar, C.R., MacLean, D.A., Quiring, D.T., & Kershaw, J.A.J. 2008. Differences in spruce budworm defoliation among balsam fir and white, red, and black spruce. Forest Science 54:158–166.

Hunter, M.L.J. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Prentice-Hall.

— 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge.

Hutto, R.L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conservation Biology 20: 984–993.

— , Pletschet, S.M. & Hendricks, P. 1986. A fixed-radius point count method for nonbreeding and breeding-season use. Auk 103: 593–602.

Imbeau, L., Savard, J.-P.L. & Gagnon, R. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. Canadian Journal of Zoology 77: 1850–1860.

— , Mönkkönen, M. & Desrochers, A. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conservation Biology 15: 1151–1162.

Le Blanc, M.-L., Fortin, D., Darveau, M. & Ruel, J.-C. 2010. Short term response of small mammals and forest birds to silvicultural practices differing in tree retention in irregular boreal forests. Écoscience 17: 334–342.

Machlis, L., Dodd, P.W.D. & Fentress, J.C. 1985. The pooling fallacy – problems arising when individuals contribute more than one observation to the data set. Journal of Comparative Ethology 68: 201–214.

Mannan, R.W., Meslow, E.C. & Wight, H.M. 1980. Use of snags by birds in Douglas-fir forest, Western Oregon. Journal of Wildlife Management 44: 787–797.

MNRF. 2003. Programme de connaissance des écosystèmes forestiers du Québec Méridional. Ministère des ressources naturelles et de la Faune du Québec.

Nappi, A., Drapeau, P., Giroux, J.-F. & Savard, J.-P.L. 2003. Snag use by foraging black-backed woodpeckers (Picoides arcticus) in a recently burned eastern boreal forest. Auk 120: 505–511.

Peet, R.K. & Christensen, N.L. 1987. Competition and tree death. BioScience 37: 586–595.

Pham, A.T., De Grandpré, L., Gauthier, S., & Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Canadian Journal of Forest Research 34: 353–364.

Pothier, D. & Mailly, D. 2006. Stand-level prediction of balsam fir mortality in relation to spruce budworm defoliation. Canadian Journal of Forest Research 36: 1631–1640.

Raymond, P., Bédard, S., Roy, V., Larouche, C. & Tremblay, S. 2009. The irregular shelterwood system: review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107: 405–413.

Reynolds, R.T., Scott, J.M. & Nussbaum, R.A. 1980. A variable circular-plot method for estimating bird numbers. Condor 82: 309–313.

Robitaille, A. & Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Sainte-Foy, Quebec.

Rouvinen, S., Kuuluvainen, T. & Siitonen, J. 2002. Tree mortality in a Pinus sylvestris dominated boreal forest landscape in Vienansalo Wilderness, Eastern Fennoscandia. Silva Fennica 36: 127–145.

Ruel, J.-C., Roy, V., Lussier, J.-M., Pothier, D.,Meek, P. & Fortin, D. 2007. Mise au point d'une sylviculture adaptée à la forêt boréale irrégulière. Forestry Chronicle 83: 367–374.

Saab, V.A. & Dudley, J.G. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in Ponderosa Pine/Douglas-Fir Forest of Southwestern. USDA Forest Service Research Paper RMRS-RP-11: 16.

Saint-Germain, M., Drapeau, P. & Hebert, C. 2004. Comparison of coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. Biological Conservation 118: 583–592.

Schieck, J., Nietfield, M. & Stelfox, J.B. 1995. Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests. Canadian Journal of Zoology 73: 1417–1431.

Smith, C.Y., Warkentin, I.G. & Moroni, M.T. 2008. Snag availability for cavity nesters across a chronosequence of post-harvest landscapes in western Newfoundland. Forest Ecology and Management 256: 641–647.

Spies, T.A. & Franklin, J.F. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal 8: 190–201.

Swallow, S.K., Gutierrez, R.J. & Howard, R.A. 1986. Primary cavity-site selection by birds. Journal of Wildlife Management 50: 576–583.

Thomas, J., Maser, C. & Rodiek, J. 1979. Snags. In: Thomas, J. (ed.). Wildlife habitats in managed forests. The Blue Mountains of Oregon and Washington. USDA Agricultural Handbook. Washington, DC. p. 60–77.

Tyrrell, L.E. & Crow, T.R. 1994. Dynamics of dead wood in old-growt Hemlock Hardwood Forests of Northern Wisconsin and Northern Michigan. Canadian Journal of Forest Research 24: 1672–1683.

Vaillancourt, M.-A., Drapeau, P., Gauthier, S. & Robert, M. 2008. Availability of standing trees for large cavity-nesting birds in the eastern boreal forest of Québec, Canada. Forest Ecology and Management 255: 2272–2285.

Van Horne, B. 2002. Approaches to habitat modeling: the tensions between pattern and process and between specificity and generality. In: Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.B. & Samson, F. (eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, DC. p. 63–72.

Wein, R.W. & MacLean, D.A. 1983. The role of fire in northern circumpolar ecosystems. John Wiley and Sons Ltd, New York.

Whitney, R.D. 1995. Root-rotting fungi in white spruce, black spruce, and balsam fir in northern Ontario. Canadian Journal of Forest Research 25: 1209–1230.

Total of 55 references