

Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics

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ABSTRACT

Extensive even-aged management of the boreal forest and its consequences on the loss of late-seral stages (>100 years) is raising concerns about the future of organisms associated with standing deadwood. The considerable reduction of deadwood not only at the stand but at the landscape level is considered to be one of the principal causes of biodiversity loss in managed forest ecosystems worldwide. Ecosystem-oriented management approaches propose a fundamental change in forestry practices whereby live and dead tree retention becomes an important consideration in forest harvesting. We use woodpecker assemblages and their association with standing deadwood for both nesting and foraging to emphasize the importance of the entire range of snag degradation stages for maintenance of key ecological processes in habitat remnants of managed landscapes. We argue that bridging foraging and nesting knowledge of woodpecker's snag requirements can refine conservation objectives for deadwood retention in the boreal forest.

Key words: deadwood, woodpeckers, hole-nesting community, late-seral forests, keystone species, foraging and nesting tree requirements, food webs, nest webs, snag management

RÉSUMÉ

L'aménagement équié de la forêt boréale transforme le couvert forestier notamment en réduisant la proportion de forêts âgées (>100 ans). Cette diminution des forêts âgées s'accompagne d'une baisse considérable du bois mort à l'échelle des peuplements et des paysages, ce qui est considérée comme l'une des principales causes de perte de diversité biologique dans les forêts aménagées à l'échelle mondiale. Les approches écosystémiques proposent un changement fondamental en foresterie, soit que la rétention des arbres vivants et morts dans les forêts aménagées devient une considération importante en aménagement forestier. Dans cet article, nous utilisons les assemblages de pics et leurs relations avec le bois mort sur pied pour statuer sur l'importance de conserver le spectre complet de stades de dégradation du bois mort dans les habitats résiduels des territoires aménagés pour maintenir les fonctions écologiques des pics, un groupe d'espèces clés dans les forêts âgées. Nous considérons l'importance de faire les liens entre les besoins d'alimentation et de reproduction des pics pour raffiner les objectifs de conservation du bois mort en forêt boréale.

Mots clés : bois mort, pics, communauté cavicole, forêts âgées, espèces clés, arbres d'alimentation et de nidification, réseaux trophiques, réseaux de cavités, aménagement des bois morts



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Introduction

The importance of deadwood for key ecological processes in forest ecosystems is recognized worldwide (Harmon *et al.* 1986, Grove 2002, Marchetti 2004). From the perspective of sustainable forest management, the retention of deadwood has become an emergent issue for allowing timber harvesting while maintaining biodiversity (Franklin *et al.* 2000, 2002). Ecosystem-oriented conservation planning or coarse-filter strategies (Noss 1987, Hunter *et al.* 1988, Franklin 1993, Galindo-Leal and Bunnell 1995, Bergeron *et al.* 1999, Hunter 1999) that provide adequate representation (distribution and abundance) of forest cover types at landscape and regional scales have been identified as crucial (Bergeron *et al.* 2002, 2007). Whereas these approaches are a first step for biodiversity maintenance through conservation of forest cover types of concern (forests older than stand rotation age in even-aged managed landscapes), their efficiency to maintain key structural elements such as deadwood and the associated processes needs to be further assessed and refined (Hunter 2005). Knowledge on habitat requirements of organisms associated with deadwood is likely to be a straightforward means to improve conservation planning of deadwood associates in managed landscapes (Block *et al.* 1995, Mikusiński *et al.* 2001, Jonsson *et al.* 2005).

Among the wide range of organisms that are associated with deadwood, hole-nesting birds, particularly woodpeckers (i.e., cavity excavators) may be considered keystone species (*sensu* Naiman *et al.* 1986) given their disproportionate influence in providing resources (cavities) to many species in forest ecosystems. The emerging concept of nest webs (Martin and Eadie 1999, Martin *et al.* 2004) has provided a strong theoretical framework to describe not only the complex interactions between cavity nesting species but also between excavators and the quality of standing deadwood (hereafter snags) for excavation. However, another critical component associated with snags for woodpeckers is the food web structure (decaying trees – saproxylic insects – foraging woodpeckers) that is related to their foraging requirements. Snags are critical habitats for saproxylic insects (Grove 2002; Jonsell *et al.* 1998; Hanks 1999; Jonsson *et al.* 2005; Saint-Germain *et al.* 2006, 2007), which are important prey for many woodpecker species (Murphy and Lehnhausen 1998, Nappi *et al.* 2003, Nappi 2009). Hence, woodpeckers represent a keystone group of species for which knowledge on both nesting and foraging requirements may help in setting deadwood conservation targets that could maintain keystone ecological processes in managed forest landscapes (Mikusiński *et al.* 2001, Schmiegelow and Mönkönnen 2002).

Retention of snags in patches, clumps of trees and single trees in new clearcuts within even-aged managed areas has often been based on guidelines derived from single-species studies with a focus on the size and density of snags to be left per unit area (BC Forest Service 1998, Watt and Caceres 1999). In the last decade, a growing body of literature has provided insights (Martin and Eadie 1999; Aitken *et al.* 2002, 2007; Bai *et al.* 2003, 2005; Martin *et al.* 2004; Wesolowski 2007) on multiple-species interactions of snag users and snags that shift the focus of snag management from a single-species to a multi-species perspective. Such a change has far-reaching implications for the maintenance of the complex ecological processes that are driven by snag dynamics.

We draw on ongoing empirical work conducted on occu-

pancy patterns of deadwood, saproxylic insects and woodpeckers in older forests at the transition zone between mixedwood and conifer-dominated forests in Québec's boreal forest to assess the importance of maintaining the entire range of snag degradation stages in habitat remnants of managed landscapes. We summarize current knowledge about the shift in age structure of forest landscapes from natural fire regimes to current forest management in this part of the boreal ecosystem. We then show how this landscape-scale change affects deadwood availability. Third, we assess snag requirements of woodpeckers for both foraging and nesting. Finally, we discuss how bridging foraging and nesting knowledge of snag requirements of woodpeckers can refine conservation objectives for deadwood retention in managed boreal ecosystems.

Shifts in the Forest Cover from Natural to Human-disturbed Landscapes

The eastern boreal forest of Canada is a dynamic ecosystem that responds to many natural disturbance agents including fire (Payette 1992), insect outbreaks (MacLean *et al.* 2005) and windthrow (Ruel 1995, Ruel *et al.* 2001). However, fire is the natural disturbance that has the most widespread influence in structuring the amount and distribution of forest cover types at regional scales (Bergeron *et al.* 2004). Forest fire frequency has a significant influence on the age structure of regional landscapes and the structural and compositional attributes of stands (Bergeron *et al.* 2002, Harper *et al.* 2002, Drapeau *et al.* 2003). Studies of natural fire history reconstruction at the transition zone between mixedwood and conifer-dominated forests in northwestern Québec showed that the natural forest mosaic contains a large proportion of stands that have not burned for over 100 years (Bergeron *et al.* 2001, 2004). Thus, naturally disturbed landscapes in this portion of the boreal forest are mainly composed of late-seral forests that have represented a major part of the forest matrix at least during the last 300 years (Bergeron *et al.* 2002; Harper *et al.* 2002, 2003). In addition, paleoecological studies (Carcaillet *et al.* 2001, Cyr *et al.* 2005) also reported that large tracts of black spruce (*Picea mariana*) forests in northwestern Québec have not burned for thousands of years, suggesting that past landscape mosaics were also dominated by late-seral forests. While variation may exist in fire frequency from region to region, fire history reconstruction records from northeastern Ontario to eastern Québec's north shore showed that most of the natural mosaic is composed of more than 50% of forests older than 100 years (Bergeron *et al.* 2006).

In contrast, the last 50 years of industrial forestry have considerably transformed the eastern Canadian boreal forest using an even-aged management approach to harvest forests that, for the most part, are older than rotation age (>100 years). The cumulative effect of even-aged management has been an increase in the proportion of early-seral habitats and concurrent decreases in late-seral habitats (Spies *et al.* 1994, Gauthier *et al.* 1996, Bergeron *et al.* 2002, MacLean *et al.* 2005). Since a landscape under even-aged management should theoretically have no stands over rotation age, the anticipated long-term effect in the current management system is a net loss of the amount of late-seral forests (>100 years) across the eastern boreal forest. Hence, late-seral forests in managed boreal landscapes are likely to be out of the range of their natural variability (Cyr *et al.* 2009, Drapeau *et al.* 2009).

Changes in Deadwood Availability

A direct consequence of this shift in the amount of late-seral forests in managed landscapes along with the increased salvage logging in recent burns (the other source of deadwood in the boreal forest), is the anticipated net reduction in the overall amount of deadwood (Hannon and Drapeau 2005). Indeed, the considerable expanse of early and mid-seral stages (Drapeau *et al.* 2009) in the landbase is likely to harbour less deadwood given the low snag densities or basal areas measured in these seral stages (Drapeau *et al.* 2002, Harper *et al.* 2003). This raises concerns about future snag conditions in second-growth forests (Sturtevant *et al.* 1997; Despons *et al.* 2002, 2004; Drapeau *et al.* 2002, 2003) as well as species responses of snag associates (Imbeau *et al.* 1999, 2001; Drapeau *et al.* 2000; Thompson *et al.* 2003; Everett and Otter 2004; Gagné *et al.* 2007). However, extensive forest management in the eastern boreal forest of North America has by no way impacted deadwood to the extent that has occurred in Northern Europe where one quarter of the species listed as endangered are deadwood associates (Jonsson *et al.* 1998, Virkkala and Toivonen 1999, Jonsson *et al.* 2005, Tikkanen *et al.* 2006). For instance, in the Abitibi region, snag densities of large trees (>20 cm) in remnant blocks and riparian or upland strips of managed landscapes, the main late-seral refuges, were similar or higher (Gagné 2006, Mascarúa-López *et al.* 2006) to those reported in unharvested late-seral stages of the boreal forest of northwestern Québec by Harper *et al.* (2003). In eastern Québec, Vaillancourt *et al.* (2008) also did not find significant differences in living and dead tree densities (>20 cm DBH) between unharvested stands and forest strips. Likewise, Vaillancourt *et al.* (2008) did not observe a truncation in the range of snag degradation stages available in remnant habitats of managed landscapes (Fig. 1). However, they found that remnant forests had a significantly lower abundance of the largest (>30 cm DBH) dead trees (Fig. 2), which are important wildlife trees for large cavity users in this region (Robert *et al.* 2000, 2008; Maisonneuve *et al.* 2002).

In summary, because the availability of snags larger than 20 cm DBH and the range of degradation stages for trees of this size have not been greatly reduced in remnant stands, cavity nesters, particularly those using smaller cavities, may not be limited by tree availability in these stands in Québec currently. Many species of woodpeckers (Imbeau and Desrochers 2002, Gagné 2006, Gagné *et al.* 2007) have been detected in these remnants even though they often represent the last older forest stands in highly harvested landscapes. However, the low densities of very large snags (>30 cm DBH) in remnants of eastern Québec (Vaillancourt *et al.* 2008) raises concerns about the long-term capacity of these remnants to provide appropriate structures for large cavity nesters in managed landscapes.

Woodpeckers Foraging and Nesting Requirements

Changes in the eastern boreal forest structure and composition associated with forest succession directly affect the composition of bird communities (Imbeau *et al.* 1999; Drapeau *et al.* 2000, 2003; Simon *et al.* 2000). Species like woodpeckers that use deadwood for nesting and foraging are among those that benefit the most from the increased structural complexity of late-seral forests (Imbeau *et al.* 2001, Drapeau *et al.* 2002). In the last decade, an important body of literature published on woodpeckers' nesting requirements has come from

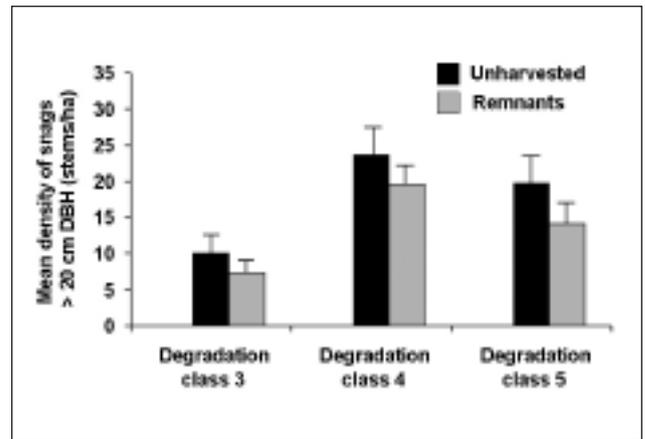


Fig. 1. Density of dead trees >20 cm DBH (mean ± SD) by degradation class in unharvested and remnant linear habitats in managed forest of eastern Québec. Tree degradation classes are: 3 = recently dead, 4 = moderate degradation, 5 = high degradation. Differences between unharvested and remnant linear habitats for all degradation classes were not significant. (Adapted from Vaillancourt *et al.* 2008).

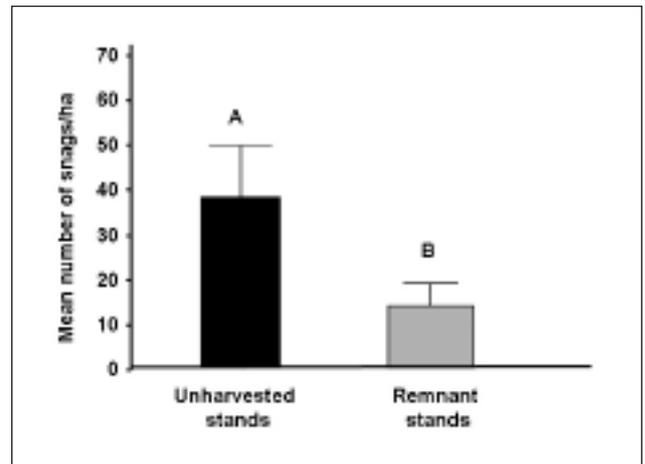


Fig. 2. Density of dead trees >30 cm DBH (mean ± SD) in unharvested and remnant linear habitats in managed forest of eastern Québec. Significant differences ($p < 0.05$) are indicated by different letters. (Adapted from Vaillancourt *et al.* 2008).

studies conducted on community organization of cavity users (nest webs, *sensu* Martin and Eadie 1999). For instance, Martin *et al.* (2004) showed that large trembling aspens (*Populus tremuloides*) made up 95% of excavated trees while this tree species represents 15% of the overall availability of large trees in the mixed forests of Interior British Columbia. Trembling aspen is thus considered a critical tree for woodpeckers in this forest ecosystem. Martin *et al.* (2004) also found that cavity users occupied the full range of snag decay whereas woodpeckers nested mostly in live trees with decay (Red-naped Sapsucker [*Sphyrapicus nuchalis*], Hairy Woodpecker [*Picoides villosus*], American Three-toed Woodpecker [*Picoides dorsalis*] and Pileated Woodpecker [*Dryocopus pileatus*] or recently dead trees (Northern Flicker [*Colaptes auratus*], Downy Woodpecker [*Picoides pubescens*]).

These nest web studies have provided baseline information on the complex linkages between woodpeckers, other cavity users and nest trees characteristics. However, we lack simultaneous information on how woodpeckers within these nest webs use deadwood for foraging. Recent knowledge on the foraging ecology of woodpeckers indicates that affinities with deadwood may vary depending on the availability of saproxylic insects (Murphy and Lenhausen 1998, Nappi *et al.* 2003), which are host-specific with regards to snag decay stage (Hanks 1999, Jonsson *et al.* 2005). In a recent study that used a novel approach of snag dissection to investigate occurrence patterns of saproxylic adults and larvae, Saint-Germain *et al.* (2007) found that host use by adults and larvae of Cerambycids showed divergent patterns on black spruce and trembling aspen in Québec's boreal forest. Insects were mostly concentrated in the early stages of decay in black spruce whereas patterns observed in aspen were opposite, with few insects in fresh snags and most of them found in middle to late stages of decay (Fig. 3). This result emphasizes the wide range of decay stages used by insects and, hence, that woodpeckers that occupy pure conifer, pure deciduous or mixed stands may use quite different foraging substrates. Cerambycids distribution patterns on deadwood are likely to affect foraging substrate preferences of woodpeckers that dig holes to access deep wood-dwelling arthropods, such as Hairy or Black-backed Woodpeckers (Nappi *et al.* 2003, Nappi 2009).

In 2003, we began a project on woodpecker foraging and nesting ecology along a natural chronosequence that extends from 60 to 240 years since fire (Bergeron 1991) in boreal mixedwood forests and in overmature conifer-dominated

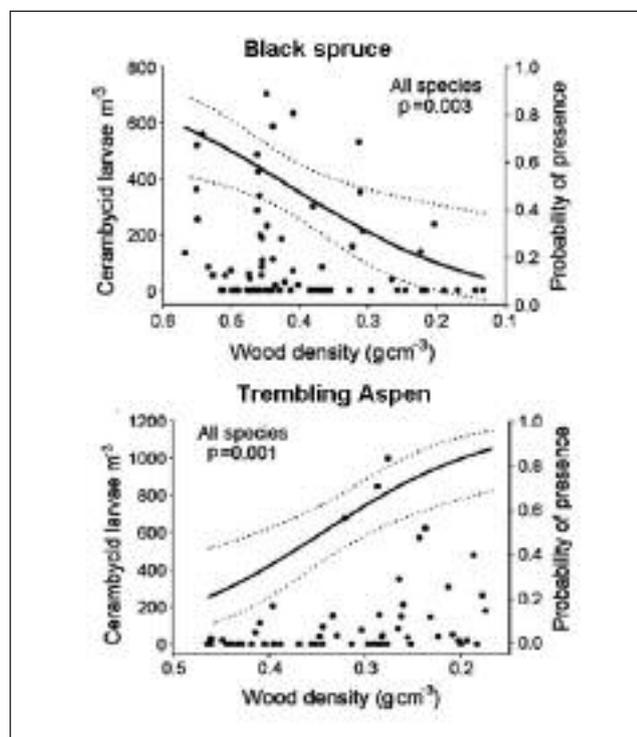


Fig. 3. Probability of presence of Cerambycid larvae along the decay gradient (wood density) for black spruce and trembling aspen in boreal forests. Logistic regressions are conducted with overall abundance and occurrence (presence-absence) of cerambycid larvae as response variables. (Adapted from Saint-Germain *et al.* 2007).

forests in northwestern Québec. Preliminary results of woodpecker substrate use with regards to tree degradation stages show differences among species for nesting and foraging requirements but also indicate, that within species, woodpeckers may or may not use trees in the same degradation stage for nesting and foraging (Fig. 4). The Yellow-bellied Sapsucker (*Sphyrapicus varius*) uses live trees for both foraging and nesting whereas the Pileated Woodpecker uses live trees for nesting but highly degraded snags for foraging. Con-

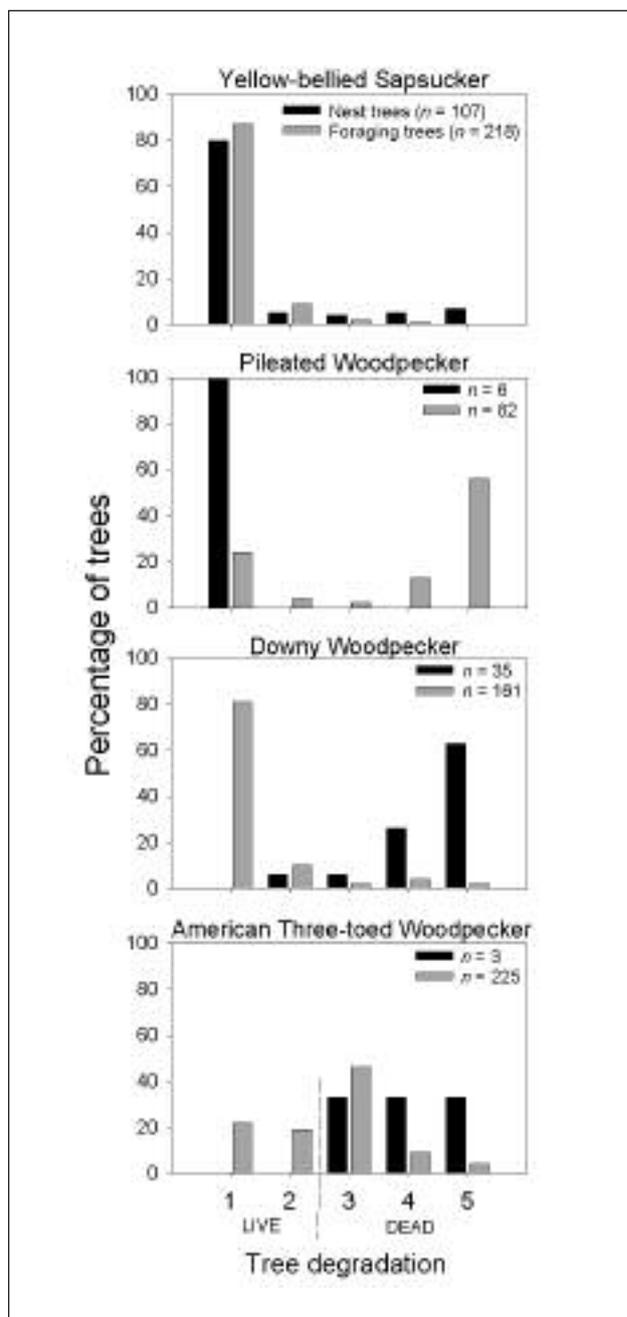


Fig. 4. Use of nest and foraging trees based on tree degradation for 4 woodpecker species in eastern boreal forests. Tree degradation classes are: 1 = healthy, 2 = declining, 3 = recently dead, 4 = moderate degradation, 5 = high degradation. "n" indicates the number of trees used for nesting or foraging for each woodpecker species.

versely, the Downy Woodpecker excavates highly degraded snags for nesting but forages mainly on live trees. Finally, the American Three-toed Woodpecker occupies an intermediate position where both foraging and nesting requirements converge towards snags in early stages of degradation. Overall, these results underscore the importance of considering the range of degradation stages of standing deadwood for maintaining keystone processes (food webs and nest webs) involving woodpecker assemblages in boreal forests.

In parallel with our woodpecker nesting and foraging ecology project in boreal mixedwood forests, we initiated in 2008 a study on woodpecker nesting ecology in habitat remnants (upland and riparian corridors) of nearby even-aged managed landscapes. Preliminary results indicate a higher number of Northern Flicker nests and a lower number of Yellow-bellied Sapsucker nests, although the total number of woodpecker nests in remnant forest strips of managed landscapes is similar to that in the natural forest (Fig. 5). Further studies on demographic parameters such as productivity or reproductive success of woodpeckers and other cavity nesters will allow assessing the potential source or sink status (*sensu* Pulliam 1988) of hole-nesting populations in these remnant habitats. That woodpeckers are nesting in these linear habitats suggests that the quality of trees (DBH, decay stage, tree species) may be adequate for many cavity-nesting species. In addition, Webb *et al.* (2008) findings on snag use by saproxylic insects in these linear remnants indicate the local persistence of prey species for woodpeckers in such habitats, at least for the timeframe investigated.

Finally, in both managed and natural mixed-wood forests, trembling aspen was the main excavated tree with 98% of cavities ($n = 278$) located in trembling aspen. However, the range of tree decay stages for which cavities were excavated by woodpeckers (Fig. 4) was wider than observed by Martin *et al.* (2004).

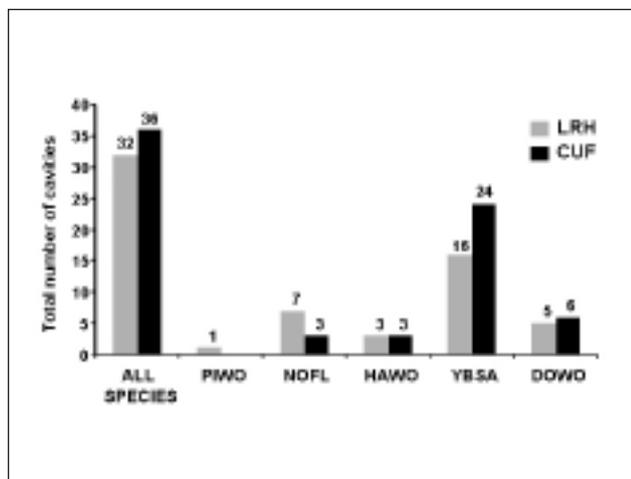


Fig. 5. Active cavities detected in plots located in linear remnant habitats (LRH) in managed landscapes and in continuous unharvested forest (CUF) in the boreal mixed forest of northwestern Québec between May and mid-July 2008. Bird acronyms are PIWO = Pileated Woodpeckers, NOFL = Northern Flicker, HAWO = Hairy Woodpecker, YBSA = Yellow-bellied Sapsucker, and DOWO = Downy Woodpecker. Numbers above bars refer to number of nests found.

Setting Conservation Objectives for Deadwood Retention

Incorporating the conservation of biodiversity in managed forest landscapes is a challenge that not only addresses maintenance of all native species in these modified environments but also the ecological processes underlying their maintenance. Scientific knowledge gained in the last decades on even-aged forest management effects on wildlife in boreal environments has efficiently targeted species, habitats and habitat attributes of concern (McLaren *et al.* 1998, Imbeau *et al.* 2001, Mikusiński *et al.* 2001, Schmiegelow and Mönkönen 2002, Drapeau *et al.* 2003, Thompson 2006). Conservation efforts should, however, be oriented strategically towards habitat features, habitats or species that are most likely to feature prominently in late-seral forest habitats. Woodpeckers and their relationships with deadwood are key indicators of the status of older forests in managed landscapes.

Maintaining the keystone processes that involve woodpeckers in boreal landscapes will require considerations of both foraging and nesting requirements. We underscore the importance of knowledge on foraging conditions because the number of trees required for foraging is considerably larger than the number of nest trees. Deadwood has been considered a limiting habitat resource for many woodpecker species (Raphael and White 1984), mostly on the basis of nesting requirements (Martin and Eadie 1999, Martin *et al.* 2004). The availability and amount of deadwood that harbours woodpeckers' insect prey is not considered in current snag management guidelines. The number of snags of a given diameter to be maintained in harvested landscapes is likely to only partially represent the snag requirements of woodpeckers and hence may fail to include key ecological processes mediated by woodpeckers for both nest webs and food webs in the boreal forest.

Consequently, we re-emphasize the comment of Bednardz *et al.* (2004) and Martin *et al.* (2004) that using the complex community of cavity users has far-reaching implications for the conservation of late-seral forest characteristics in even-aged managed landscapes. We add that better understanding of the foraging ecology of woodpeckers and their association to deadwood is a critical dimension that needs to be incorporated in the conservation of deadwood attributes in our managed landscapes. This calls for a conservation strategy of standing deadwood that shifts from guidelines on snag numbers to a broader consideration of snags dynamics that should involve 1) quantitative assessments of recruitment, persistence and degradation pathways of nesting and foraging snags 2) better knowledge of relationships between trees degradation stage, insect abundance patterns and woodpeckers foraging behaviour and 3) quantification of cavity occupancy by excavators and secondary users and 4) quantification of fall rates of cavity trees. Retention of forest patches that incorporate standing deadwood attributes based on the complex interactions of woodpeckers' assemblages should upgrade the quality of remnant habitats and be able to maintain keystone processes that involve woodpeckers in late-seral forests. Finally, as for any other management strategy, the efficiency of conservation objectives for standing deadwood in managed forest landscapes should be assessed directly through monitoring of woodpecker demographic parameters (Block *et al.* 1995, Mikusiński *et al.* 2001, Drapeau *et al.* 2008).

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