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How important is dead wood for woodpeckers foraging in eastern North American boreal forests?

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ABSTRACT

Dead and decaying trees may be a limited resource for woodpeckers in managed forests, especially for species that rely on dead wood for nesting and foraging. Whereas recent nest web studies greatly increased our understanding of nest tree use by woodpeckers, knowledge on woodpeckers foraging requirements is much less developed. We quantified and compared tree selection patterns and foraging behavior of six bark-foraging woodpeckers – downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), yellow-bellied sapsucker (*Sphyropicus varius*) and pileated woodpecker (*Dryocopus pileatus*) – that co-occur in eastern boreal forests of North America. A total of 271 observation bouts and more than 600 foraging trees were recorded at three study sites characterized as mixedwood, conifer, and burn. Our results show that dead wood represents an important foraging substrate for most bark-foraging woodpeckers in Canadian eastern boreal forests. However, significant differences in individual species were found with regard to substrate use patterns, foraging behavior and associated prey. Woodpeckers were categorized according to their selection for specific stages of tree degradation, with the yellow-bellied sapsucker and the pileated woodpecker representing opposite ends of this gradient. The black-backed woodpecker showed the highest use of dead wood and was very specific in its tree selection by using mostly recently dead trees. We emphasize that providing foraging substrates for most woodpecker species not only requires maintaining dead wood but also paying heed to the underlying dynamics of dead wood (e.g. recruitment and degradation) in managed boreal forest landscapes.

1. Introduction

Dead wood is a key component of biodiversity in forest ecosystems worldwide. Decaying and dead trees provide habitat resources for thousands of species such as wood-inhabiting fungi, saproxylic invertebrates and cavity-nesting vertebrates (Raphael and White, 1984; Grove, 2002; Cockle et al., 2011; Stokland et al., 2012). Saproxylic species – defined as “species that depend, during some part of their life cycle, upon wounded or decaying woody material from living, weakened or dead trees” (Stokland et al., 2012) – show strong affinities to specific tree hosts, decay stages, tree sizes and microhabitat conditions and are sensitive to the abundance of their preferred dead wood substrates in both managed and unmanaged forests (Siitonen, 2001; Stokland et al., 2012).

In the boreal forest, forestry practices still include the extensive use of low tree retention clearcuts and short harvest rotations, which result in a significant decrease in the abundance and diversity of dead wood as well as its associated biodiversity (Siitonen, 2001; Grove, 2002; Jonsson and Siitonen, 2012). In European boreal forests, intensive forest management has led to the decline or to the local extirpation of several saproxylic species (Angelstam and Mikusiński, 1994; Berg et al., 1994; Siitonen, 2012). In North American boreal forests, maintaining dead wood in managed forests is often identified as a critical issue given the extent of even-aged management and the increase of salvage logging after natural disturbances (Hannon and Drapeau, 2005). In different regions of the North American boreal forest, ecosystem-based management strategies are now aimed at providing an adequate representation of cover types and stand age structure at landscape scales (Bergeron et al., 2002; Gauthier et al., 2009), with harvesting practices such as variable retention harvest or partial cutting that maintain variable amounts of dead trees as well as significant green-tree retention in harvested blocks (Sullivan et al., 2001; Serrouya and D’Eon, 2004; Fenton et al., 2009). Although these

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new approaches likely contribute to the conservation of biodiversity, their efficiency to maintain saproxylic species still needs to be assessed (but see Cooke and Hannon, 2012). Specifically, decisions regarding management targets and prescriptions (e.g. amount of old-growth forests at landscape scales, levels and types of retention of live and dead trees in harvested blocks) will likely influence the persistence of saproxylic species populations in managed landscapes. Knowledge on these species habitat requirements as well as their dependence to dead wood may help identify the species most sensitive to the effects of forest management (focal species *sensu* Lambeck, 1997) and may be used to improve conservation planning of saproxylic species assemblage in managed landscapes.

Woodpeckers play an important ecological role in forest ecosystems by providing cavities to a broad range of vertebrate and invertebrate species (''nest-web''; Martin and Eadie, 1999; Wesolowski, 2011). These keystone species may be particularly important in conifer-dominated boreal forests where natural cavities are much less abundant (e.g. Aitken and Martin, 2007; Cockle et al., 2011). Dead wood is often identified as a critical habitat attribute for woodpeckers nesting, given that many species are known to prefer snags or living trees with decaying heartwood for their nest cavities (e.g. Raphael and White, 1984; Blanc and Martin, 2012). Yet, dead wood may also be a critical component of woodpeckers' food web. Indeed, snags are critical habitats for saproxylic insects (Saint-Germain et al. 2004, 2007), which are important prey of many woodpecker species (Murphy and Lehnhausen, 1998; Imbeau and Desrochers, 2002; Nappi et al., 2003). Given the number of trees required for foraging, woodpecker populations could be much more limited by the availability of suitable foraging substrates than by potential nest trees, and may thus in turn be more sensitive to the reduction of decaying and dead trees in managed landscapes (Imbeau et al., 2001). A decrease in the abundance of woodpeckers may thus have a cascading effect on the abundance of cavity-nesting species and on the nest-web community structure. Knowledge on woodpecker foraging requirements, in addition to nesting habitat features, may thus be crucial for setting dead wood conservation targets that could maintain the complex ecological network associated with dead wood (i.e. saproxylic food and nest webs).

Use and partitioning of foraging resources among sympatric woodpecker species has received much attention in North America and Europe (e.g. Hogstad, 1971; Bull et al., 1986; Török, 1990). Although use of decaying and dead trees has often been reported, few studies have documented the selection *per se* (disproportionate use of resources as compared to their availability; Johnson, 1980) of dead wood by foraging woodpeckers and their differential tree selection patterns. In the North American boreal forest, the few studies on foraging ecology of woodpeckers have mostly focused on single species in one habitat type and were restricted to coniferous landscapes (e.g. Imbeau and Desrochers, 2002; Tremblay et al., 2010; Nappi and Drapeau, 2011). Foraging requirements and the relative importance of dead wood as a foraging substrate have yet to be quantified for most boreal woodpeckers.

We studied the foraging ecology of the six bark-foraging woodpecker species that co-occur in the eastern North American boreal forest: downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), yellow-bellied sapsucker (*Sphyropicus varius*) and pileated woodpecker (*Dryocopus pileatus*). Foraging ecology was examined by analyzing foraging tree selection, foraging behavior and woodpeckers' prey. Our study was conducted in different forest cover types – mixedwood, conifer and burned conifer stands – representative of the natural forest landscape in eastern Canada. More specifically, our study addresses the following questions: (1) what is the relative importance of dead wood as a foraging substrate for woodpeckers in the boreal forest? and (2) how do these species differ in foraging tree selection and foraging behavior?

2. Methods

2.1. Study sites

The study area is part of the northern Clay Belt of Quebec and Ontario, a large physiographic region dominated by clay deposits. Forest composition shows a latitudinal transition from mixedwood forests in the south (*Abies balsamea–Betula papyrifera* bioclimatic domain) to conifer-dominated forests in the north (*Picea mariana*-moss bioclimatic domain; Saucier et al., 1998). Fire and insect outbreaks are the main natural disturbances in these forest landscapes. We selected one study site in the southern mixedwood and two sites in the northern coniferous forest. Whereas these three sites are part of the same physiographic region, they are spatially dispersed one from another because we were interested in studying woodpeckers' foraging in unmanaged forests that represented the range of natural forest conditions (composition and structure) in this region.

The mixedwood site (''MXW'') is located at the Lake Duparquet Research and Teaching Forest (LDRTF; 48°30′ N, 79°22′ W; Fig. 1). The LDRTF is a 8045-ha forest landscape composed of mainland, islands and peninsulas. The mainland fire regime is characterized by stand-replacement fires: thirteen fires within LDRTF over the last three centuries have created a complex natural forest mosaic (Harvey, 1999). Stand composition varies according to time since fire, from early seral stands dominated by deciduous (trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*)), to mixed stands (with white spruce (*Picea glauca*)), to coniferous stands (balsam fir (*Abies balsamea*), eastern white cedar (*Thuya occidentalis*)) (Bergeron, 2000). Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) occur in localized areas as well. Three spruce budworm (*Choristoneura fumiferana*) outbreaks occurred in the last century, the most recent between 1970 and 1987, an event that was especially severe in balsam fir-dominated stands (Bergeron et al., 1995). Our study took place in the eastern part of the LDRTF mainland, a conservation area that has been lightly affected by anthropogenic disturbances.

The conifer-dominated study site (''CON'') is located at the Muskuuchii Hills Projected Biodiversity Reserve (50°12′ N, 78°43′ W; Fig. 1). The biodiversity reserve covers 80,100 ha, of which half consists of peat bogs on organic deposits that support black spruce stands of varying densities. The other half is composed of terraces and hills characterized by well-drained till, sand and fine sediment deposits (Gouvernement du Québec, 2008). Our study took place in a portion of the landscape dominated by mature stands (>120 years) on mesic sites. From 1998 to 2000, experimental partial cuts were conducted in a case-control manner that resulted in a mosaic of intact and partial cut stands. Black spruce and jack pine dominate forest composition. Other species include balsam fir, trembling aspen and paper birch.

The third study site is a 8-year-old coniferous burn landscape (''BURN''), located 200 km east of the ''CON'' site (50°30′ N, 75°43′ W; Fig. 1). Vegetation is dominated by black spruce and jack pine with scattered white birch and trembling aspen. Burn severity was highly variable, with close to 50% of the area consisting of unburned and low-severity burned stands (details in Nappi et al., 2010).

Woodpecker foraging observations were collected in predefined large sampling blocks at the MXW and CON sites (Fig. 1). At the MXW site, sampling blocks were distributed in four 60-year classes (60–120, 120–180, 180–240 and >240 years), based on fire history mapping (Dansereau and Bergeron, 1993). We selected three sampling blocks in forests of each age class (total of 12 blocks). Each