Nest webs and woodpecker ecological services: the role of woodpeckers in tree cavity-using wildlife communities in North America

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Abstract: Woodpeckers are exceptional in their ability to excavate cavities in trees for their nesting and roosting activities. Since they tend to use these cavities only once for breeding but cavities often persist for one to several decades, woodpeckers play an important ecological role by providing nesting and roosting habitat for a broad range of fauna, including birds, mammals, reptiles, amphibians and insects. Thus, woodpeckers have the ability to provide critical resources to other wildlife species and to influence structure and function in forest and savannah wildlife communities. The mixed forests of interior British Columbia support a rich community of cavity-nesters, accounting for about one third of forest vertebrate species. Nest-cavity and nest-tree characteristics were measured over 11 years for 20 cavity-nesting bird and six cavity-nesting mammal species, representing excavators and secondary cavity-nesters, in Interior Douglas-fir (*Pseudotsuga menziesii*) forest ecosystems. We constructed a Nest Web to describe community structure that showed most cavity resource use flowed up the community through aspen trees and cavities excavated by Northern Flickers. There was overwhelming selection for trembling aspen (*Populus tremuloides*); 95% of all cavity nests were in aspen trees, which comprised only 15% of trees available. The full range of live and dead trees were used, but cavity-nesters showed a strong preference for live trees with decay (~48% of nests) or dead trees (~45% of nests). Woodpecker species varied in their selection of decay conditions of trees in which they excavated cavities with Downy Woodpeckers selecting trees with the most advanced decay. Overall, aspen was the critical nesting tree, with trees that were alive but with signs of decay preferred, and Northern Flickers were the keystone excavators in endemic conditions. Tree species and decay condition influence cavity persistence and thus cavity availability for the community of cavity-using vertebrates. An outbreak of bark beetles (food pulse) resulted in variation in the importance of specific woodpecker species as cavity providers.

Key words: Nest webs; Cavity-nesting birds; Keystone excavators, Community structure, Tree decay, Tree cavity persistence.

Introduction

Cavity-nesting vertebrates comprise a major component of many forest communities. About 10% of all birds and many other vertebrates use cavities in trees for nesting or roosting, and these species use either cavities that are excavated or holes formed by natural decay processes (Cockle et al. 2011). Cavity-nesting species in forest ecosystems constitute a structured wildlife community that interacts through the creation of, and competition for, nest-sites. Cavity-nesting species may be classified into three guilds according to their mode of cavity acquisition. Woodpeckers, or primary cavity excavators, create cavities in trees for nesting and roosting. Secondary cavity-nesters, include a variety of passerines, ducks, birds of prey and small mammals, that require but cannot excavate cavities. Thus, they rely on those shelters created by excavators or a limited number of naturally occurring holes. A third guild, weak cavity excavators (e.g., nuthatches chickadees,) may excavate their own cavities in decayed trees, use naturally occurring holes, or reuse cavities created by other species. The interdependence between the three groups with respect to the creation and use of nest cavity resources was termed a Nest Web by Martin and Eadie (1999). They proposed that cavity-nesting vertebrate communities exist within 'nest webs', directly analogous to food webs whereby, some species depend partly (i.e., weak cavity excavators) or entirely (secondary cavity-nesters) on primary cavity excavators to produce a critical resource (cavities) for them to use. Thus, cavity-nesting communities exhibit a hierarchical structure with potentially strong inter-dependencies among community members. By viewing cavity-using vertebrate communities as Nest Webs, one can employ a broader community perspective in studying connectance, linkage and interactions among members of these webs, and use established theory to predict more precisely the structure and function of cavity-using vertebrate communities. These ecological dependencies may vary with habitat features such as forest type or tree condition and with the stage of forest succession (Martin et al. 2004).

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A number of bird species excavate cavities as part of their nesting, roosting, or feeding activities. Cavity-excavating birds can be considered ecosystem engineers because they transform the physical environment in ways that create resources for other species (JONES et al. 1994; ROBLES and MARTIN 2013). Multiple species can excavate tree cavities (e.g., Sittidae, Paridae, Capitonidae (Barbets), and Trogonidae), but the most powerful excavators are in the family Picidae (WINKLER et al. 1995). Woodpeckers are the most widely recognized avian ecosystem engineers given their abilities and behavior of excavating holes into trees and other woody plant tissues. Woodpeckers are morphologically and taxonomically diverse and occur on all continents except Antarctica, with 214 species ranging in size from the 6 to 8 gm piculets to the over 370 g Black Woodpecker (WINKLER et al. 1995). Most woodpeckers use their cavities for only one season and then abandon them, thus woodpecker-excavated cavities in trees can provide shelter year round for many other cavity-dwelling species for one to two decades (BLANC & MARTIN 2012, EDWORTHY et al. 2012).

Managing for potential woodpecker nest trees requires an understanding of factors that influence woodpecker nest tree selection, and thus, the ecological processes involved in creating trees that are suitable for cavity excavation. One such process is fungal decay, which causes the progressive softening of heartwood and sapwood in trees (THOMAS et al. 1979, BULL et al. 1997, JACKSON & JACKSON, 2004). As trees become unhealthy, decay and die, they change in form and function to wildlife. Classification schemes that characterize trees from live healthy trees into a gradation of decay classes, ranging from recently dead trees to fully decayed and downed logs, are used to inform management guidelines for cavity-using wildlife habitat (THOMAS et al. 1979, CLINE et al. 1980). The stage of tree decay can also influence the longevity of the nest tree and cavity (EDWORTHY et al. 2012), and thus cavity abundance.

As the principle primary excavators of tree cavities, woodpeckers play a crucially important ecological role in wildlife communities by providing critical ecological services such as required nesting and roosting habitat for a broad range of fauna, including birds, mammals, reptiles, amphibians and insects (DENNIS 1971, MARTIN et al. 2004, MIKUSI SKI 2006; FLOYD & MARTIN 2015). In fact, there is a strong general relationship between woodpecker species richness and richness of forest birds at both the stand and landscape levels (MIKUSI SKI et al. 2001, DREVER et al. 2008) and woodpeckers may be reliable indicators of overall forest health (LINDENMAYER et al. 2000, VIRKKALA 2006, DREVER et al. 2008). Thus, managing to improve woodpecker habitat in general may benefit forest biodiversity (DREVER & MARTIN 2010), and managing for potential woodpecker nest trees in particular may contribute to forest biodiversity by facilitating the process of cavity excavation and ensuring a reliable supply of good nesting and roosting cavities.

Methods

Study area

The data reported in this chapter were collected between 1995-2011. We located cavities and monitored nests of cavity-nesting birds and mammals on 28 study sites in the Cariboo-Chilcotin region of central interior British Columbia, Canada (51º 52'N, 122º 21'W). The study sites were comprised of mixed coniferous and deciduous forest embedded in a matrix of grassland and shallow ponds within the warm and dry Interior Douglas-fir Biogeoclimatic Zone (MEIDINGER & POJAR 1991). Predominant tree species were trembling aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and white and hybrid spruce (*Picea glauca* x *engelmannii*). Twenty-six sampling sites were mature forest (80-200 years old), nine of which were selectively cut for pine and/or spruce in 1997-2002. Our sampling sites (7 to 32 ha in size) varied in character from continuous forest to two sites that were a series of 'forest islands' (0.2 to 5 ha) within the grassland matrix. Additional details for study area and study design are given in MARTIN & EADIE (1999), AITKEN et al. (2002), MARTIN et al. (2004), BLANC & MARTIN (2012), and EDWORTHY et al. (2012).

Nest location and monitoring

The cavity-nesting community in the area consists of 31 bird and 12 mammal species (MARTIN & EADIE 1999). From 1 May to 31 July, we searched for all occupied cavity nests on our sites. We found cavity nests by following adult birds; listening for begging chicks; watching for birds to enter and leave cavities; and observing cavity contents using ladders, mirrors, pole-mounted video cameras, and by climbing trees. Once located, nest cavities were checked every year thereafter, to determine whether they were still usable; cavities were considered to be no longer usable when the tree fell; the branch supporting the cavity fell from the tree; the cavity walls collapsed; or the bark grew over and closed the cavity opening. Our goal was to determine the extent of use by cavity-nesters across a range of forest stand types, and not to maximize the number of nests for any single species. Thus we conducted systematic nest searches across all sites for an average of 6-7 observer-hours of nest search/sampling site/week.

Nests were considered occupied if they contained at least one egg or nestling. We also monitored cavities occupied by cavity-nesting mammals such as red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), bushy-tailed woodrat (*Neotoma cinerea*), and fisher (*Martes pennanti*). We also reported occasional use by facultative cavity users such as chipmunk (*Eutamias* spp.), deer mouse (*Peromyscus maniculatus*) and short-tailed weasel (*Mustela erminea*). Occupied cavities were assigned unique numbers and nest-trees were marked with numbered aluminium tags to facilitate relocation within and across seasons. For each nest of a secondary cavity-nester, we determined the excavator species that produced the cavity based on previous observations of excavation (including from field work in the same area from previous years), and occasionally from the size and shape of the cavity (MARTIN et al. 2004). The persistence of individual cavities and trees were monitored over a period of up to 17 years.

Nest-tree and cavity characteristics

After nest cavities were vacated, we recorded tree and cavity variables. Tree characteristics data included species, diameter at breast height (DBH) and decay class. We used a tree decay classification system that ranged from 1-7, with 1 indicating a live and healthy tree with no external indicators of decay, 2 indicating a live tree with visible signs of decay, and 3-7 indicating dead trees with advancing stages of decay (THOMAS et al. 1979, See Fig. 3 for decay class icons adapted for aspen). Tree condition was assessed using visible signs of decay such as the presence of fungal conks, bark beetle sign, and broken top.

To examine tree species and characteristics available in the landscape, we measured trees and cavities in 11.2 m radius circular plots around each nest-tree and at point count stations 100m apart along transect lines throughout each sampling site to assess available trees. On continuous forest sites, transects were spaced systematically in a 100 × 100 m grid starting at a grassland or wetland edge and extending 500 m into the forest. On sampling sites with forest islands where it was not possible to establish a grid, we placed vegetation plots at least 100 m apart. Most sites covered an area that included one or several territories of most cavity-nesting species present, and thus the habitat characteristics averaged over all vegetation plots on a sampling site represented availability of nesting resources with a sampling effort of approximately one vegetation plot/ha. Within an 11.2 m radius for both nest plots and systematically-selected point count station plots on sampling sites, we recorded for all trees 12.5 cm DBH (British Columbia Ministry of Forests inventory standard) tree species, size (DBH), decay class, and the number of cavities (used or unused) present (more details given in MARTIN et al. 2004).

Kaplan-Meier survival estimates were used to quantify median cavity survival rates and to produce survival curves for cavity trees. Cox proportional-hazards regression models were used to estimate the effects of aspen cavity characteristics on hazard of loss, which is related to longevity. These methods of survival analysis allow the inclusion of right-censored data (where individuals were not monitored through to the time of loss) and do not require that the data fit a particular survival distribution (FOX 2001). Median life spans for cavities were calculated as the age when survival reached 0.50. Survival analyses were done using the survfit and coxph functions from the "survival" package in the statistical program R, version 2.9.2 (THERNEAU & LUMLEY 2009, R DEVELOPMENT CORE TEAM 2010). For additional details, see EDWORTHY et al. (2012).

Results

The Nest Web

The application of the Nest Web concept was first demonstrated in a community ecology study of cavity-nesting vertebrates in British Columbia, Canada (Fig. 1; updated from Fig. 5, MARTIN et al. 2004). We located and tagged a total of 2503 occupied cavity nests representing 17 species of birds and five species of small mammals from 1995 to 2006. When nest-site use was summarized for the cavity-nesting vertebrate community in interior British Columbia, we found that nidic structure was organized in discrete levels and nesting resource use was strongly structured through cavities excavated by Northern Flickers *Colaptes cafer* and in aspen trees (Fig. 1). Some of the larger secondary cavity-nesters such as Barrow's Goldeneye (*Bucephala islandica*) strongly preferred using cavities excavated by Pileated Woodpeckers (*Dryocopus pileatus*), Bufflehead, American Kestrel and European Starling used flicker-excavated cavities almost exclusively while Northern Saw-whet Owl used cavities excavated by Pileated Woodpeckers or flickers in about the same proportions. Other species such as Tree Swallow and red squirrel used cavities excavated by seven excavator species. Nidic relationships for species with less than 15 nests must be interpreted cautiously (i.e., for one excavator (Black-backed Woodpecker), and six secondary cavity nesters in our study, Fig. 1). However, the depicted woodpecker-secondary cavity nester linkages for Barrow's Goldeneye in our study was supported by a concurrent study that included our study area as most of the 39 natural cavities occupied by Barrow's Goldeneye were exca-

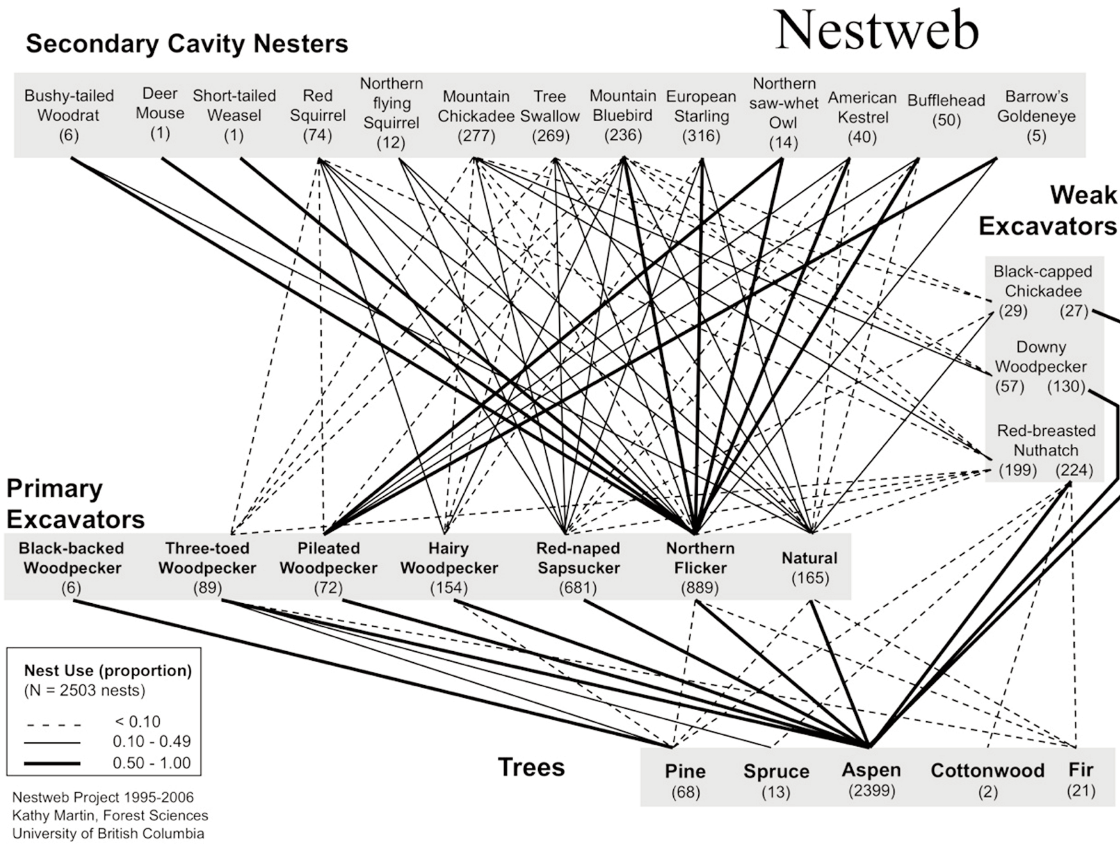

Fig. 1: A nest web diagramming resource flow (cavity or tree) through the cavity-nesting vertebrate community in interior British Columbia. Resource use in the nest web shows links between species using nests (secondary cavity nesters and excavators) and the excavator or tree species that provided the resource. For example, Bufflehead (N = 50 nests) primarily used flicker cavities, but regularly occupied cavities excavated by Pileated Woodpecker, and occasionally used naturally occurring cavities. Numbers under each species indicate the number of occupied nests for which there was information on the excavator or tree species used.

vated by Pileated Woodpeckers (EVANS et al. 2002). Finally, although Red-naped Sapsuckers were almost as abundant as flickers on the sites, they appeared relatively less important in the Nest Web with no secondary cavity-nester specializing strongly in using their cavities, but see ROBLES & MARTIN (2013) for preferential use of sapsucker cavities by Tree Swallows on the forested sites.

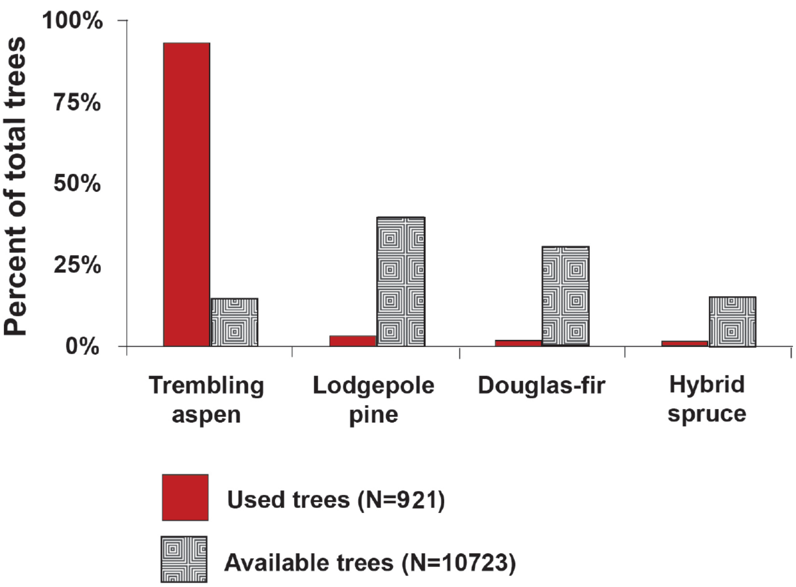

Fig. 2: Selection of tree species used by cavity nesting birds in relation to availability of trees (trees > 12.5 cm dbh) in interior Douglas-fir forest stands in interior British Columbia. Each used or available tree was included only once, although used trees may have been used more than once during the study, and some trees supported multiple used cavities. 'Available trees' includes the most complete and most recent pre-harvest vegetation data set. Updated with additional years of data from Fig. 1a, MARTIN et al. (2004).

Tree selection for excavation and nesting - species and decay conditions

With respect to tree species used for excavation and nesting by all species, there was overwhelming selection for aspen on all study sites across all years, despite aspen representing only 15% of the trees on our sites (Fig. 2). Over 95% of 1714 nesting cavities were in trembling aspen, 2.8% were in lodgepole pine, 1.3% in Douglas-fir, and 0.5% in spruce (EDWORTHY et al. 2012, updated from MARTIN et al. 2004).

There was strong selection for cavities in aspen across all guilds and all species (MARTIN et al. 2004). Over a 12 year period, in the study, 96.7% of 1271 woodpecker nests located were in aspen trees (BLANC & MARTIN 2012). Among the common excavators, American Three-toed Woodpeckers (*Picoides dorsalis*) used aspen the least, but still selected for aspen for 79% of their nests (BLANC & MARTIN 2012). Only the rare Black-backed Woodpecker excavated exclusively in lodge pole pine trees (6 of 6 nests, updated from BLANC & MARTIN 2012). All other tree species on the sites were used for nesting and excavation to a limited extent (Fig. 2).

Cavity-nesters selected trees across a wide range of decay classes for nesting, but showed the strongest selection for live trees with onset of decay (decay class 2) and dead trees (3-7; Fig. 3). Trees in each decay class were used by a surprising range of woodpeckers and secondary cavity nesters, with the greatest diversity of species using decay classes 2 to 4 (15-16 species for each decay class, see Fig. 2 in Martin et al. 2004). As expected, a greater range of woodpecker species used trees in the lower decay classes (Fig. 4, reprinted from Blanc & Martin 2012). Pileated Woodpeckers, Hairy Woodpeckers and Red-naped Sapsuckers primarily used live trees, while Downy Woodpeckers selected trees with advanced decay (Fig. 4). Northern Flickers used the full range of decay classes for nesting (Blanc & Martin 2012). However, since flickers are essentially weak excavators, there was a tendency for the flicker cavities in live trees to have been renovated from a previous excavator (Unpublished data). Thus woodpeckers and other excavators such as nuthatches and chickadees strongly influence the selection of trees used for nesting by secondary cavity-using vertebrates.

Persistence of cavity trees related to decay class of trees

Woodpeckers produce a multi-annual resource and thus the value of the ecological services provided by woodpeckers strongly relates to the persistence of the cavities they form. Edworthy et al. (2012) applied the demographic concepts of survival and longevity to populations of tree holes to investigate rates of loss for cavities. As well, they examined how the characteristics of nest trees, habitat type, and excavator species affected the persistence of tree cavities in trembling aspen (95% of cavities were in aspen trees) in interior British Columbia, Canada. Three models were used to produce an average model for aspen that included decay class, DBH, distance to edge, and an interaction of DBH and distance to edge (Edworthy et al. 2012). The decay stage of the nest tree was the most important factor determining cavity longevity when survival of 1635 nesting cavities in aspen was modeled over a time span of 16 years (Fig. 5). The predicted median longevity for cavities in live trees was >15 years (predicted survival rate after 15 years = 0.56; Fig. 5). Cavities in recently dead trees were 2.7 times more likely than live trees to be destroyed in a year, and had a median longevity of 9 years. Cavities in dead trees with advanced decay had the lowest persistence, with a risk of loss 3.6 times greater than for cavities in live trees; their median longevity was only about 7 years (Fig. 5). Cavity longevity was greater in continuous forest than in aspen grove habitat (Edworthy et al. 2012).

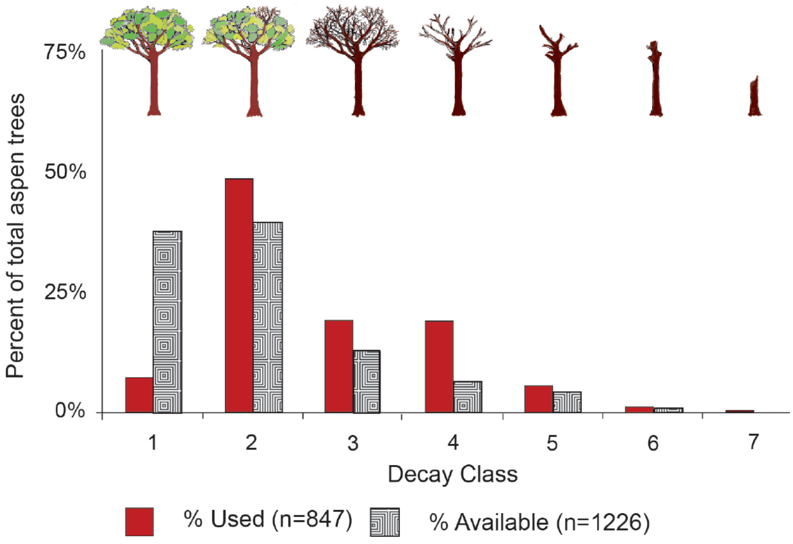

Fig. 3: Selection of tree species and decay class characteristics used for nesting by cavity-nesting birds in relation to availability in interior British Columbia. See text for description of decay classes. Each occupied or available tree was included only once, although multiple cavities may have been occupied in a tree or individual cavities occupied multiple times. Occupied trees refer to the sample of nest-trees that included only the most recent nesting attempt, and available trees were the most complete and recent set of vegetation plot data. Updated with additional years of data from Fig. 1c, Martin et al. (2004).

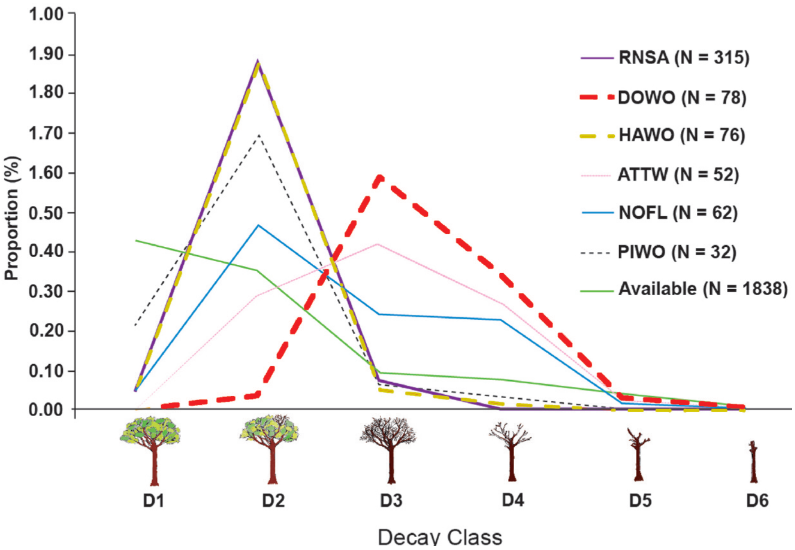

Fig. 4: Nest cavity excavation profiles of six woodpecker species in comparison to the mean annual aspen tree decay availability in interior British Columbia, 1997 - 2008. Proportional use of decay classes is based on total nests found for each species within freshly excavated nest cavities over the 12-year period (N = 615). Tree availability data reflect the mean annual decay class distribution of 1,838 trees that were re-sampled over the 12-year period. Woodpecker species are RNSA = Red-naped Sapsucker, DOWO = Downy Woodpecker, HAWO = Hairy Woodpecker, ATTW = American Three-toed Woodpecker, NOFL = Northern Flicker, and PIWO = Pileated Woodpecker. After Blanc & Martin (2012).

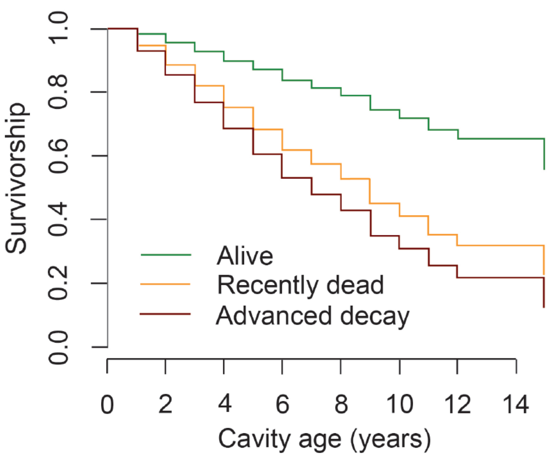

Fig. 5: Cox proportional-hazards predicted survival curves across three decay stages at average values of DBH and distance to edge for aspen tree cavities in central British Columbia, Canada. Green lines represent cavities in live trees (decay classes 1 and 2; median survival > 15 years), yellow lines represent cavities in recently dead trees (decay class 3; median survival 9 years), and brown lines represent cavities in snags with advanced decay (decay classes 4, 5, and 6; median survival 7 years). After Edworthy et al. (2012).

Discussion

There is an extensive literature documenting the use of woodpecker nest holes by secondary cavity-nesters (Newton 1994). For example, in our survey of the origin of the cavities used by secondary cavity nesters in interior British Columbia, most cavities used were excavated by Northern Flickers, Red-naped Sapsuckers and Hairy Woodpeckers in trembling aspen, and these holes provided nesting or roosting habitat for at least 12 other bird species and six mammal species (Martin et al. 2004; Aitken & Martin 2007; Cockle & Martin 2015). In aspen woodlands of the Colorado Rocky Mountains, Violet-green Swallows (*Tachycineta thalassina*) and Tree Swallows (*T. bicolor*) nested almost exclusively in cavities excavated by Red-naped Sapsuckers (Daily et al. 1993). Studies of cavity-nesting bird communities in forests of central interior British Columbia, Quebec, western Florida, and central Estonia revealed that the great majority of suitable cavities were excavated by woodpeckers (Martin et al. 2004, Remm et al. 2006; Blanc & Walters 2008; Ouellet-Lapointe et al. 2012). The importance of woodpeckers is especially striking in the case of large-bodied secondary cavity-nesters. Aubry & Raley (2002) reported that at least five species of ducks, five species of owls, and nine species of mammals nested in cavities produced by North America's largest extant woodpecker, the Pileated Woodpecker. Similarly, nest holes of the Black Woodpecker, Europe's largest avian excavator, were used for nesting by the Jackdaw (*Corvus monedula*), Tengmalm's Owl (*Aegolius funereus*), and Stock Dove (*Columba oenas*; Mikusinski 1995).

A number of mammal species use tree cavities. Tree cavities provide shelter for hundreds of species of bats (Kunz & Lumsden 2003; Ruczynski & Bogdanowicz 2005). In the Cascade Range of southern Oregon, nests of female fishers were primarily in cavities excavated by pileated woodpeckers (Aubry & Raley 2006). Multiple studies have documented use of woodpecker-excavated cavities by flying squirrels (*Glaucomys* sp), red squirrels (*Tamiasciurus hudsonicus*) bushy-tailed woodrats (*Neotoma cinerea*; Aubry & Raley 2002; Martin et al. 2004).

In addition to providing nesting cavities, woodpeckers contribute additional important ecological resources for the wildlife community as they excavate other types of cavities or holes and remove tree bark while feeding in trees. These services include the excavation of feeding holes and sap wells in trees. Woodpeckers create abundant holes and associated wood fragments when they forage for wood-dwelling invertebrates that can allow smaller woodpeckers and songbirds access to tree dwelling invertebrates under the bark loosened by woodpeckers (Winkler et al. 1995). Sapsuckers drill sap wells in deciduous and coniferous trees that are visited by a wide range of sap-feeders including other birds, mammals and insects (Daily et al. 1993; Montellano et al. 2013). Woodpeckers may thus contribute significantly to trophic structure and decomposition cycles in forests (Bednarz et al. 2004; Fayt et al. 2005; Drapeau et al. 2009). Floyd & Martin (2015), describe the different forms of cavity-excavation, review the ecological effects of woodpecker activities, and discuss ecosystem services that potentially flow from tree cavity excavation activities by woodpeckers. Other studies on the ecological services of birds discuss the impacts of feeding excavations for wildlife communities (Wenny et al. 2011).

Previous studies have used the decay classes of woodpecker nest trees to inform woodpecker habitat management, with a particular emphasis on retaining dead standing trees (snags) for nesting habitat (Mannan et al. 1980, Raphael & White 1984; Schreiber & deCalesta, 1992; Laudenslayer et al. 2002, Blanc & Walters 2008). However, many woodpeckers prefer to excavate new nest cavities in live trees with soft spots of decay, and some excavators avoid excavating in trees with multiple cavities (Robles et al. 2007), suggesting that trees with advanced decay and many cavities may be more reflective of past excavation value (Aitken & Martin 2004). Woodpeckers often excavate nest cavities in live trees, including sections of the bole of trees that contain heart rot (Hart & Hart 2001, Martin et al. 2004, Pasinelli 2007, Zahner et al. 2012), dead portions of living trees (Conner et al. 1976), and within decaying limbs of living trees (Reller 1972, Jackson 1976, Stauffer & Best 1982, Ingold 1994, Jackson & Ouellet 2002). Some woodpecker species choose live trees for nesting more often than snags (LAWRENCE 1967, INGOLD 1994, ROBLES et al. 2007, MATSUOKA 2008, GYUG et al. 2009) or use live trees exclusively (JACKSON 1994). Thus, focusing only on snags (either dead standing trees or the dead section of live trees) for conservation of woodpecker nesting habitat may be limited (JACKSON & JACKSON 2004).

Temporal variation in the ecological roles of woodpeckers in Nest Web Communities

Early studies of the role of woodpeckers in Nest Web networks used a static approach that did not take into account how the Nest Web might change over time (MARTIN et al. 2004). However, the need for a dynamic approach became apparent when the ecosystem experienced a dual resource pulse of food and cavities precipitated by an outbreak of mountain pine beetle (*Dendroctonus ponderosae*), which killed 100% of mature pine trees (NORRIS & MARTIN 2010). When COCKLE & MARTIN (2015) studied the Nest Web dynamics of a network of 25 cavity-nesting vertebrate species over 14 years, they found that after a bark beetle outbreak, secondary cavity-nester use of cavities created by Northern Flickers and cavities formed by natural decay processes declined by one half and one third, respectively, while the use of cavities created by Red-naped Sapsuckers (*Sphyrapicus nuchalis)*, Pileated Woodpecker and Hairy Woodpeckers (*Picoides villosus)* doubled, tripled, and quadrupled, respectively. Use of cavities created by Downy and American Three-toed Woodpeckers peaked in 2005 and 2006, one and two years after the peak of the beetle outbreak. Thus during an increase in the abundance of a critical resource (food for insectivores), there was a shift in the importance of flickers, the most common but perhaps less-preferred woodpecker, as cavity providers toward the less common, preferred woodpeckers (Hairy and Pileated Woodpeckers, sapsuckers). Whereas a static approach suggested that the Northern Flicker was a keystone species whose management would permit conservation of most cavity-nesting vertebrates in the community (MARTIN et al. 2004), a dynamic approach revealed that under some ecological conditions (such as during and after a bark beetle outbreak), the importance of specific excavators as cavity providers can vary. Rather than a keystone species, Northern Flickers might best be considered a generalist facilitator, that can provide cavities for most species of secondary cavity-nesters when better alternatives are scarce (COCKLE & MARTIN 2015).

Generally, cavity-nesting vertebrates comprise a major component of many forest communities. About 10% of all birds and many other vertebrates use cavities in trees for nesting or roosting, and many species use cavities excavated or naturally formed in other substrates (COCKLE et al. 2011). About 25-30% of forest vertebrate species in the northwestern North America nest or roost in cavities and most are obligate hole-nesters (BUNNELL et al. 1999; MARTIN et al. 2004). In most cases woodpeckers excavate a new cavity for each nesting attempt (BLANC & MARTIN 2012), but see WIEBE et al. (2007) for a review of the frequency of nest cavity reuse among woodpecker species. These fresh excavations ensure a continuous supply of available shelters for secondary cavity-nesters that require cavities but cannot construct their own (AITKEN & MARTIN 2004; COCKLE et al. 2011; REMM & LÕHMUS 2011). Without woodpecker holes, secondary cavity nesters are largely dependent on the slow formation of natural cavities by decay or on human-provided nest boxes near some urban areas. The ecological roles that woodpeckers play appear most pronounced in North America where most cavity-using vertebrates use mainly excavated cavities in contrast to the other continents where secondary cavity-nesting birds and mammals rely exclusively or extensively on decay-formed holes (COCKLE et al. 2011). Additional studies that examine entire assemblages of tree cavity-using vertebrates will enable further new insights into the ecological roles of woodpeckers and their influence on forest biodiversity, community ecology and wildlife conservation.

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