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Research Article

Tree Cavity Occupancy by Nesting Vertebrates across Cavity Age

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ABSTRACT Cavity-nesting birds and mammals exhibit species-specific nest-site selection for tree characteristics and cavity dimensions. Although trees and their cavities change as they age, with trees becoming softer and cavities becoming larger, it is not known how their value as nesting resources varies with age. In the context of wildlife and forest management, we investigated the relative value of generating a supply of fresh cavities, which are thought to be of high quality, versus protecting cavities as they age and expand in interior volume. For 21 years (1995–2016), we monitored the formation and occupancy of tree cavities used by >30 species of birds and mammals in interior British Columbia, Canada. Cavity occupancy by secondary users was highest 1 year post-excavation (53%), then declined to 40% after 2 years, remained at $33 \pm 7\%$ (SD) between 3 and 16 years of age, and increased to 50% use from 17–20 years post-excavation. Excavators that reused cavities (woodpeckers [Picidae], nuthatches [*Sitta* spp.]) strongly selected 1- and 2-year-old cavities, large-bodied non-excavators (ducks, raptors, squirrels) selected mid-aged cavities, and mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*) selected most strongly for the oldest cavities. Cavities created in living aspen trees (*Populus* spp.), especially those excavated by northern flickers (*Colaptes auratus*), maintained high occupancy by secondary users across cavity age, and provided the bulk of cavities used in this system. Altogether, these results show that a diverse excavator community is needed to generate a supply of fresh cavities in the ecosystem, and retention of the mid-aged and older cavities will help support larger species.

KEY WORDS cavity-nesting bird, forest management, habitat complexity, keystone resource, nesting habitat, tree cavity, tree hollow, woodpecker.

Tree cavities are an important reusable nesting resource for communities of cavity-nesting birds and mammals globally (Cockle et al. 2011, van der Hoek et al. 2017). Cavities support up to 30% of forest vertebrate biodiversity in some forest systems (Bunnell et al. 1999) but are often a limiting resource, especially in landscapes affected by forestry, agriculture, and urbanization (Newton 1994, Marzluff et al. 1998, Aitken and Martin 2008, Cockle et al. 2010, Wiebe 2011). To sustain populations of cavity-nesting vertebrates in the context of forest harvesting, managers can retain cavity-bearing trees or promote recruitment of new cavities. Retained cavities may be reused across many years; however, tree cavities may decline in occupancy and quality as they age (Mazgajski 2007, Gentry and Vierling 2008). Understanding the value of old cavities, which persist and are available across many years, versus fresh cavities, which may provide high-quality preferred nest sites, will help to inform better forest management for cavity-nesting communities.

Trade-offs involved in the use of fresh versus older tree cavities make it difficult to predict the overall change in cavity quality with age, and these trade-offs may vary across species (Wiebe et al. 2007). Cavities can persist from a few weeks to >30 years (Wesołowski 2011, 2012; Cockle et al. 2017), and their characteristics change over time (Edworthy and Martin 2014), influencing their suitability as nest sites (Aitken and Martin 2004, Robles and Martin 2013). As they age, cavity trees advance through decay classes (Thomas et al. 1979), whereby cavity walls soften and microclimate regulation provided by the cavity chamber is reduced (Wiebe 2001). Risk of nest predation can also increase as cavity walls decay and mammalian predators learn the nest site

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locations (Nilsson 1984, Sonerud 1985, Wesołowski 2002, Brightsmith 2005, Paclík et al. 2009, Tozer et al. 2012). In some systems ectoparasites accumulate as cavities age (Rendell and Verbeek 1996*a*, *b*), although this problem may be negligible in regions with cold winters (Wiebe 2009). In at least one respect, however, cavities may improve with age: cavities in living aspen trees (*Populus* spp.) increase in chamber depth by approximately 1 cm per year while maintaining relatively constant entrance diameters (Edworthy and Martin 2014). For a wide range of species, internal cavity dimensions are positively related to occupancy, brood size, and nest survival (Wiebe and Swift 2001, Aitken and Martin 2004, Gibbons et al. 2008, Politi et al. 2009, Møller et al. 2014).

As cavities change in characteristics with age they may also change in suitability for various species in the community, resulting in species-specific variation in occupancy with cavity age. For example, cavity expansion over time might allow larger species to occupy cavities that were originally excavated by smaller species. If cavity occupancy by different species in the community is partitioned across cavity age, then managing for a diverse array of cavity ages may be an important strategy for protecting and enhancing the diversity of cavity-nesting wildlife communities. Within cavity-nesting communities, nest site selection varies among species and guilds (Li and Martin 1991, Aitken et al. 2002). Whereas most woodpeckers (Picidae) create and use a fresh cavity each year, rarely occupying an old cavity (Aitken et al. 2002, Saab et al. 2004, Blanc and Martin 2012), other excavators sometimes excavate fresh cavities and sometimes reuse existing cavities (e.g., northern flickers [*Colaptes auratus*], red-breasted nuthatches [*Sitta canadensis*]; Norris and Martin 2012, Wiebe 2016). Non-excavators (e.g., mountain bluebirds [*Sialia currucoides*]) rely on existing cavities and exhibit interspecific variation in nest site selection, most notably a positive correlation between body size and cavity size but also variation in the use of trees at different stages of decay (Saunders et al. 1982, Poonswad 1995, Martin et al. 2004). Among non-excavators, limited cavity availability may force weak competitors into sub-optimal cavities (Aitken and Martin 2008, 2012).

The relationship between cavity age and occupancy by vertebrates may also be mediated by the initial characteristics of the cavity. Excavator species, tree species, and decay class exert a strong influence on rates of cavity persistence (Wesołowski 2011, 2012; Edworthy et al. 2012; Cockle et al. 2017) and changes in dimensions over time (Edworthy and Martin 2014). For example, in interior British Columbia (Canada), cavities produced by strong excavators in living broadleaf trees (e.g., quaking aspen [*Populus tremuloides*]) persisted longer and advanced through decay classes more slowly than those produced by weak excavators in decaying or dead aspen (Edworthy et al. 2012, Edworthy and Martin 2014), suggesting that cavities in living trees may best maintain their value to secondary cavity-users as they age.

We examined the occupancy of tree cavities as they age, in a community of 31 birds and mammals in interior British Columbia (Table 1). Our objective was to investigate the relative value of generating a supply of fresh cavities versus protecting cavities as they age and expand in interior volume. If cavities decline in value (as nesting resources) as they age, we predicted that cavity occupancy would decline with age. If expansion of internal dimensions over time increases the value of a cavity to large-bodied species, or if weak competitors are displaced into older cavities, then we predicted occupancy of cavities would increase with cavity age for ducks, raptors, and the less competitive passerines (e.g., tree swallows [*Tachycineta bicolor*], mountain bluebirds) but not for smaller-bodied species (e.g., mountain chickadee [*Poecile gambeli*]), strong competitors (e.g., European starlings [*Sturnus vulgaris*]), or excavators. Lastly, if the quality of cavities in dead trees declines rapidly, we predicted occupancy would remain relatively stable with age for cavities formed by strong excavators in living trees but would decline

Table 1. Cavity-nesting vertebrates and size classes of cavities excavated and reused by each species in interior British Columbia, Canada, 1995–2016. Cavity size classes were categorized as small (S; entrance width <3.5 cm), medium (M; 3.5–5 cm), and large (L; >5 cm). For excavators, size formed is the size of cavity each species creates, and for all species bullet points indicate the size of cavities suitable for use (size used).

		Size used		
Species common name	**Size formed**	**S**	**M**	**L**
Excavator or formation agent				
Natural decay	S, M, L			
Northern flicker	L			●
Pileated woodpecker	L			●
Red-naped sapsucker	M		●	
Hairy woodpecker	M		●	
American three-toed woodpecker	M		●	
Black-backed woodpecker (*Picoides arcticus*)	M		●	
Downy woodpecker	S	●		
Black-capped chickadee	S	●		
Red-breasted nuthatch	S	●	●	
Non-excavators—bird				
Wood duck (*Aix sponsa*)				●
Bufflehead				●
Barrow's goldeneye (*Bucephala islandica*)				●
Hooded merganser (*Lophodytes cucullatus*)				●
Flammulated owl (*Psiloscops flammeolus*)				●
Northern hawk owl (*Surnia ulula*)				●
Northern saw-whet owl				●
American kestrel				●
Tree swallow			●	●
Mountain chickadee		●	●	
Boreal chickadee (*Poecile hudsonicus*)		●		
Mountain bluebird			●	●
European starling			●	●
Non-excavators—mammal				
Little brown bat (*Myotis lucifugus*)				●
American marten (*Martes americana*)				●
Fisher (*Martes pennanti*)				●
Short-tailed weasel (*Martes erminea*)			●	●
Bushy-tailed woodrat (*Neotoma cinerea*)			●	●
Deer mouse (*Peromyscus maniculatus*)		●	●	●
Yellow pine chipmunk (*Tamias amoenus*)			●	●
American red squirrel			●	●
Northern flying squirrel (*Glaucomys sabrinus*)			●	●

with age for cavities formed by weak excavators in dead or decaying trees. To test these hypotheses, we investigated community- and species-level occupancy of tree cavities across cavity age, and patterns of occupancy with age according to cavity formation agent, decay class, and tree species.

STUDY AREA

We combined data from 2 long-term studies (Nestweb and Flicker) of cavity-nesting birds in the Cariboo-Chilcotin region of interior British Columbia, Canada. The Nestweb study was conducted May–July, 1995–2011, at 28 study sites ranging from 7 ha to 32 ha in area, and 815 m to 911 m above sea level (ASL) all within 50 km of Williams Lake, British Columbia (51° 52′ N, 122° 21′ W). The Flicker study was conducted May–June, 1998–2016, and encompassed a 100-km^2 area around Riske Creek, British Columbia (51° 58′ N 122° 31′ W; 911 m ASL) and included several of the Nestweb sites. All sites were on the broad, rolling Fraser Plateau in the interior Douglas-fir (*Pseudotsuga menziesii*) and sub-boreal pine-spruce biogeoclimatic zones, characterized by dry, warm summers and cool winters (Meidinger and Pojar 1991). Forest types ranged from mixed coniferous-deciduous forest surrounded by grassland, small lakes, and wetlands, to dry coniferous forest often with deciduous strips next to small creeks. The predominant coniferous species were Douglas-fir, lodgepole pine (*Pinus contorta*), and hybrid white-Engelmann spruce (*P. glauca* x *engelmannii*), with occasional Rocky Mountain juniper (*Juniperus scopulorum*). The predominant broadleaf species was quaking aspen with occasional alder (*Alnus* spp.), paper birch (*Betula papyrifera*), and willow (*Salix* spp.), and over 95% of nesting cavities are in quaking aspen trees. Cavity-nesting birds in these forests included 9 species of excavators, 13 species of non-excavator birds, and 9 species of mammals (Table 1), comprising >30% of forest vertebrate diversity (Bunnell and Kremsater 1990). Land-use included forest harvesting and cattle grazing. Between 1998 and 2010, 11 of the Nestweb sites were harvested, removing either 15–30% of trees in partial harvests or 50–90% of trees in clearcut with reserves. Managers retained most of the aspen and mature Douglas-fir trees on harvested sites to provide nesting habitat for cavity-nesting vertebrates and winter range for ungulates, in both harvest plans. Martin et al. (2004), Drever et al. (2008), Drever and Martin (2010), and Wiebe (2001, 2016) provide additional study site details.

METHODS

Cavity Occupancy and Characteristics

The Nestweb study monitored cavities used by any species of cavity-nesting vertebrates (Martin et al. 2004, Cockle and Martin 2015), and the Flicker study tracked occupancy of cavities first used by northern flickers (Wiebe 2001, 2014). We located nests by following birds to their nest sites and by inspecting previously occupied cavities. We used ladders, mirrors, and flashlights to inspect cavities up to approximately 6 m above the ground. Starting in 2003 we also used video cameras on extendable poles, which allowed us to view the contents of cavities ≤15 m above the ground. We considered a cavity to be occupied if it contained ≥1 eggs (excluding dumped eggs) or young. We considered cavities inaccessible by ladder or camera to be occupied if we observed adults entering or exiting the cavity on ≥2 occasions 1 to several days apart. After a cavity was occupied initially, we continued to check it every year until it was destroyed, usually when the tree fell (90% of cavity losses; Edworthy et al. 2012), or we stopped monitoring the site (because of small numbers of nesting birds or difficult access). Each breeding season (May–Jul), we checked known cavities every 4–5 days for signs of nesting activity. We discovered many cavities (55%) in the year they were excavated, and thus we have full histories for these cavities throughout their lifetime over the 2-decade field study. We first discovered others (45%) when occupied by a secondary cavity-nester (min. age), and their use before this entry into our study was unknown (see Table S1, available online in Supporting Information, for the number of nests by species by age). Methods involving animals were approved by the University of British Columbia Animal Care Committee (protocol #A07-0130).

When we first found a cavity, we recorded the formation agent (excavator species or natural decay), tree species, and decay class. We scored the decay class of the cavity tree as 1) live and healthy, 2) live unhealthy (e.g., fungal fruiting bodies, wood-boring insect attack), 3) recently dead (hard wood, minor branches intact), 4–5) advanced decay with soft sections, and loss of minor or major branches (Thomas et al. 1979, Martin et al. 2004). If we observed excavation or we discovered a fresh cavity occupied by a strong excavator with fresh woodchips or excavation hammering, we designated the observed species or nest occupant as the excavator. If we initially discovered a cavity occupied by a secondary user, we were often able to determine whether the cavity excavator was a pileated woodpecker (*Dryocopus pileatus*), northern flicker, sapsucker, or nuthatch because of the distinctive size, shape, or bark staining typical of the entrance holes of these species. We were able to assign an excavator for 80% of excavator-formed cavities. We designated cavities formed by decay or damage, often in knotholes or cracks, as natural ($n = 80$ cavities; 3.3% of cavities in our dataset). All natural cavities entered the dataset as age 1 (min. age of 1 yr) when first used. For all other cavities we designated the excavator or formation agent as unknown.

Statistical Analysis

As described above, cavities entered our dataset either as fresh cavities (i.e., excavated in the year we first located them), or as existing cavities, for which we could only designate a minimum age. We designated cavities found fresh as age zero in the year they entered the dataset, and existing cavities as minimum age 1 in the year they entered the dataset. We examined differences in the proportion occupied across cavity ages between known-age cavities (found freshly excavated) versus minimum-age cavities, and found that differences in proportion occupied diminished below 5% at age 3 (Fig. S1, available online in Supporting

Information, compares occupancy and sample size of known- *vs.* minimum-age cavities across all ages). Thus, for most analyses, we dropped minimum-age cavity years 1 and 2 but pooled known- and minimum-age cavities for cavities aged 3–20 years. The exception was analyses specific to natural cavities, which we designated as minimum age when found, and we retained all age classes of these cavities. We also pooled data from cavities ≥18 years for all cavity types because of low sample sizes in the older age classes.

We examined patterns in cavity occupancy across age for individual species of users, formation agent, tree species, and initial tree decay class. To test for positive or negative linear and non-linear trends in occupancy across cavity age, we fit generalized additive models (GAMs) using the gam package in R (Hastie 2016, R Core Team 2017). These models enabled us to capture patterns in the data that might include both linear trends and non-linear patterns generated by complex interactions among change in cavity characteristics, species selection preferences, and inter-specific competition. For the non-linear component, we allowed up to third-order polynomial terms to achieve a balance between capturing biological patterns and avoiding over-fitting. We constructed separate GAMs for each species of occupant, formation agent, tree species, and decay class. We modeled the proportion of cavities occupied as the response variable, and cavity age as the sole predictor variable in each model. For the analyses by secondary user, we calculated the proportion of cavities occupied by each species (in each age class) as the number of cavities occupied by the species divided by the number of cavities in the appropriate size class. We divided cavities into small, medium, and large size classes, based on excavator or entrance diameter (Table 1). We excluded cavities for which we were unable to assign a size class (i.e., formation agent and size measurements unknown) from these analyses ($n = 339$ cavities excluded; 11%). We weighted all models by sample size of cavities in each age class, using the weights argument in the gam R package, such that a weight of 2 was the same as making a given observation twice (Hastie 1992, 2016). Statistical significance reported for GAMs represents a deviation from a null model of zero

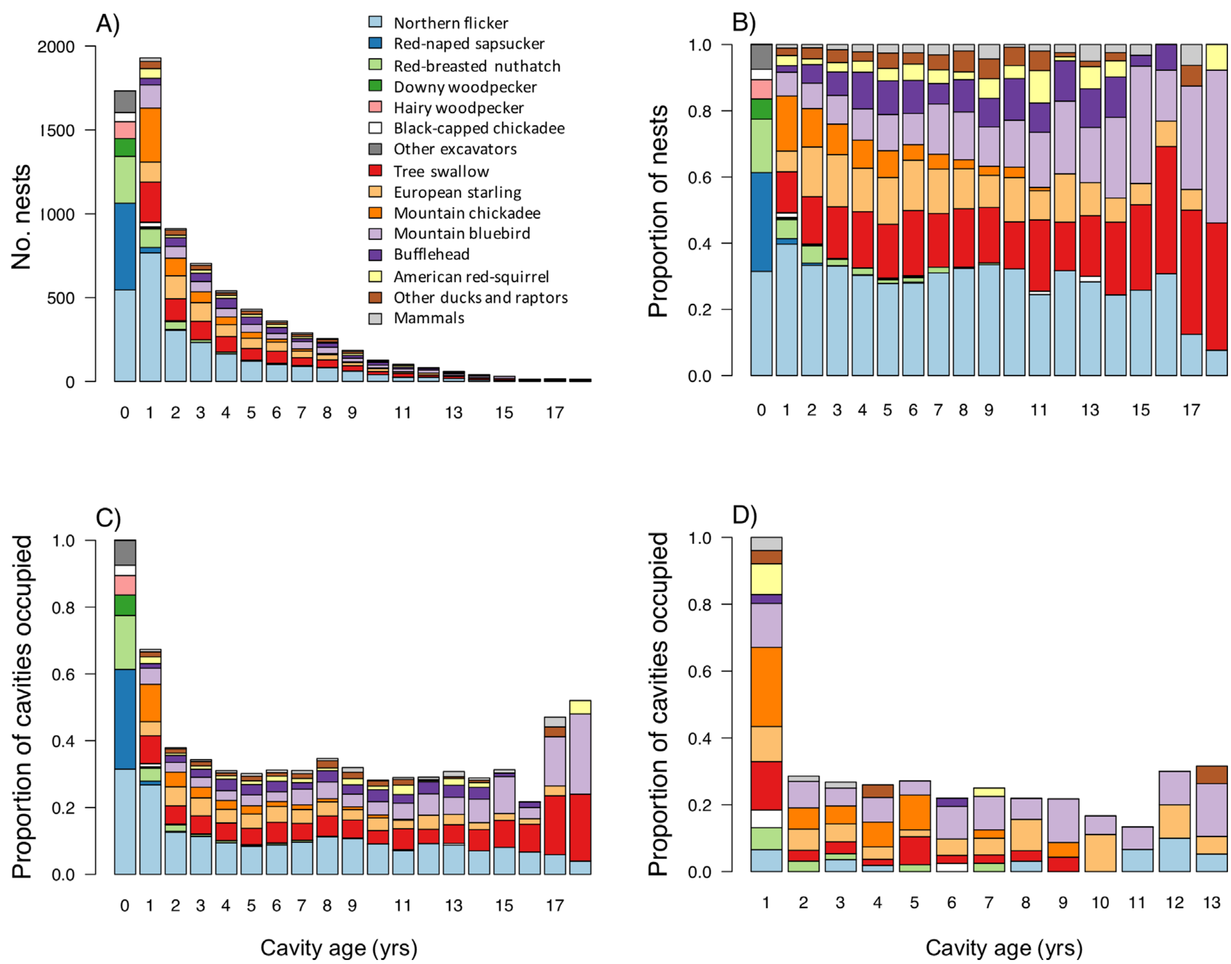

Figure 1. Summary of cavity occupancy by 31 species, including 6,736 nests in 2,876 cavities ages 0–20 years in interior British Columbia, Canada, 1995–2016. Age classes 0–2 years include known-age cavities, and ages >3 years include pooled known-age and minimum-age cavities. A) Number of nests across cavity age for the 12 most common species ($n \geq 190$ nests) and 3 groups of remaining species (other primary excavators, secondary cavity-nesting ducks and raptors, and secondary cavity-nesting mammals). B) Proportion of nests by species out of all nests examined. C) Proportion occupied out of the total number of excavated cavities ($n = 15{,}682$ cavity-years). D) Proportion occupied of the number of natural (decay-formed) cavities occupied ($n = 495$ cavity-years occupied; age is minimum known age).

change in occupancy across age. Some species had too few nest records to model patterns of occupancy, and thus we included only species with sample sizes of >40 nests in existing cavities (age > 0).

RESULTS

Community-Level Patterns of Cavity Occupancy

Results were generated from 3,130 cavities monitored from 1995 to 2016, for 15,682 cavity-years (occupied = 6,767 cavity-use years, unoccupied = 9,915 cavity non-use years; Fig. 1A). Most (80%) of these cavities were of known age, and mean age was 4.0 years. Cavities were used by 31 species across ages 0 (freshly excavated) to 20 years (Fig. 1A, B; Table S1). Excavated cavities ($n = 3{,}059$) comprised 86% of cavities and were occupied by 21 bird and 6 mammal species. The remainder of cavities (14%) were formed by natural decay or the excavator was unknown, and were occupied by 9 bird and 4 mammal species.

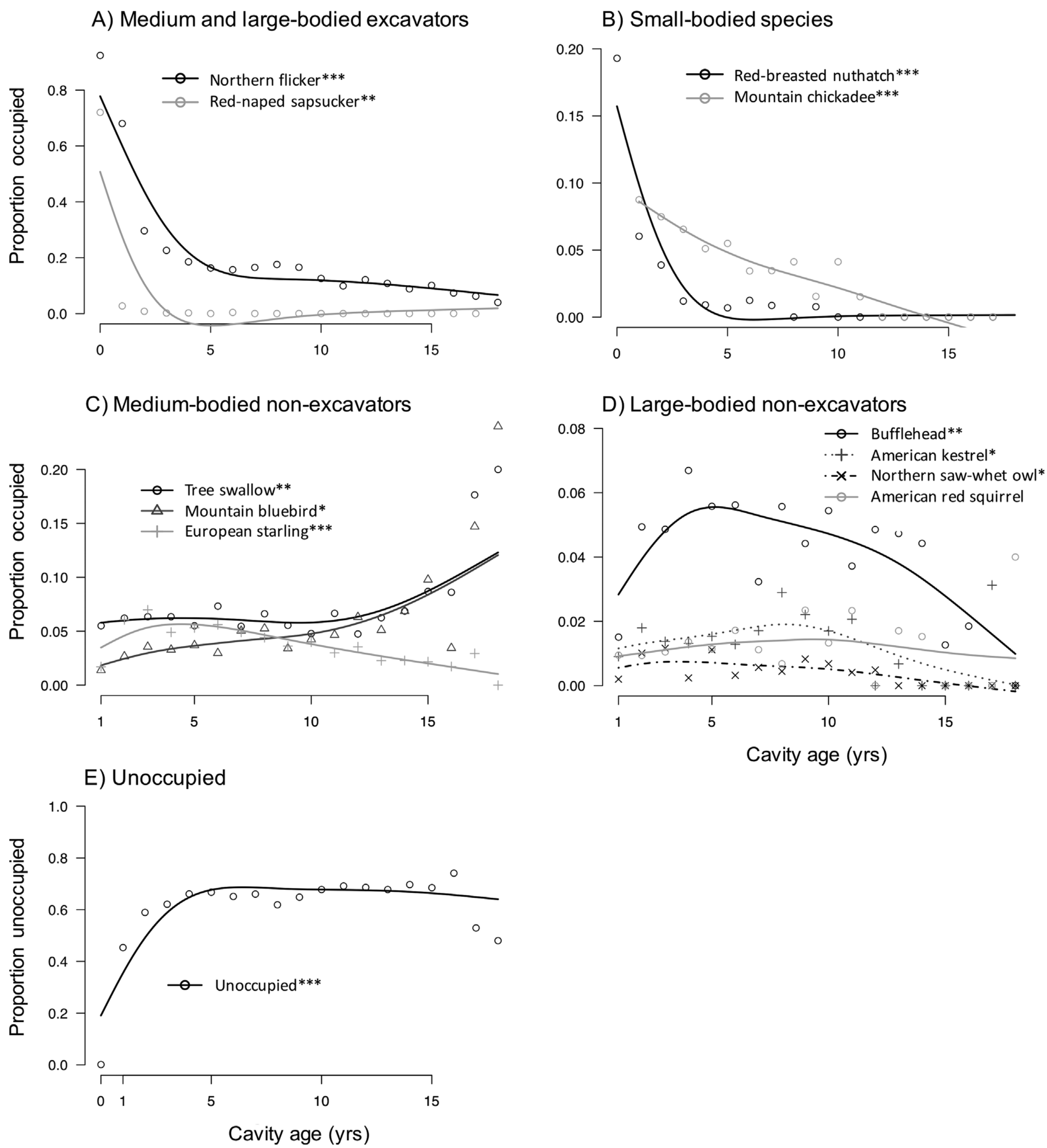

Figure 2. Species-level patterns of occupancy across cavities aged 0–≥18 years (excluding minimum age 1 and 2 cavities) in interior British Columbia, Canada, 1995–2016. Panels show trends for A) medium and large excavators, B) small-bodied species (including excavators and non-excavators), C) medium-bodied non-excavators, D) large-bodied non-excavators, and E) the proportion of unoccupied cavities. Trends are based on generalized additive models and stars denote level of statistical significance in deviation from a null model of zero change in occupancy across age (* <0.05, ** <0.01, *** <0.001).

Reuse of existing cavities by any species was highest 1 year post-excavation (age 1), but remained constant from ages 2–15 years. All excavated cavities were used at age 0, the year they were formed. At age 1, occupancy fell to 67%, and by age 2, occupancy was 38% (Fig. 1C). Between ages 3 and 16, mean proportion occupied was 33% (range = 29–38%; Fig. 1C). Occupancy of the oldest cavities (17–20 years; $n = 59$ cavity-years;) increased to 50%. Natural cavities showed a pattern of occupancy like that of excavated cavities, but because natural cavities were designated as minimum age 1 in the year they were first found occupied, 100% of these age-1 cavities were occupied. Between ages 2 and 16, occupancy of natural cavities was 25% (range = 13–31%) with a slight increase in occupancy of the oldest cavities (Fig. 1D).

Species-Level Patterns of Cavity Occupancy

Many species showed strong selective preferences across cavity age, with different trends between excavators versus non-excavators and across the range of body sizes. Most excavators created and occupied a fresh cavity every year (Table S1); however, northern flickers and red-naped sapsuckers (*Sphyrapicus nuchalis*) sometimes reused existing cavities rather than excavating a fresh one. Northern flickers exhibited a hockey-stick-shaped pattern of occupancy, using 68% of the age-1 large cavities available (entrance width >5 cm), and 29% of age-2 cavities, followed by a steady decline from 22% of age-3 cavities to 9% of ≥18-year-old cavities. When they reused, red-naped sapsuckers predominantly used 1-year-old cavities (3.5–5 cm wide) but occupied just 2% of the medium-sized cavities available (Fig. 2A). Other strong excavators reused cavities only occasionally (≤9%), predominantly in age-1 cavities (Table S1).

Among small-bodied cavity-nesters, red-breasted nuthatches (excavators) reused cavities aged 1 to 2 years post-excavation, and rarely up to 9 years post-excavation (Fig. 2B). Mountain chickadees, small-bodied non-excavators, used small and medium-sized cavities. Their occupancy declined linearly from 9% of the age-1 cavities available to 0% of cavities age 12 and older (Fig. 2B).

We monitored 3 medium-bodied secondary cavity-nesting passerines: tree swallow, mountain bluebird, and European starling, all of which used medium- and large-sized cavities. Tree swallows and mountain bluebirds were the most frequent users of older cavities across the whole community. For cavities aged 1 to 10 years, tree swallows had a steady occupancy of 5–7%, whereas bluebirds showed a linear increase; occupancy for both species peaked at 19–24% in the oldest age class (≥18 years; Fig. 2C). Occupancy by European starlings peaked at age 3 (7%) and then declined steadily to 0–3% in cavities >15 years old.

Large-bodied secondary cavity-nesters included bufflehead (*Bucephala albeola*), American kestrel (*Falco sparverius*), northern saw-whet owl (*Aegolius acadicus*), and American red squirrel (*Sciurus vulgaris*). Occupancy by bufflehead increased from 1.5% of age-1 cavities to 6.5% of age-4 cavities, and then declined in older-aged cavities. The other large-bodied species used cavities more consistently across age classes, with slightly higher occupancy in cavities aged 1–10 years than in those >10 years old (Fig. 2D). Overall cavity vacancy (all size classes) increased from 44% of age-1 cavities to 67% of age-4 cavities, and was nearly constant after age 4 (Fig. 2E).

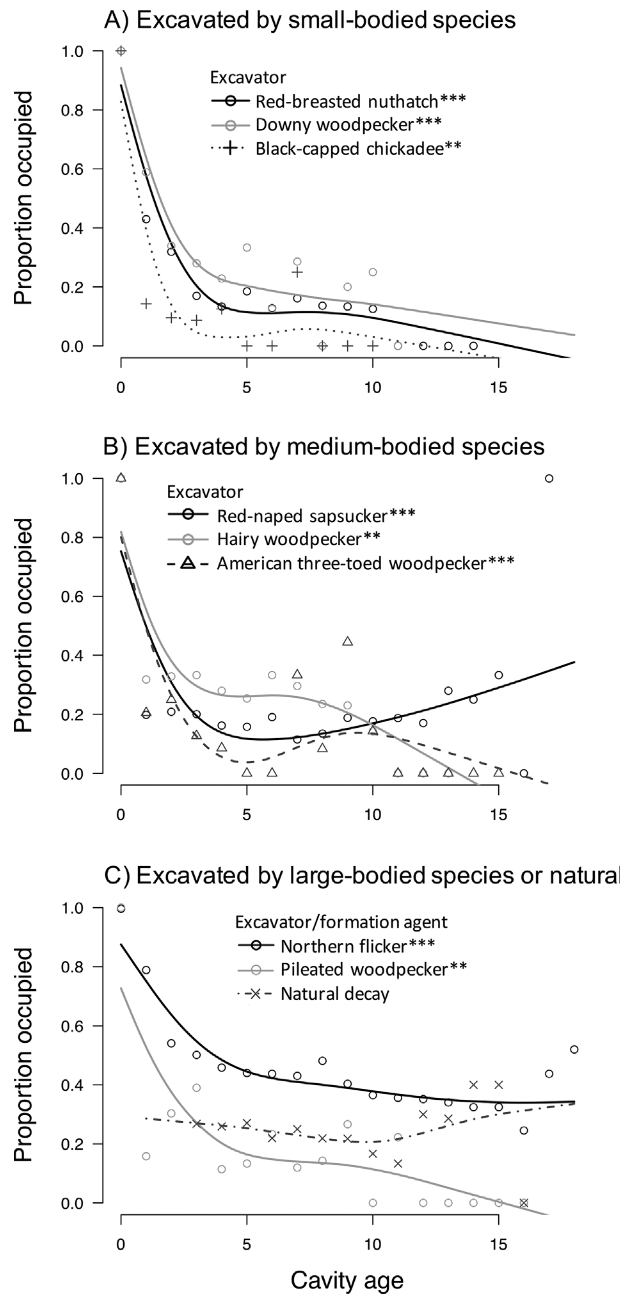

Figure 3. Patterns of cavity occupancy across age within formation agent and size categories, in cavities ages 0–≥18 years (excluding minimum age 1 and 2 cavities) in interior British Columbia, Canada, 1995–2016. Cavities were formed by A) small-bodied excavators (all weak), B) medium-bodied excavators (strong), and C) large-bodied excavators (strong) and natural decay. Sample of cavity ages were ≥150 for all the excavators and 356 for cavities formed by natural decay. Trends are based on generalized additive models and stars denote level of statistical significance in deviation from a null model of zero change in occupancy across age (* <0.05, ** <0.01, *** <0.001).

Patterns of Cavity Occupancy Across Formation Agent, Tree Species, and Tree Decay

Cavities excavated by small-bodied species, including downy woodpecker (*Picoides pubescens*), red-breasted nuthatch, and black-capped chickadee (*Poecile atricapillus*), were most likely to be reused in their first 3 years post-excavation (Fig. 3A). Among medium-bodied woodpeckers, hairy woodpecker (*Picoides villosus*) cavities had the highest occupancy between 1 and 9 years post-excavation, and the proportion occupied declined slowly with age (Fig. 3B). Occupancy of red-naped sapsucker cavities declined between ages 1–7 years but then increased from ages 8 to ≥18 years. Occupancy of American three-toed woodpecker (*Picoides dorsalis*) cavities declined in the first 4 years post-excavation, and was more variable after age 6, possibly because of low sample sizes. Most large cavities were excavated by northern flickers, and flicker cavities had relatively high occupancy across all ages, with 80% occupancy of age-1 cavities, declining to 55% at age 2, and approximately 38% occupancy at ages >15 years (Fig. 3C). In contrast to flicker cavities, occupancy of cavities excavated by pileated woodpeckers averaged approximately 25% in age 1–3 year cavities and declined to 0% by age 11. Cavities formed by natural decay were used consistently at 26–30% across age classes.

Cavities excavated in aspen or pine trees were occupied >24% throughout their lifespans, whereas those excavated in fir and spruce were rarely used after 6 years post-excavation (Fig. 4A). Among cavity-tree decay classes, all trends in cavity occupancy were similar to the pattern in the overall dataset, with the highest occupancy in age-1 cavities but consistent occupancy across the remainder of the lifespan (Fig. 4B).

DISCUSSION

In central British Columbia, we found that tree cavities were used by about 30 species of cavity-using vertebrates for up to 20 years, with patterns of occupancy influenced by cavity age, entrance size, formation agent, and tree species. Relatively fresh cavities had the highest occupancy, suggesting that they were the highest quality resources; however, older cavities were occupied throughout their lifespans. Fresh cavities were used disproportionately more by excavators and several small- or medium-bodied non-excavators, whereas older cavities were used more often by medium- to large-bodied non-excavators. The partitioning of these nesting resources by cavity age and size suggests that an age-structured cavity supply generated by a diversity of formation agents contributes to the biodiversity of cavity-nesting communities. In the context of forest management, maintaining a regular supply of high quality fresh cavities and retaining existing cavities, will help to support these diverse communities.

Except for northern flickers and red-breasted nuthatches, excavators in our system typically excavate a fresh cavity for nesting each year, and these cavities became available for secondary users in subsequent years. At the community-level, our result that occupancy was highest in cavities age 1 year post-excavation is similar to the results of shorter-term and single-species studies (Conner et al. 1998, Aitken et al. 2002, Mazgajski 2007, Gentry and Vierling 2008). These findings support hypotheses predicting that fresh cavities offer an advantage to secondary cavity users in terms of lower predation risk, better microclimate regulation, or fewer ectoparasites, compared to older cavities (Nilsson 1984, Sonerud 1985, Wesołowski 2002, Tozer et al. 2012). Despite the initial decline in occupancy, there was no further decline in community-level use of cavities age 3 to ≥18 years old in which occupancy was maintained at 29–34%.

Our species-specific results suggest that cavity resources are partitioned across cavity age, and we suggest that cavity quality increases with age for some species and declines for others. When excavators reused cavities, they predominantly

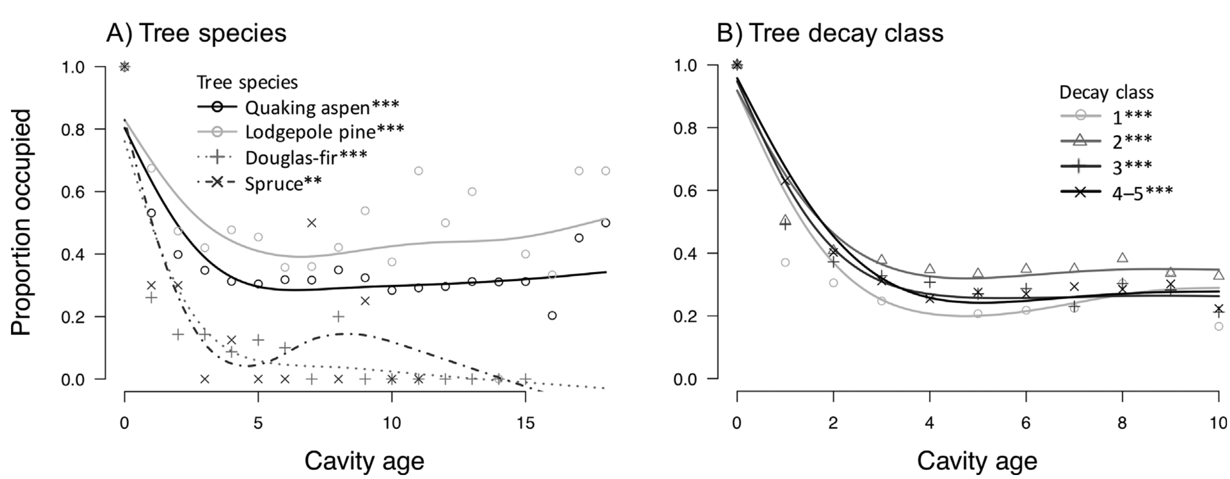

Figure 4. Patterns of cavity occupancy across age within A) tree species and B) initial tree decay class categories, in cavities ages 0–≥18 years (excluding minimum age 1 and 2 cavities) in interior British Columbia, Canada, 1995–2016. We defined decay classes as alive and healthy (1), alive with signs of fungal, insect, or mechanical decay (2), recently dead with major and minor branches intact (3), and advanced decay with branches lost, possible broken top, hard wood or spongy wood (4–5). Tree species include those listed in panel A. Trends are based on generalized additive models and stars denote level of statistical significance in deviation from a null model of zero change in occupancy across age (* <0.05, ** <0.01, *** <0.001).

used newer cavities. Northern flicker was the only excavator that frequently reused cavities >5 years post-excavation. Flickers are facultative excavators; in general about 70% of flicker pairs reuse cavities annually at our sites (Wiebe 2016). Relatively high conspecific densities coupled with weak competitive abilities against other users of large cavities such as starlings and raptors may contribute to the use of older cavities by flickers (Wiebe 2003, Edworthy et al. 2011). Non-excavators used cavities more evenly across ages than the excavators did, although mountain chickadees and European starlings selected newer cavities. As the only abundant small-bodied non-excavating bird at our study area, mountain chickadees occupy a distinct nest niche compared to most other non-excavators, relying in large part on cavities produced by red-breasted nuthatches and downy woodpeckers, cavities that are rarely used by other species of non-excavators (Cockle and Martin 2015). As a result, they may experience less competition for young (age 1–2 yr) cavities, compared to medium- and large-bodied species. European starlings also selected newer cavities, consistent with their selection of nest trees in early stages of decay (Martin et al. 2004) and their strategy of aggressive competition for cavities (Weitzel 1988, Ingold 1998).

Bluebirds and swallows showed the strongest selection for older cavities, which may be related to displacement by similar-sized competitors from newer cavities. As medium-bodied species using primarily flicker and sapsucker cavities, mountain bluebirds and tree swallows must compete with a large range of secondary cavity-using species, including European starlings and flickers, which are abundant and occupied 67% of the available age-1 cavities and 30% of age-2 cavities. When co-existing with European starlings, mountain bluebirds and tree swallows delay breeding by 1 and 2 weeks, respectively, and are relatively weak competitors (Koch et al. 2012). Large-bodied species used cavities across a wider range of age classes (American kestrel, northern saw-whet owl, American red squirrel), or showed peak use of mid-aged cavities (bufflehead), likely in response to gradual increases in cavity volume with age (Bortolotti 1994, Edworthy and Martin 2014).

Cavity decay and persistence are linked to formation agent, tree species, and initial decay class of the cavity tree (Edworthy et al. 2012). Northern flickers excavate cavities that are used by a large proportion of the community (Martin et al. 2004, Cockle and Martin 2015). Flicker cavities had among the highest occupancy across their lifespan, in part because their large size can accommodate most cavity-using vertebrates in our system. Additionally, flickers excavate cavities close to edges, which makes their cavities attractive to edge-associated species (e.g., tree swallows, mountain bluebirds), contrasting with pileated woodpeckers, which also excavate large cavities but farther inside the forest (Martin et al. 2004). Although occupancy of cavities created by most formation agents declined with age, occupancy of red-naped sapsucker cavities increased from ages 7 to $\geq$18 years. Sapsuckers excavate medium-sized cavities, usually in live trees (Martin et al. 2004); after 1–2 decades, the cavity volume will have expanded considerably, but the tree supporting the cavity is still quite robust (Edworthy and Martin 2014), perhaps increasing the value of the cavity to non-excavators. Occupancy of cavities excavated by weak, small-bodied excavators declined most rapidly, suggesting that these cavities decline in quality with age more rapidly than cavities excavated by larger and stronger excavators, or are predominately used by species that select for young cavities. During a mountain pine beetle (*Dendroctonus ponderosae*) outbreak at our study area, downy woodpecker and red-breasted nuthatch populations increased, generating a supply of fresh cavities that resulted in increased abundance of species relying on small cavities, confirming that a fresh supply of cavities is important for these species (Norris and Martin 2010).

Consistent with earlier findings from this system (Aitken et al. 2002), we found that cavities in aspen trees were used across their lifespans. Additionally, cavities of all decay classes were occupied across their lifespans; however, cavities formed in living trees have greater persistence in many forests (Cockle et al. 2017), with median lifespans of 15 years in our study area (vs. 7–9 years for cavities in dead and decaying trees; Edworthy et al. 2012). Altogether, the abundance, long lifespan, and consistent occupancy of cavities in living aspen trees makes them a central resource supporting diverse cavity-nesting communities in mixed coniferous-deciduous forests in British Columbia.

MANAGEMENT IMPLICATIONS

We recommend forest habitat management plans that promote diverse and abundant excavator communities to generate a regular supply of new cavities. Our discovery that species occupancy patterns vary with cavity age highlights the additional roles of cavity lifespan, and timing of cavity production, in maintaining the diversity of these communities, especially medium- and large-bodied species, and possibly poor competitors. Harvesting typically results in loss of most existing cavities; however, retention of trees suitable for excavation and existing old cavities, provides a supply of nesting cavities critical for the conservation of cavity-nesting bird and mammal communities. After harvesting, in interior British Columbia, woodpeckers can respond positively to increased insect abundance and edge habitat (Drever and Martin 2010), generating a supply of fresh cavities (Edworthy and Martin 2013). Management plans that retain aspen or other preferred cavity-bearing trees as clusters, including young, healthy trees for future recruitment as cavity-bearing trees, may help maintain a long-term supply of cavities.

Although we focus on use during the breeding season, old and fresh cavities are often used year-round, especially for roosting and storing food. Thus, the value of tree cavities is much greater than we have measured here. Overall, the resiliency of cavity-nesting communities will depend on maintaining excavator abundance and richness, ensuring a supply of suitable trees for future excavation, and developing silvicultural prescriptions that retain existing cavities to provide a diverse age-structured supply of tree cavities for nesting and roosting.

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