



Long-term dynamics of the characteristics of tree cavities used for nesting by vertebrates



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ABSTRACT

Many cavity-nesting vertebrates rely on tree cavities for nesting, and these cavities are often a limiting resource. The availability of tree cavities depends on rates of formation, persistence, and degradation or change in characteristics (e.g., entrance area, chamber volume, level of decay). Understanding how cavity characteristics change over time is key to understanding the value of cavities for wildlife as they age. We measured physical characteristics of 960 tree cavities for up to 17 years (2490 measures of cavity dimensions, involving 23 species of cavity-using vertebrates) to estimate rates of change in cavities in relation to their age, whether they were in living versus dead trees, and their formation agent. We also analyzed the effects of cavity expansion by renovators. Overall, we found that cavity depth increased by 0.35 cm yr^{-1} (1.7%), horizontal depth increased by 0.09 cm yr^{-1} (0.8%), cavity entrance diameter increased by 0.06 cm yr^{-1} (1.2%), and the decay class of the cavity tree advanced by one category every 12.5 years. Cavities in living trees increased in depth by 0.84 cm yr^{-1} versus 0.14 cm yr^{-1} in dead trees; both showed relatively small increases in entrance diameter, with a non-significant trend toward greater increase of entrance diameter in dead trees. Cavities excavated by northern flickers [*Colaptes auratus*] maintained relatively constant dimensions compared with those created by other excavators, although cavity trees selected by northern flickers decayed 3.3 times more rapidly than those selected by strong excavators (hairy woodpeckers [*Picoides villosus*], American three-toed woodpeckers [*Picoides dorsalis*], pileated woodpeckers [*Dryocopus pileatus*], and red-naped sapsuckers [*Sphyrapicus nuchalis*]). Northern flickers were the most frequent renovators with 13.5% of cavities they used renovated from cavities formed by other excavators or decay. Renovations by northern flickers increased cavity depth by a mean of $16.5 \pm 11.8 \text{ cm}$. We show that cavities in living trees significantly increase in cavity volume as they age and likely increase in quality over time, while cavities in dead trees maintain relatively constant dimensions. Thus, retention of living trees as “wildlife trees” is at least as important as retention of dead trees (snags) to support a diverse community of cavity-nesting birds and mammals.

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1. Introduction

Resource characteristics can change dramatically over time, especially in non-consumable, persistent resources like tree cavities. Tree cavities are a multi-annual resource, which can persist for one to several decades, and support complex communities of cavity-nesting birds and mammals (Martin and Eadie, 1999; Edworthy et al., 2012; Wesolowski, 2011, 2012). Tree cavities are formed by excavator species or natural decay, and may be used in subsequent years by secondary cavity-nesting birds, which

require existing cavities in order to breed, but cannot form these cavities. Facultative excavators sometimes excavate and sometimes use existing cavities for nesting and roosting (Norris and Martin, 2012). The availability of suitable cavities limits populations of many secondary cavity-nesting birds (Newton, 1994; Aitken and Martin, 2008; Cockle et al., 2010; Wiebe, 2011). Superficially, cavity availability appears to be determined by rates of formation and loss. However, cavity characteristics, including hole size, location, and quality of the surrounding habitat, influence whether a cavity is usable or not, and requirements vary by species of user (Aitken et al., 2002; Lohmus and Remm, 2004). These characteristics are dynamic temporally as growth and decay of trees and expansion by predators or secondary excavators (renovators) cause changes in cavity dimensions and structure (Aitken et al.,

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2002; Mazgajski, 2003; Blanc and Walters, 2008). As cavities progress through demographic stages (fresh to old), changes in their characteristics may have a strong impact on their quality as a nesting and roosting resource.

A high quality nesting cavity will provide protection from predators, regulate temperature and moisture, and allow enough space for nestlings to develop (Nilsson, 1984; Gauthier and Smith, 1987; Li and Martin, 1991; Wesolowski, 2002). Cavity-nesting birds balance the need to have large enough entrances to accommodate their body size and small enough ones to exclude predators (Cockle et al., 2011). Selecting a deep cavity also reduces predation risk (Sedgwick and Knopf, 1990). To a point, increasing interior width allows greater clutch sizes (Wiebe and Swift, 2001). Finally, the degree of tree decay, or structure of the chamber walls, affects vulnerability to predation, risk of blowdown, and microclimate regulation (Wiebe, 2001; Clement and Castleberry, 2013).

In North America, cavity-nesting vertebrates have a large range of body sizes, including passerine species (6–100 g), squirrels (150–220 g), woodpeckers (20–350 g), raptors (80–700 g), and waterfowl (up to 1800 g; Martin et al., 2004). The differences in cavity characteristics help to partition nest cavities among these diverse groups (Aitken et al., 2002). Even small differences in cavity size results in partitioning of cavity resources among species with similar nesting site niches, such as mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*; Robles and Martin, 2013). Thus, as cavity characteristics change over time, cavities may be used by changing sets of species, before they finally become unusable.

Processes of decay and expansion by excavators (renovations) enlarge cavity dimensions, but other processes, including growth of living trees, decrease cavity dimensions (Wesolowski, 1995; Lucan et al., 2009). Cavities in dead trees have decreased persistence compared with those in living trees, due to blowdown and more rapid decay (Blanc and Martin, 2012; Edworthy et al., 2012). Because excavators select different decay classes of trees (weak excavators select dead and decaying trees, while strong excavators prefer living trees with heart rot), patterns of cavity dynamics may vary across excavators (Blanc and Martin, 2012). Finally, the dynamics of cavities used will reflect both the ways that usable cavities change with time and the selection preferences of the users. In this study we focus mostly on cavities that were occupied (and which we could be certain were usable nest cavities), but we also compare them with a sample of unused cavities (cavities occupied earlier in the study, to ensure they were legitimate cavities, but that were not occupied in the year they were re-measured).

At our field sites in British Columbia, Canada, more than 32 species (30% of forest vertebrates) use tree cavities for nesting (Bunnell and Kramsater, 1990). Cavities are formed primarily in aspen trees (*Populus tremuloides*), but also form in lodgepole pine (*Pinus contorta* var. *latifolia*), hybrid spruce (*Picea engelmannii* x. *glauca*), interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and birch (*Betula* sp.). Most tree cavities in this system last for a median of 7–15+ years, depending on the level of cavity tree decay, and exit the system when either the tree blows down (93% of cavity loss events) or the chamber decays (Edworthy et al., 2012). Here, we focus on the rates of change of cavity characteristics and several factors that influence these rates of change during a 17 year period. Our objectives were to (1) describe the dynamics (rates of change) of cavity characteristics from their initial values, (2) investigate the impact of tree decay and renovators on cavity characteristics, (3) determine whether rates of change vary across the excavators that formed the cavity, and (4) assess the patterns of change in used versus unused cavities.

2. Material and methods

2.1. Study sites

We studied change in tree cavity characteristics at 27 field sites (7–32 ha), within 40 km of William's Lake, British Columbia, Canada (51°52'N, 122°21'W). Sites included aspen groves surrounded by grasslands and shallow ponds and continuous mixed-wood forests. Aspen groves were dominated by trembling aspen and continuous forests were dominated by lodgepole pine, hybrid spruce, interior Douglas-fir, and birch. We included cavities formed in any of these tree species in this study, but the majority of cavities used were in aspen trees (95%, $n = 914$ of 960 cavities). Additional details on the study sites are given in Martin et al. (2004), Drever and Martin (2010), Edworthy and Martin (2013), and Robles and Martin (2013).

2.2. Field data collection

We located nest cavities and monitored their use, persistence, and characteristics over 17 years (May to July, 1995–2011). Nest cavities were defined as cavities that contained at least one egg or nestling (excluding single dumped eggs). In the year a cavity was initially found, we determined whether it was newly excavated or a pre-existing cavity. We identified newly excavated cavities by directly observing excavations, and also inferred that a cavity was new when we observed a large amount of fresh woodchips at the base of the tree. In some cases woodpeckers expanded or “renovated” existing cavities. We classified cavities as renovated when a cavity that we had discovered in previous years had fresh woodchips at the base. If there were few fresh woodchips and we were uncertain whether the cavity was freshly excavated or renovated, we classified the formation agent as unknown and excluded these cavities from the analysis.

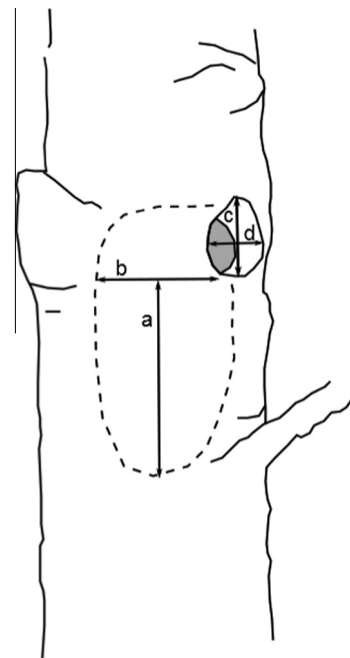


Fig. 1. Dimensions of cavities measured. Vertical cavity depth (a) was measured from the base of the entrance hole to the bottom of the cavity. Horizontal depth (b) was measured from the interior edge of the entrance hole, horizontally to the back of the cavity. Entrance diameter was measured at the maximum height (c) and width (d) of the cavity.

We measured cavity characteristics including interior vertical and horizontal depths, height and width of the entrance area, and tree decay class for cavities up to 6 m high (Fig. 1). We took the mean of height and width of the cavity entrance to create a single mean diameter value (cm). Decay classes were defined as (1) alive and healthy, (2) alive with signs of fungal, insect, or mechanical decay, (3) recently dead with major and minor branches intact, (4) dead with major branches, possible broken top, hard wood, (5) dead with remnants of major branches, broken top, spongy wood, and (6) dead with a broken top, no branches, and soft portions of wood (Thomas et al., 1979; Martin et al., 2004). Cavities were re-measured at the end of the breeding season (mid to late July) in each year that they were used for nesting. In almost all cases, nesting effort was completed before we took the measurements. In 2009 we also re-measured all cavities that had been used earlier in the study but were unoccupied in the present year and in trees that were still standing.

2.3. Data analysis

The year a cavity was excavated was designated as age = 1. For cavities that were found after the year of excavation, the year they were first found was designated as age = 2. The age of some cavities was uncertain because we found them one or more years after they were excavated, and here we tested for differences in rates of cavity change between known age and minimum age (i.e. where we defined age = 2 at the first year of known use during the study) cavities using linear mixed-effects models (see below). Renovations by northern flickers (*Colaptes auratus*; $n = 22$) were treated as fresh excavations and the change they caused in cavity dimensions was analyzed separately (see below). The amount of change in cavity characteristics was calculated as the difference from the initial value, which removed the effects of initial size. The cavity dimension variables—change in vertical depth, change in horizontal depth, change in mean entrance diameter—are continuous variables. Although decay class is an ordinal measure, the degree of change in decay class with cavity age gives a probability of transitioning through decay classes over time, which we also treated as a continuous variable.

We classified cavities by status of the cavity tree (living versus dead), cavity excavator type (strong, weak, and northern flicker), and occupancy status (used versus unused) on cavity dynamics. Cavity tree status and occupancy status were re-assessed each year a cavity was measured and cavities were allowed to transition annually between these categories (e.g., tree alive to dead). Because excavator guilds and tree status (living versus dead) were correlated (Blanc and Martin, 2012), we constructed separate models to explore patterns in rates of cavity change among excavator guilds (strong, weak, and northern flicker). Excavators were classified by excavator strength into (1) strong (red-naped sapsucker [*Sphyrapicus nuchalis*], hairy woodpecker [*Picoides villosus*], American three-toed woodpecker [*Picoides dorsalis*], black-backed woodpecker [*Picoides arcticus*], pileated woodpecker [*Dryocopus pileatus*]), (2) weak (red-breasted nuthatch [*Sitta canadensis*], black-capped chickadee [*Parus atricapillus*], downy woodpecker [*Picoides pubescens*]), and (3) northern flicker, a moderate-strength excavator that often reuses existing cavities or avoids excavating through living sapwood by excavating in dead trees or renovating existing cavities (61% in dead trees or renovated, $n = 230/377$ nests).

To determine the overall change in the average cavity dimensions at our sites we first fit linear mixed-effects models estimating the change from initial value for each cavity dimension as a function of cavity age, with cavity ID as a random factor to account for repeated measures of individual cavities across years. We tested for non-linear effects by including a quadratic term (age^2) in our

models of change in cavity characteristics, but this term was non-significant in all models (all $p > 0.28$, Fig. 2). To explore factors influencing rates of change in cavity dimensions we constructed more complex linear mixed-effects models of cavity dimensions which included fixed effects of age as well as categorical variables describing (1) cavity tree status (living versus dead), (2) cavity occupancy status (used versus unused), (3) whether we knew the age of a cavity or not, and two-way interactions of age with each categorical variable. Cavity ID was included as a random effect. Whether we knew the exact age of a cavity or not did not affect rates of change of cavity characteristics (all $F < 3.21$, $p > 0.074$), except for tree decay ($F = 21.07$, $p < 0.001$), so we only included cavities of known age in the final models of tree decay. In an earlier analysis we also found similar survivorship of known and minimum age cavities (Edworthy et al., 2012). For all models, we used ANOVA F -tests to determine the significance of fixed effects in our models, and t -tests to determine whether differences among factor levels were significant.

To determine the impact of renovators on cavity characteristics, we calculated the differences in interior dimensions and entrance diameter before and after renovation. Northern flickers were the only renovators with a sufficient sample size (cavities measured before and after renovation) for this analysis. All analyses were done using the statistical program R, including the “nlme” package for linear mixed-effects models (R Core Team, 2013; Pinheiro et al., 2014).

3. Results

We collected repeated measures of characteristics of 960 cavities in years when they were used as nest sites, for up to 2490 measurements of cavity characteristics across the study (see Table 1 for distribution of sampling across cavity age classes). Cavities were measured between 1 and 17 times (mean = 2.7). Most cavities (95% or 914 cavities) were in aspen trees, 26 were in lodgepole

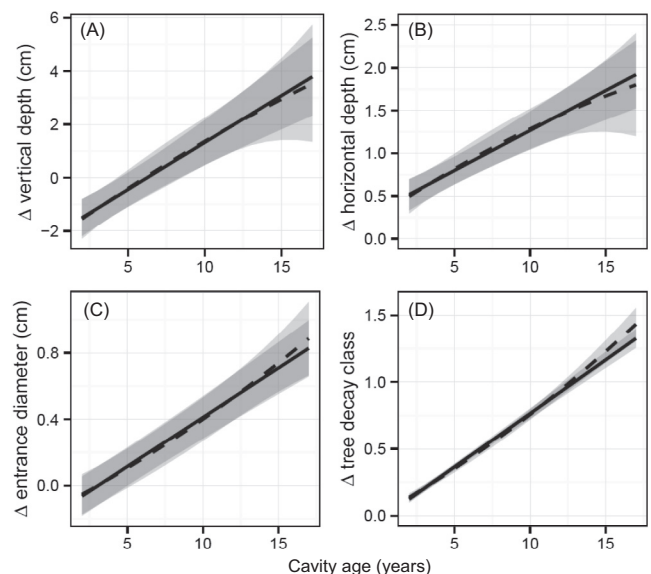


Fig. 2. Change in cavity characteristics relative to their initial dimensions (year = 1) for vertical depth (A), horizontal depth (B), mean entrance diameter (C), and tree decay class (D) of cavities used for nesting in interior British Columbia, Canada (1995–2011). The majority of cavities were in trembling aspen (95%), and the rest were in lodgepole pine, interior Douglas fir, hybrid spruce, and birch. Solid lines represent the results of linear mixed-effects regression models with age as the fixed effect and cavity ID as a random effect. Dashed lines represent models with an added quadratic term (age^2), and shaded regions represent standard errors. All cavity characteristics increased significantly with cavity age ($p < 0.002$).

Table 1

Sample sizes of cavity characteristic measures across cavity age. See Section 2.2 for a description of the variables.

Cavity age	Vertical depth (n)	Horizontal depth (n)	Mean entrance diameter (n)	Decay class (n)
1	241	269	280	333
2	162	180	184	249
3	113	135	143	182
4	102	115	121	146
5	83	94	101	125
6	69	79	81	108
7	56	66	68	87
8	43	48	48	63
9	40	45	45	51
10	22	25	25	41
11	26	29	29	40
12	17	22	23	23
13	14	16	17	19
14	12	15	15	16
15	6	6	6	6
16	5	6	6	6
Total	1011	1150	1192	1495

pine, 16 were in Douglas-fir, 3 were in spruce, and 1 was in birch. For used cavities, we recorded 2490 repeated measures of decay stage, 1495 of which were for cavities of known age. We recorded 1011–1192 repeated measures of cavity dimensions. Tree decay stages were available for all cavity trees, but we only obtained cavity dimension measures for cavities 6 m or less above the ground and we were unable to take vertical depth measures for the 150 cavities that contained active nests at the time of measurement. In 2009 we re-measured an additional 94 cavities that were used for nesting earlier in the study, but were subsequently unused. Initial cavity dimensions did not differ between living and dead cavity trees, except for strong excavators having deeper cavities in live trees (Table 2). Cavity dimensions were altered by decay from fungus and insects over time, by renovating species (including northern flickers, red squirrels, red-naped sapsuckers, and red-breasted nuthatches), by secondary cavity users, and by sapwood growth in living trees.

Overall vertical depth increased by 0.35 ± 0.11 cm yr⁻¹ (\pm SE) ($F = 11.00$, $p = 0.001$), horizontal depth increased by 0.09 ± 0.03 cm yr⁻¹ ($F = 3.18$, $p = 0.002$), mean entrance diameter increased by 0.06 ± 0.01 cm yr⁻¹ ($F = 35.66$, $p < 0.001$), and mean tree decay class advanced by one decay class every 12.5 years (Fig. 2). In living trees, vertical cavity depth increased by nearly 1 cm yr⁻¹ (0.84 ± 0.18 cm or 3.6% yr⁻¹), compared with a

significantly slower rate of increase for cavities in dead trees (0.14 ± 0.27 cm yr⁻¹, difference = 0.70 cm yr⁻¹, $t = 3.80$, $p < 0.001$; Fig. 3A). Horizontal depth in live trees increased by 0.14 ± 0.05 cm yr⁻¹, but did not differ significantly from rate of change of horizontal depth in dead trees (0.11 ± 0.07 cm yr⁻¹, $t = 0.46$, $p = 0.640$; Fig. 3B). Mean entrance diameter showed modest rates of increase in both live and dead trees and did not differ significantly between live and dead trees (Fig. 3C; difference = 0.02 ± 0.03 cm yr⁻¹, $t = 0.70$, $p = 0.483$).

Excavator group (strong, northern flicker, weak) was not a significant predictor of rate of change of vertical depth ($F = 0.65$, $p = 0.522$), horizontal depth ($F = 1.27$, $p = 0.282$), or entrance diameter ($F = 0.34$, $p = 0.715$); however, there was a consistent trend toward the greatest expansion occurring in cavities formed by weak excavators, followed by cavities formed by strong excavators, and cavities formed by northern flickers were the most stable in their dimensions (Fig. 4A–C). Cavities excavated by strong excavators showed an immediate decrease in depth (4.2 ± 1.6 cm) in the first year after excavation, likely due to addition of nest material by secondary users (Fig. 4A). Excavator group was a significant predictor of rate of progression through cavity tree decay classes ($F = 18.23$, $p < 0.001$). In contrast to their slow rates of change in cavity dimensions, northern flicker cavities advanced most rapidly through decay classes, at a rate of 0.19 ± 0.02 classes per year, which was 0.14 ± 0.03 classes yr⁻¹ more than cavity trees selected by strong excavators ($t = -5.44$, $p < 0.001$). Weak excavators advanced by 0.10 ± 0.02 decay classes yr⁻¹ more rapidly than strong excavators ($t = 4.42$, $p < 0.001$), but rate of change of decay class did not differ significantly among northern flicker and weak excavators ($t = -1.25$, $p = 0.211$; Fig. 4). Finally, unoccupied cavities showed more rapid increase in entrance diameter than cavities that were occupied (0.11 ± 0.03 cm yr⁻¹, $t = -2.75$, $p = 0.006$). Occupied cavities had a very small, but significant increase in rate of change of decay class compared with unoccupied cavities (0.05 ± 0.02 classes yr⁻¹, $t = 2.67$, $p = 0.008$). Differences between occupied and unoccupied cavities in vertical and horizontal depth were not significant ($t = 1.09$, $p = 0.276$, and $t = 1.22$, $p = 0.221$, respectively; Fig. 5).

Northern flickers were the most frequent renovators; renovating 80 of 424 (13.5%) of the cavities they used. These included cavities in living (74%) and dead (26%) trees, initially excavated by red-naped sapsuckers, hairy woodpeckers, northern flickers, American three-toed woodpeckers, red-breasted nuthatches, or formed by decay. Other renovators included red-breasted nuthatches (8), red-naped sapsuckers (4), and one each for black-capped

Table 2

Initial values of cavity dimensions (in freshly excavated cavities, year = 1, or minimum age cavities, year = 2) across excavator groups (strong, northern flicker, weak) and living versus dead cavity trees. Differences between initial characteristics of living and dead trees were assessed using Student's *t*-tests, and bold font denotes significance ($p < 0.05$).

Cavity dimension	Excavator group	Cavity tree status		<i>t</i>	<i>p</i>
		Mean ± SE (<i>n</i>)			
		Alive	Dead		
Vertical depth (cm)	Strong	19.5 ± 0.4 (217)	17.5 ± 0.7 (89)	2.54	0.01
	Northern flicker	28.6 ± 1.6 (91)	30.8 ± 1.3 (116)	−1.08	0.28
	Weak	12.7 ± 0.8 (26)	13.3 ± 0.4 (95)	−0.65	0.52
	All excavators	20.8 ± 0.6 (457)	20.2 ± 0.6 (475)	0.72	0.47
Horizontal depth (cm)	Strong	10.8 ± 0.2 (234)	10.8 ± 0.3 (92)	0.00	1.00
	Northern flicker	15.1 ± 0.4 (93)	14.4 ± 0.3 (122)	1.29	0.20
	Weak	7.6 ± 0.5 (30)	7.2 ± 0.2 (107)	0.76	0.45
	All excavators	11.4 ± 0.2 (488)	10.9 ± 0.3 (504)	1.56	0.12
Mean entrance diameter (cm)	Strong	4.5 ± 0.1 (241)	4.3 ± 0.1 (93)	1.52	0.13
	Northern flicker	6.8 ± 0.3 (94)	7.0 ± 0.2 (122)	−0.58	0.56
	Weak	3.5 ± 0.1 (30)	3.4 ± 0.1 (111)	0.62	0.53
	All excavators	4.9 ± 0.3 (500)	5.2 ± 0.9 (516)	−1.89	0.06

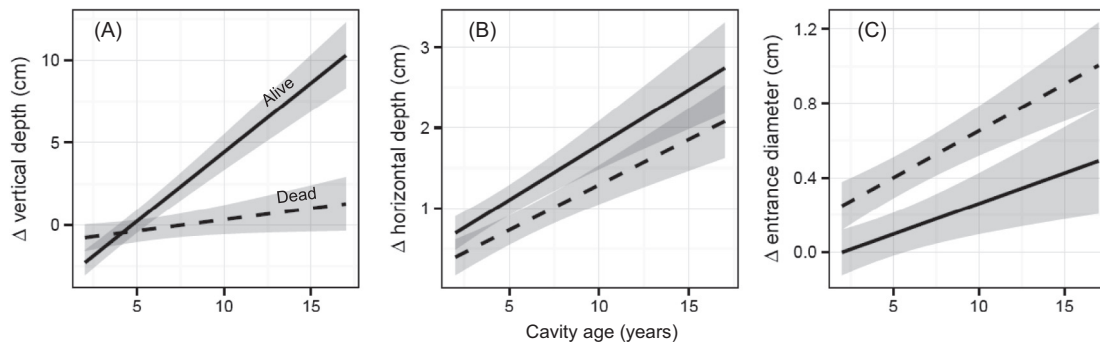


Fig. 3. Change in cavity characteristics relative to their initial dimensions (year = 1) for vertical depth (A), horizontal depth (B), and mean entrance diameter (C) of cavities used for nesting in living versus dead trees in British Columbia, Canada (1995–2011). Solid black lines represent rates of change of cavities in living trees ($n = 243$ cavities, 675 repeated measures) and dashed represents cavities in dead trees ($n = 280$ cavities, 740 repeated measures).

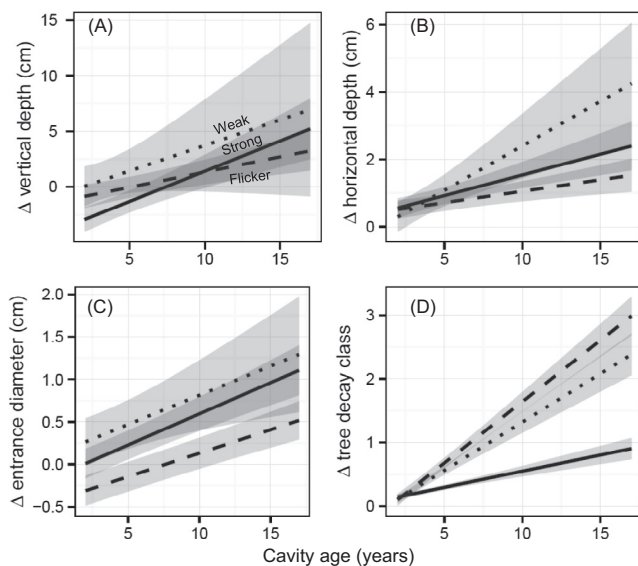


Fig. 4. Change in cavity characteristics relative to their initial dimensions (year = 1) for vertical depth (A), horizontal depth (B), mean entrance diameter (C), and decay class (D) across nesting cavities formed by three excavator groups (black solid = strong, dashed = northern flicker, dotted = weak) in British Columbia, Canada (1995–2011). Strong excavators included red-naped sapsucker, hairy woodpecker, American three-toed woodpecker, and pileated woodpecker ($n = 131$ cavities, 520 repeated measures); northern flickers were a moderate strength excavator ($n = 231$ cavities, 507 repeated measures); and weak excavators included red-breasted nuthatch, downy woodpecker, and black-capped chickadee ($n = 242$ cavities, repeated measures).

chickadee, black-backed woodpecker, downy woodpecker, and pileated woodpecker. We were able to access by ladder and measure changes in cavity characteristics for 22 renovations by northern flickers and less than 2 each for all other species. In the year of their renovation, northern flickers increased vertical depth by 16.5 ± 2.7 cm, horizontal depth by 3.1 ± 0.5 cm, and entrance diameter by 1.5 ± 0.4 cm (Fig. 6).

4. Discussion

Tree cavities are dynamic multi-annual resources that increase in interior depth, interior width, entrance diameter, and level of tree decay with age. Despite their long life spans and importance as nesting resources, this is the first study to monitor long-term changes in tree cavity characteristics for the cavity-using vertebrate community. These changes in cavity characteristics affect

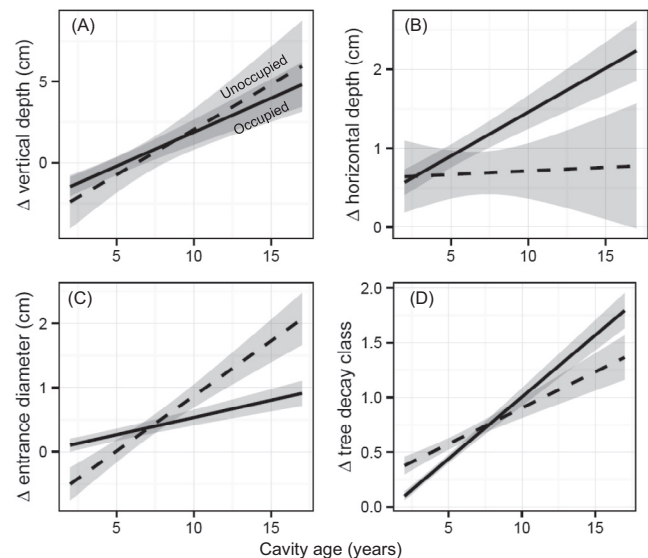


Fig. 5. Change in cavity characteristics relative to their initial dimensions (year = 1) for vertical depth (A), horizontal depth (B), mean entrance diameter (C), and tree decay class (D) for occupied (used for nesting) versus unoccupied cavities in British Columbia, Canada (1995–2011). Black lines represent rates of change of occupied cavities ($n = 429$ cavities, 1495 repeated measures, see methods for explanation of sampling variation) and grey lines represent unoccupied cavities ($n = 94$ cavities, 94 repeated measures).

the quality and availability of useable nesting and roosting sites over time. In systems where tree cavities are a limiting resource, the dynamics of cavity characteristics will affect the abundance and community composition of cavity-using birds and mammals. Additionally, species preferences will determine the quality of the supply of cavities, and changes in cavity dimensions have important implications for secondary cavity users (Robles and Martin, 2013, 2014). While forest management practices for conservation of cavity-nesting vertebrates often focus on retention of dead trees (snags), we found that cavities in living trees likely increase in quality over time as they experience a gradual increase in cavity volume, thus offering suitable cavities for an increasing range of species as they age, while cavities in dead trees showed relatively little change in dimensions.

Cavities in living trees likely provide high quality resources over many years, compared with cavities in dead trees. Fresh cavities in live trees have the protection of robust entrances and chamber

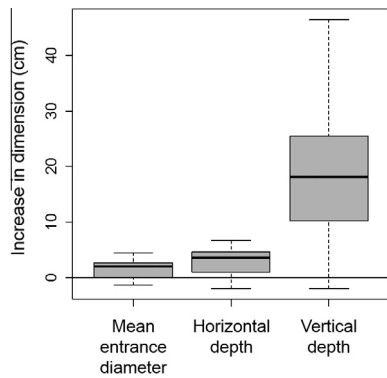


Fig. 6. Effects of renovations by northern flickers ($n = 22$) on mean entrance diameter, horizontal depth, and vertical depth of tree cavities in British Columbia, Canada. Boxplots show the median (solid line), quantiles (boxes), and inter-quantile ranges (whiskers).

walls, and may harbor fewer parasites, but are relatively more shallow and provide less space for growing nestlings than older cavities. Older cavities are protected by greater chamber depth and provide more space for nestlings to develop. But over their full lifespans, cavities in living trees likely provide the most valuable nesting resources. Cavities in living trees had the greatest increase in chamber depth, while their mean entrance diameter changed little. Cavities in live trees also persist longer before the tree falls down or the chamber decays (>15 years versus 7–9 years for cavities in dead trees; Edworthy et al., 2012).

The strong difference in increased vertical depth of cavities in living compared to dead trees was not anticipated, and we have not determined the processes driving the strong increases in vertical depth of cavities in living trees. However, we suggest that during the lifetime of cavities in living trees, decay is occurring mostly at the cavity level (internal heart rot), while decay for cavities in dead trees occurs primarily at the tree level (more external). In aspen trees, which contained the majority of cavities in our system (95%), heart rot infects living trees and expands from the point of entry, followed by active decay by insects such as carpenter ants (*Camponotus herculeanus*; Basham, 1958). McCoomb and Noble (1981) found greater insect abundance in cavities in living trees compared to dead trees, which may accelerate decay of these cavities. Additionally, Daily (1993) found that red-naped sapsuckers select nesting sites at the highest point affected by heart rot decay, which often enters at the roots and spreads upward (Shigo, 1965). Thus, these fresh cavities freshly excavated in living trees are in the relatively early stages of decay, and tree decay may progress more rapidly after cavity excavation.

Chamber dimensions may also increase when woodpeckers reuse cavities and generate fresh woodchips from the chamber walls, which will contribute to increasing chamber dimensions, especially horizontal depth. However, the effect of woodpeckers in driving the greater expansion of cavities in living trees in comparison to cavities in dead trees is likely small, as rates of change in occupied versus unoccupied cavities did not differ. In many systems globally, natural tree hollows formed in living trees are a major source of nest cavities, and the mechanisms behind cavity formation and expansion in living trees warrant further study (e.g., Cockle et al., 2012).

Because strong excavators select nest sites in living trees and northern flickers more often (61%) excavate in dead trees or renovate an existing cavity, the dynamics of living versus dead trees are reflected across these excavator groups. Cavities formed by both weak and strong excavators showed non-significant trends toward greater increase in vertical and horizontal depth than those created by northern flickers. As well, cavities formed by strong excavators

advanced through decay stages significantly slower than those formed by weak excavators or northern flickers. As a result, cavities created by strong excavators may retain their ability to regulate temperature and humidity longer, and are more resistant to blow-down than cavities created by weaker excavators (Wiebe, 2001; Edworthy et al., 2012; Maziarz and Wesolowski, 2013). These results provide further evidence that cavities created by strong excavators are high quality resources, throughout their longer lifespans, whereas flicker cavities provide abundant, but consistently poorer quality nesting resources.

Most of our cavity-measures were taken in years when the cavities were used for nesting, but we also re-measured a sample of 94 unused cavities to help evaluate the relationship of selection by secondary users with dynamics of cavity characteristics. Entrance diameter expanded more rapidly in unoccupied cavities than in occupied cavities, indicating that secondary cavity nesters selected cavities which maintained relatively small entrance diameters. We did not detect differences in change in vertical and horizontal cavity depth between occupied versus unoccupied cavities, but the non-significant trend toward increased horizontal depth in occupied cavities may reflect selection by secondary users for larger chamber volume (Aitken and Martin, 2004).

The most dramatic changes in cavity dimensions occur when cavities are renovated. Rather than starting a fresh cavity, excavators may expand an existing cavity, originally created by a smaller species. At our sites, renovations were relatively infrequent (1.9% of nests, and 4.8% of all cavities used by excavators were renovated). However, in some systems renovations over several years play an important role in generating new cavities for some large species, but can also reduce the availability of cavities for some species. In south-eastern USA, red-cockaded woodpeckers (*Picoides borealis*) excavate cavities in living pine trees and it can take them up to a decade to complete a cavity (Conner and Rudolph, 1995). Further renovation of these cavities by northern flickers and pileated woodpeckers causes a major problem for the red-cockaded woodpeckers in living longleaf (*Pinus palustris*) and loblolly pine (*Pinus taeda*) systems where cavity availability is limited and predation by snakes is a major limiting factor unless there is resin flowing around the cavity entrance (Saenz et al., 1998; Blanc and Walters, 2008).

5. Conclusions

Just as the demographic stages of trees, including saplings, mature trees, and dying and dead trees, increase complexity and biodiversity in forests, aging in tree cavities also increases the complexity of available tree cavity resources, providing a greater range of nesting resources for different species (Drapeau et al., 2009). In harvested landscapes, retaining cavities across the demographic spectrum of fresh and older cavities, especially in living trees, will help to maintain a greater range of cavity availability and conditions and support a diverse community of cavity-using vertebrates. Further research into the sequence of users as cavities change with age is needed in order to understand how changes in cavity characteristics and quality affect the composition of cavity-nesting communities.

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