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Survival analysis of a critical resource for cavity-nesting communities: patterns of tree cavity longevity

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Abstract. Tree cavities are a vital multi-annual resource used by cavity-nesting birds and mammals for nesting and shelter. The abundance of this resource will be influenced by the rates at which cavities are created and destroyed. We applied the demographic concepts of survival and longevity to populations of tree holes to investigate rates of loss for cavities in three tree species, as well as how characteristics of nest trees, habitat type, and species of excavator affected the persistence of tree cavities in trembling aspen, *Populus tremuloides* (95% of cavities were in aspen trees), in interior British Columbia, Canada. By modeling survival of 1635 nesting cavities in aspen over a time span of 16 years, we found that the decay stage of the nest tree was the most important factor determining cavity longevity. Cavities in trees with advanced decay had a relatively short median longevity of 7 years (95% CI 6–9 years), whereas those in living trees had a median longevity of more than 15 years. We found that cavity longevity was greater in continuous forest than in aspen grove habitat. Interestingly, cavities formed by weak excavators survived as long as those created by Northern Flickers (*Colaptes auratus*), despite occurring in more decayed tree stems. Thus, weak excavators may be selecting for characteristics that make a tree persistent, such as a broken top. Our results indicate that retention of cavities in large, live aspen trees is necessary to conserve persistent cavities, and that cavity longevity will have a large effect on the structure and function of cavity-using vertebrate communities.

Key words: cavity-nesting birds; Colaptes auratus; *forest management; keystone species; nesting resources; Northern Flicker;* Populus tremuloides; *tree cavities; trembling aspen; Williams Lake, central British Columbia, Canada; woodpeckers.*

Introduction

Structural elements of habitat, or nonconsumable, resources can have an important role in how biological communities function (Dennis 2004). In some ecosystems, a single type of structure (e.g., coarse woody debris, tree cavities, snowpack) can have a disproportionate impact on species diversity (Tews et al. 2004). Hence, it is important to understand how these structural elements are maintained and what factors determine their abundance and characteristics. Cavity-nesting communities are excellent systems in which to examine the dynamics of a structural resource because numerous bird, mammal, and insect species could not breed without access to tree cavities for nesting. Cavity availability can limit nest density and probably population size for many species of cavity-nesting vertebrates (Newton 1994, Aitken and Martin 2008, Cockle et al. 2010). In interior British Columbia, more than 40 species, or ~30% of forest vertebrates, use tree holes (Bunnell and Kremsater 1990). Thus, cavity availability and quality potentially have a strong influence on the structure and function of cavity-dependent communities (Martin and Eadie 1999, Aitken and Martin 2008).

Cavities are formed either by excavators such as woodpeckers or by natural decay processes, such as branch fall followed by fungal and insect decay, and they may be reused for many years in sequence (Sedgwick 1997, Aitken et al. 2002, Aitken and Martin 2007). Although most primary excavators prefer to excavate a fresh cavity each year (90–98% for five of the six primary excavators at our sites), Northern Flickers frequently reuse existing cavities (84% at our sites) and secondary cavity-nesters rely on existing cavities for nesting; one cavity at our sites was reused 17 times during its 13-year life span (L. Blanc and K. Martin, *unpublished data*). Eventually, cavities are lost from the system when trees fall over or break below the cavity, when cavity walls or floors decay (chamber decay), or when cavity entrances closer over or collapse. A stable supply of tree holes in forest communities requires a balance in the rate of cavity creation with the rate of

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cavity loss (Sedgwick and Knopf 2002, Cockle et al. 2011*a*). To understand the density of existing tree holes and to predict future trends in cavity abundance, it is useful to apply the demographic concepts of survival and longevity to populations of tree cavities. Here, we use the terms survival and longevity to refer to tree cavities that are in standing trees and stems such that they could be used for nesting or roosting by vertebrates.

Despite the critical role cavity persistence plays in the cavity supply, few studies have tracked the persistence of nest cavities to determine survival in relation to nest tree or stand characteristics over time. Because tree blowdown seems to be the main cause of cavity disappearance (e.g., Sedgwick and Knopf 2002), we predicted that cavities in the stems of large, living aspen trees would survive longest in the system, whereas cavities located in trees closer to forest edges would be more susceptible to destruction or breakage from the wind. A previous study of cavity longevity in mountain ash forests of Australia found that cavities were most persistent when they were in large-diameter, less-decayed trees (Lindenmayer and Wood 2010). Studies that investigate the survival of live and dead trees, regardless of whether they support cavities, consistently find relationships with decay stage and tree diameter in a variety of forest systems (Raphael and Morrison 1987, Lee 1998, Russell et al. 2006, Lindenmayer and Wood 2010, Cockle et al. 2011*a*). However, these studies of tree survival do not directly address the survival of nesting cavities and do not take into account sources of cavity loss in standing trees (chamber decay and healing over). Cavities are often excavated in live trees: 55% in interior British Columbia (Martin et al. 2004) and 100% by Red-cockaded Woodpeckers in Florida (Harding and Walters 2002), and the dynamics of these trees are not accurately reflected in studies of dead tree fall-down rates. Additionally, most of these studies have been too short (e.g., <10 years) to track most cavities throughout their entire life spans.

The longevity of tree cavities may also influence the availability of cavities in different forest types or in different size classes created by different excavators. Forest types are defined by factors including tree species composition, climate, disturbance regimes, and topography, all of which may affect cavity longevity and contribute to the strong differences found in cavity abundance among forest types (Aitken and Martin 2008, Koch et al. 2008). We also expect to find patterns in cavity longevity across excavator species; excavators are known to prefer different sizes and decay states of trees, with smaller, weaker excavators selecting smaller trees with more advanced decay (Martin et al. 2004, Wesolowski 2011). If weaker excavators select nest tree characteristics that result in high risk of degradation, their cavities may be more ephemeral than those of stronger excavators. Such differences in cavity longevity across excavators potentially impact cavity availability for secondary cavity-nesters (species that cannot create their own cavities), which often selectively use holes created by a particular species of excavator (Martin et al. 2004).

Here, our goal was to assess rates of cavity loss in three tree species and to model factors influencing cavity persistence in trembling aspen (*Populus tremuloides*), the tree species that contains 95% of all active cavity nests found in interior British Columbia (Aitken and Martin 2007). We also tested whether cavity persistence varied across two habitat types (aspen in isolated groves in a grassland matrix and aspen in continuous mixed forests), and whether the cavities formed by three major excavating groups (strong excavators, Northern Flickers, and weak excavators) differed in persistence. We used failure-time analysis techniques to track survival of individual cavities over time for an entire cavity-nesting community to evaluate these questions.

METHODS

Study sites

We monitored the fates of 1714 tree cavities during 16 years (1995–2010) on 27 study sites and the surrounding area within 50 km of Williams Lake (51°51′ N, 122°21′ W) in central British Columbia, Canada (Wiebe and Swift 2001, Martin et al. 2004). The study included two forest types: continuous mixed forest and aspen groves. Continuous forest sites were dominated by lodgepole pine (*Pinus contorta*; 42% of trees) and Douglas-fir (*Pseudotsuga menziesii*; 28%) and contained hybrid white spruce (*Picea engelmannii* × *glauca*; 18%) and aspen (12%). Aspen groves contained 54% aspen, 38% lodgepole pine, and 9% Douglas-fir, and were surrounded by grasslands and shallow ponds. Continuous coniferous forest patches ranged from 8 to 32 ha, whereas aspen groves on the grassland ranged from ~0.2 to 5 ha. All sites were warm and dry, as is characteristic of the interior Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991). A few of the continuous patches were subjected to selective harvesting, and on these plots we only used the survival data until cutting occurred to model cavity persistence in unmanaged forest types. Additional study area details are given in Martin and Eadie (1999), Aitken et al. (2002), and Martin et al. (2004).

Eight excavating species were common on our sites: Pileated Woodpecker (*Drycopus pileatus*), Red-naped Sapsucker (*Sphyrapicus nuchalis*), American Three-toed Woodpecker (*Picoides dorsalis*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), Downy Woodpecker (*Picoides pubescens*), Red-breasted Nuthatch (*Sitta canadensis*), and Black-capped Chickadee (*Poecile atricapillus*). Cavity formation agents were grouped into four categories: (1) strong excavators that prefer living trees, but most often excavate in parts of the tree with fungal infection (i.e., Pileated Woodpecker, Red-naped Sapsucker, American Three-toed, Hairy Woodpecker); (2) Northern Flickers, strong excavators that use a range of decay classes including many dead stems, and, given their abundance and cavity type, are considered keystone excavators in our system (Martin et al. 2004); (3) smaller, weak excavators that typically use decayed, soft wood (Downy Woodpecker, Red-breasted Nuthatch, Black-capped Chickadee); and (4) cavities formed naturally through decay, which were found predominantly in live, unhealthy trees and recently dead trees.

Cavity location and monitoring

From May to July, 1995–2010, we systematically searched our sites for nests in tree cavities by listening for fresh excavations and following birds, and we checked all cavities occupied in previous years to determine if the trees were still standing and if the cavities were usable. We considered a cavity freshly excavated if we observed a bird excavating or found many fresh wood chips at the base of the nest tree. Cavity interiors up to 5.2 m high were visually inspected for nest suitability and nesting status using mirrors, and flashlights; from 2005 on, cavities up to 15 m high were inspected using a video camera system on an extendable pole (TreeTop Peeper, Sandpiper Systems, Manteca, California, USA). Inaccessible cavities were checked by observers tapping or scratching at the base of the tree and watching for activity. When a cavity was first occupied (containing at least one egg or nestling), we considered it a suitable nest cavity and continued to monitor it in subsequent years until it was destroyed. A cavity was considered destroyed in three cases: (1) the cavity tree fell or broke off below the cavity; (2) the cavity entrance grew over; (3) the chamber decayed or was ripped apart by predators. All cavity loss that was caused by human activity, including firewood cutting, timber harvest, and prescribed burning, was censored in the analysis. Additionally, cavities that still existed when we stopped monitoring a site or during the last season of the study (2010) were censored. Thus, we could determine the year the cavity was first excavated (new, known age) or first found occupied (minimum age) and its subsequent survival.

We found 798 cavities in the year they were first excavated (fresh), but we also found 837 cavities that had been excavated in an earlier year (minimum age). A preliminary analysis showed that the survival for cavities found freshly excavated was nearly identical to that for cavities found as reused holes (likelihood ratio test = 0.2, df = 1, $P = 0.66$; Fig. 1). Because the life spans of known-age and minimum-age cavities did not differ statistically (probably because we found cavities within the first few years after they were created), we used year of first occupancy as the start date for subsequent analyses of all cavities pooled ($n = 1635$). An earlier study calculated overall cavity life span using some of these data for a shorter time series on a subset of the study area than are included here (818 cavities over 13 years; Cockle et al. 2011*a*).

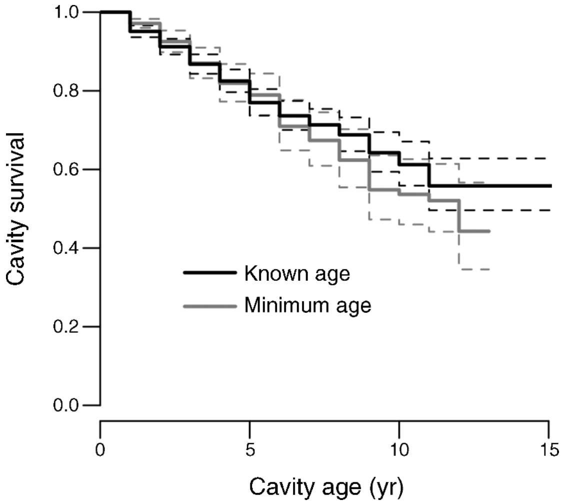

FIG. 1. Kaplan-Meier survival curves (solid lines) and 95% confidence intervals (dashed lines) for aspen (*Populus tremuloides*) tree cavities in central British Columbia. Black lines represent cavities of known age (found freshly excavated, $n = 798$ cavities), and gray lines represent cavities for which the excavation date is unknown (found used; age is a minimum estimate, $n = 837$ cavities).

Cavity characteristic measurements

We measured survival in relation to cavity characteristics including dbh (diameter at breast height, 1.3 m) of the cavity tree, its distance to the nearest open edge, and tree condition. Tree condition was classified as decay class 1 (live healthy), 2 (live unhealthy), 3 (recently dead), or 4–8 (progressively softened and decayed snags) (Backhouse and Louiser 1991). All nest trees were in decay classes 1 through 6 (Fig. 2). For the analyses, we grouped decay classes 1 and 2 into an "alive" category, decay class 3 was designated "recently dead" (tree stem still hard with all major and minor branches present), and decay classes 4 through 6 were grouped as "dead with advanced decay."

Data analysis

Kaplan-Meier survival estimates were used to quantify median survival rates and to produce survival curves for tree species, excavator groups, and forest types. 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). The general form of a Cox proportional-hazards model is a linear model for the log-hazard (Formula 1), where $h_i(t)$ represents the hazard of loss at time t (cavity age) for an individual cavity (i):

$$\log h_i\,(t) = \alpha + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_k x_{ik}. \tag{1}$$

The constant α is the baseline hazard and the x's are

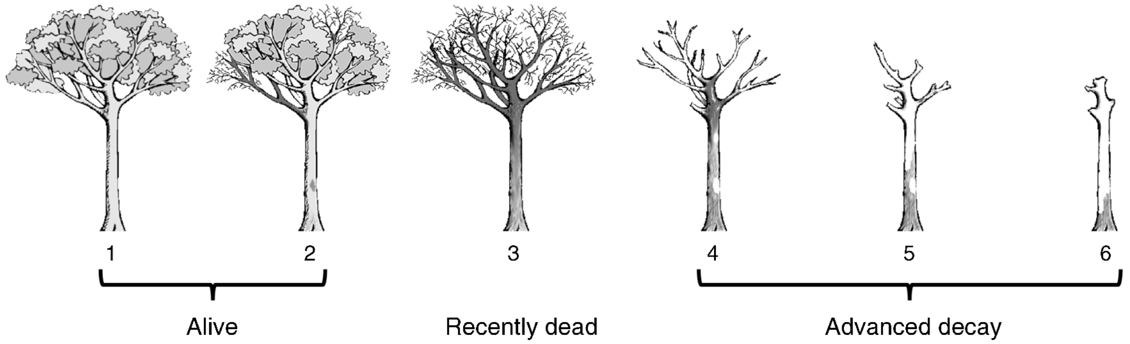

FIG. 2. Aspen decay classes based on Backhouse and Louiser (1991). Our "alive" grouping included decay classes 1 (alive and healthy) and 2 (alive with signs of fungal, insect, or mechanical decay); "recently dead" included decay class 3 (recently dead with major and minor branches intact); and "advanced decay" included decay classes 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).

covariates that modify the baseline hazard. Because Cox proportional-hazards models are semiparametric, we used partial likelihoods in place of full likelihoods for our calculations of AIC values (Cox 1975). Tied cavity loss times were dealt with using the Efron approximation method, which assumes that ties were a result of imprecise measurement (Efron 1977).

To determine which explanatory variables (decay class, dbh, distance to edge) were important predictors of cavity longevity, we used Akaike's Information Criterion (AIC) to rank all possible subsets of a global model that included our three explanatory variables and their two-way interactions (Burnham and Anderson 2002). These interactions were included because the variables were all potentially related to tree stability and may have modified one another's effects. The two continuous variables (dbh, distance to edge) were not intercorrelated ($P = 0.12$). Models that had a ΔAIC value >2 were included in the top model set and were used to produce averaged parameters (Burnham and Anderson 2002). Model-averaged parameters were used to predict probabilities of cavity loss with decay class, diameter, and distance to edge, which are properties of cavity trees that could potentially be managed. After investigating which characteristics of the tree itself were important predictors of longevity, we developed two separate models, which modeled hazard of loss in relation to forest type and excavator species to assess predicted differences in longevity across these groups. Median life spans 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 and Lumley 2009, R Development Core Team 2010).

RESULTS

At our sites, 95.3% of cavities used for nesting were in aspen trees, 2.8% were in lodgepole pine, 1.3% were in Douglas-fir, and 0.5% were in hybrid white spruce. At the 5-year mark, cavities in aspen trees had the highest survival (0.78), followed by cavities in pine trees (0.65; Table 1). After 10 years, aspen tree cavity survival declined to 0.59, while survival of cavities in pine trees did not change. Sample sizes for Douglas-fir and hybrid white spruce were too small to obtain reliable survival rates. Considering all the cavities that were lost from the system naturally ($n = 402$), 90% disappeared when the tree stem blew over or cracked, 7% when the chamber decayed, and 3% when the entrance hole grew shut. The cases in which the entrance hole grew shut were restricted to cavities excavated in living trees. Because the main sources of mortality were blow-over and chamber decay, we next modeled the potential factors affecting these sources of cavity loss (97%) in aspen trees for which we had the largest sample.

Underlying factors for cavity loss due to tree blow-over or stem breakage

Three of the 17 models that we fit to predict hazard of cavity loss received considerable support ($\Delta\text{AIC} < 2$; Table 2). We used these three models to produce an average model that included decay class, dbh, distance to edge, and an interaction of dbh and distance to edge (Table 3). Decay class was the most important variable and had the largest effect sizes, with lower survival rates at more advanced stages of decay (Fig. 3). Live trees were the most persistent and their hazard rates were used as "baseline" rates in comparison to higher decay stages (Table 3). The predicted median longevity for cavities in live trees was >15 years (predicted survival rate after 15 years $= 0.56$; Fig. 3). Cavities in recently dead trees were 2.70 times more likely than live trees to be destroyed in a year, and had a median longevity of 9 years (95% CI $=$ 7–11 years), conditional based on average values of the other variables (Table 3, Fig. 3). Cavities in dead trees with advanced decay were the least persistent, with a risk of loss 3.56 times greater than for cavities in live trees; their median longevity was only 7 years (95% CI $=$ 6–9 years; Table 3, Fig. 3). Investigation of the dbh × distance to edge interaction showed that trees with larger dbh persisted longer than trees

TABLE 1. Survival of cavities in two tree species (trembling aspen, *Populus tremuloides* and lodgepole pine, *Pinus contorta*) in interior British Columbia based on Kaplan-Meier estimates.

Cavity age (yr)	Trembling aspen				Lodgepole pine			
	No. cavities at risk	No. censored	No. lost	Survival rate	No. cavities at risk	No. censored	No. lost	Survival rate
1	1635	605	63	0.96	45	15	2	0.96
2	962	110	41	0.92	28	5	2	0.89
3	811	111	42	0.87	21	4	3	0.76
4	658	96	35	0.82	14	0	1	0.71
5	527	78	31	0.78	13	1	1	0.65
6	418	71	25	0.73	11	4	0	0.65
7	322	60	12	0.70	7	2	0	0.65
8	250	51	12	0.67	5	1	0	0.65
9	187	39	16	0.61	4	0	0	0.65
10	132	25	5	0.59	4	1	0	0.65
11	102	33	7	0.55				
12	62	21	3	0.52				
13	38	27	0	0.52				
14	11	5	0	0.52				
15	6	6	0	0.45				

Notes: Number of cavities at risk represents the number of usable cavities monitored up to a given age; the number of events gives the number of cavities that were lost. Censored cavities were still standing at the end of the study, when we stopped monitoring a site, or were lost through human causes (e.g., prescribed burns, logging).

with smaller dbh when in the interior of the forest, and that there was no effect of dbh at the forest edge (Fig. 4).

Longevity patterns across habitat types and excavator groups

Cavities in aspen groves were in more decayed trees with greater mean dbh and were closer to the edge than those in continuous forest (Table 4). Correspondingly, cavities in aspen groves were at 52% higher risk of loss than those in continuous forest habitat (median life span in aspen groves was 12 years; after 15 years, survival in continuous forest was 0.64; Fig. 5).

All predictors of cavity longevity (decay class, dbh, and distance to edge) differed significantly ($P < 0.001$) across excavators (Table 5). Weak excavators created cavities in dead trees with small diameters and advanced decay (82% in dead trees), whereas strong excavators used the highest percentage of live trees (80%). Northern Flickers excavated a majority of cavities in live trees (52%), but they also used dead trees with advanced decay (34%), as well as recently dead trees (13%). Both weak and strong excavators tended to excavate in the interior of the forest, whereas Northern Flickers excavated near the edge (Table 5). Cavities formed by strong excavators lasted the longest (median longevity, lower 95% CI = 15 years) and their hazard rates were used as the baseline. The loss rate of cavities formed by weak excavators was 1.87 times greater than the loss rate of cavities formed by strong excavators, and their survival rates had not yet declined to a median value (0.50 survival) after 12 years (Fig. 6). Cavities formed by Northern Flickers were the least persistent, with loss rates 2.17 times greater than for cavities formed by strong excavators; their median longevity was 12 years (95% CI = 10–13 years). Multiple comparisons among these groups, with a Bonferroni correction to the α level ($\alpha = 0.017$), revealed that cavities created by strong excavators had lower hazard of loss and greater longevity compared to those created by both Northern Flickers (likelihood ratio test = 26.4, df = 1, $P < 0.0001$) and weak excavators (likelihood ratio test = 6.07, df = 1, $P = 0.014$), but there was no difference in longevity between cavities created by weak excavators and Northern Flickers (likelihood ratio test = 0.22, df = 1, $P = 0.64$). We did not include natural cavities in this analysis because of the small sample size of nest sites that we located in these cavities. Further, because natural cavities make up a small portion of available cavities (3%), any differences in survival patterns of these cavities would not be important for this cavity-nester community.

TABLE 2. Model selection results based on Cox proportional-hazards models of hazard of loss in relation to tree diameter (dbh), decay stage, and distance to edge for 1635 cavities in interior British Columbia, Canada (1995–2010).

Models	K	logLik	AIC	ΔAIC	w
Decay stage	2	−1828.9	3661.8	0.00	0.45
dbh + decay stage + distance to edge + dbh × distance to edge	5	−1826.1	3662.1	0.35	0.38
dbh + decay stage	3	−1828.8	3663.7	1.92	0.17

Notes: Models included here had $\Delta\text{AIC} < 2$ and are ranked from most plausible to least plausible. For each model, we give the number of parameters (K), the maximum log(likelihood) ratio (logLik), the Akaike's Information Criterion (AIC), the difference in AIC compared to the model with the least AIC value (ΔAIC), and its weight, *w*.

TABLE 3. Effect of tree dbh, decay stage, and nearest edge variables on the life span of an aspen tree cavity based on averaged Cox proportional-hazards models for 1635 cavities from 1995–2010 in Riske Creek, British Columbia.

Parameter	Estimated coefficient	SE	Hazards ratio†	95% CI for HR‡
dbh (0.1 m)	0.027	0.08	1.03	0.89–1.19
Decay = live§				
Decay = recently dead	0.99	0.17	2.70	**1.95–3.74**
Decay = advanced decay	1.27	0.13	3.56	**2.74–4.63**
Distance to edge (10 m)	0.04	0.03	1.04	0.97–1.11
dbh × distance to edge	0.98	1.02	1.02	**0.96–0.99**

† The hazards ratio is equal to exp(estimated coefficient) and represents the change in hazard per unit for continuous variables (dbh = 0.1 m, nearest edge = 10 m), and compared to a "control" for categorical variables (decay stage). A hazards ratio (HR) of 1 means that there is no change in hazard, a HR above 1 indicates an increase in hazard (shorter life span), and HR below 1 indicates a decrease (longer life span).

‡ When the 95% CI for the hazards ratio (HR) does not include 1, the coefficients differ significantly from 1 at the $\alpha < 0.05$ level, as designated in boldface.

§ The live tree decay stage was used as the "control" with which the other two decay stages were compared.

DISCUSSION

Our demographic model of life span of aspen tree cavities in two habitat types helps to explain the dynamics of cavity resources and to predict the abundance of tree cavities based on characteristics of the tree and landscape in interior British Columbia. In both North and South America, secondary cavity-nesting birds select cavities based on their characteristics and abundance, and not in relation to their formation agent (Aitken and Martin 2007, Cockle et al. 2011*b*). Long-lived cavities make substantial contributions to the pool of cavity resources available for nesting and roosting. For example, a cavity that survives 14 years (the median longevity of cavities in interior BC) is potentially available for 14 or more pairs of breeding birds, whereas a cavity that survives a single year can only be used once or twice. These long-lived cavities are most valuable to secondary cavity-nesters (which require existing cavities in order to nest) and to excavators that frequently reuse cavities (e.g., Northern Flickers). Cockle et al. (2011*a*) found that cavity longevity was a strong determinant of the relative importance of excavated vs. natural cavities globally. In tropical South America and in European forests, loss rates of excavated cavities were much higher than loss rates of natural cavities (12.7 and 2 times higher, respectively); thus excavated cavities were a less available resource for secondary cavity-nesters. In North America, both natural and excavated cavities had similar persistence times, resulting in excavated cavities being a far more important resource for secondary cavity-nesters, because excavated cavities were much more abundant than cavities formed by natural decay only (Cockle et al. 2011*a*). Our detailed analysis of excavated aspen tree cavities in North America revealed that tree and forest context characteristics strongly influenced cavity longevity. These effects resulted in patterns of cavity persistence across both habitat types and excavator groups, which have implications for the availability of cavity resources for use by secondary cavity-nesters.

Underlying factors for cavity loss due to tree blow-over or stem breakage

Contrary to the widely accepted idea that dead trees in advanced stages of decay are the best contributors to nesting tree resources for wildlife, we found that cavities in live, unhealthy trees lasted more than twice as long as those in dead, decaying trees. This pattern is consistent across other studies of snag longevity involving both coniferous trees (Russell et al. 2006) and deciduous trees such as aspen (Lee 1998, Yamasaki and Leak 2006, Lindenmayer and Wood 2010). Decay class is a good

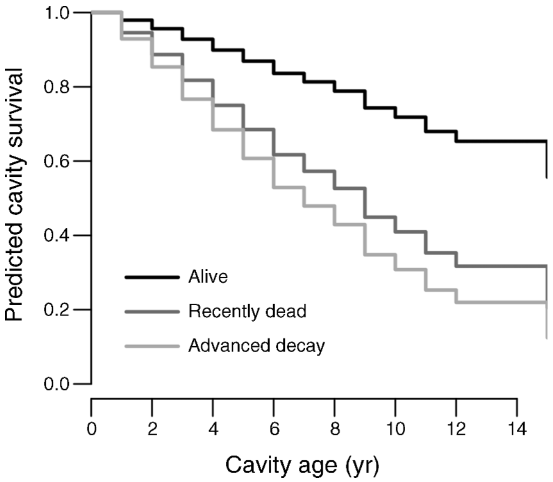

FIG. 3. Cox proportional-hazards predicted survival curves across three decay stages at average values of dbh and distance to edge for aspen tree cavities in central British Columbia, Canada. Black lines represent cavities in live trees (decay classes 1 and 2; median survival >15 years), medium gray lines represent cavities in recently dead trees (decay class 3; median survival 9 years), and light gray lines represent cavities in snags with advanced decay (decay classes 4, 5, and 6; median survival 7 years).

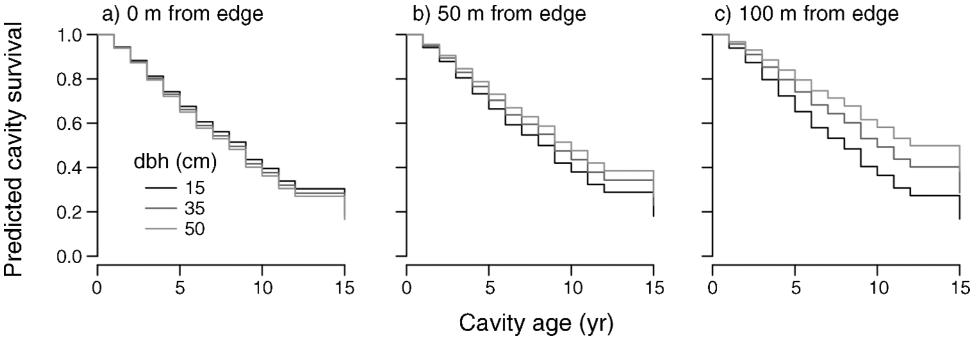

FIG. 4. Predicted survival curves, based on a Cox proportional-hazards model, showing the effect of dbh and distance to edge for aspen tree cavities in interior British Columbia. These graphs show predictions for cavities in recently dead aspen trees (decay class 3), but the pattern of increasing survival for large-dbh trees with increasing distance to the edge was consistent across decay classes.

indicator of susceptibility to blowdown, breakage, and chamber decay because of its relationship with tree stem strength, root mass integrity, canopy presence, and heartwood hardness. As a result, decay class was a better predictor of cavity longevity than tree dbh. Raphael and White (1984) found that, in coniferous forest, excavators select dead trees and prefer advanced stages of decay; however, live cavity trees are critical nesting and roosting habitat in many systems, including those in which aspen is the dominant nest tree (95% of nests at our study sites), where non-excavated cavities predominate (83% of cavities in the Atlantic forest of Argentina; Cockle et al. 2011*a*), or where excavators prefer live trees. Red-cockaded Woodpeckers excavate and reuse cavities exclusively in live pine trees (mainly *Pinus palustris* and *P. taeda*), possibly because their flowing resin is a predator deterrent (Harding 1997). Heart rot fungus (*Phellinus* spp.) infects live aspen and pine trees, creating a soft core surrounded by hard sapwood that enables woodpeckers to create structurally sound cavities (Harding 1997, Jackson and Jackson 2004). At our sites, live, unhealthy aspen trees represented 45% of the trees chosen by excavators, but these trees represented only 15% of the trees in our forest stands (Martin et al. 2004). Because they are both long-lived and selected for nesting by almost all of the excavators and secondary cavity-nesters, live, unhealthy aspen trees provide the greatest contributions to the pool of cavity resources.

By including both live and dead trees as well as a spectrum of edge and interior forest habitats, we were able to detect complex patterns in cavity longevity that would be masked in a more limited sample. In the interior of the forest, large-diameter trees were more persistent than small-diameter trees, but there was no effect of dbh at the forest edge. The benefits of a large dbh may decrease at the forest edge, where there is higher wind exposure and where the tree height and large crown that come with increasing dbh are liabilities (Scott and Mitchell 2005). Differing results may be due to the large degree of variability in study systems, including tree decay stages, forest types, and forest contexts. Most past studies found that large-dbh trees last longer than small-dbh trees, including systems in mixed temperate forests in central Maine (Garber et al. 2005), northern hardwood forests of New Hampshire (Yamasaki and Leak 2006), deciduous forests of southern Illinois (Nielsen et al. 2007), and mountain ash forests of southeastern Australia (Lindenmayer and Wood 2010). Studies by Moorman et al. (1999) and Lee (1998) were exceptions, finding that dbh is independent of snag longevity in mixed forest of South Carolina Piedmont and in the boreal forest of Alberta, respectively. In Alberta, aspen death rates were high for both small trees in dense stands due to self-thinning, and for large-dbh canopy trees, but once these trees were dead, they fell down at the same rate, regardless of dbh (Lee 1998).

Longevity patterns across habitat types and excavator groups

Large differences in cavity density across forest types suggest that some characteristics of the forest result in either greater cavity formation rates or longer persis-

TABLE 4. Cavity characteristics (mean ± SE) for 1635 aspen tree cavities in two types of forest habitats in interior British Columbia.

Cavity characteristic	Forest habitat type			
	Aspen grove (n = 771)	Continuous forest (n = 864)	F	P
Tree dbh (cm)	32.5 ± 0.3	28.5 ± 0.3	80.5	<0.0001
Decay class	2.85 ± 0.04	2.67 ± 0.04	11.1	0.0009
Distance to edge (m)	13.4 ± 2.1	52.3 ± 2.2	162.8	<0.0001

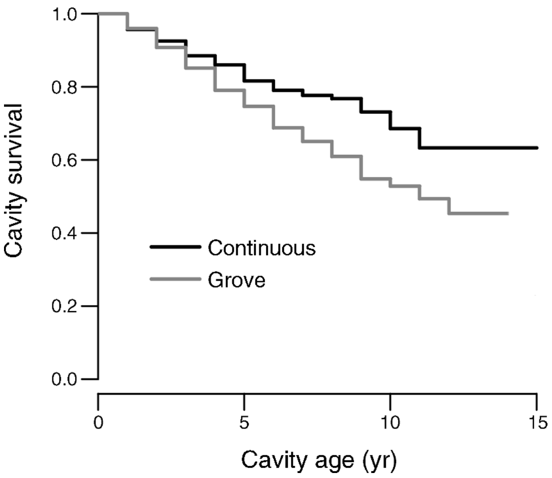

FIG. 5. Kaplan-Meier survival curves across forest habitat types for tree cavities in central British Columbia. Black lines represent aspen grove habitat ($n = 771$ cavities), and gray lines represent continuous mixed-coniferous forest habitat ($n = 864$ cavities).

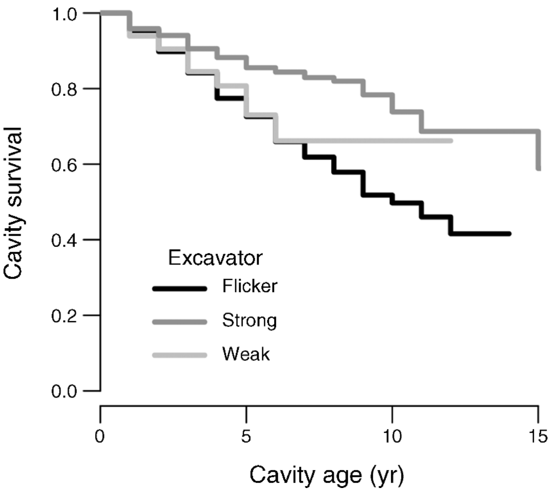

FIG. 6. Kaplan-Meier survival curves across excavator groups for aspen tree cavities in central British Columbia. The black line represents cavities formed by Northern Flicker ($n = 583$ cavities), the dark gray line represents cavities formed by strong excavators ($n = 433$ cavities), and the light gray line represents cavities formed by weak excavators ($n = 180$ cavities).

tence (e.g., Koch et al. 2008). Cavity densities, in turn, influence abundance and richness of secondary cavity-nesters (Aitken and Martin 2008). In both primary and managed forest, experimental increases in cavity density result in increased abundance of some cavity-nesters (Aitken and Martin 2008, Cockle et al. 2010, Wiebe 2011). In interior British Columbia, cavity density is much higher in aspen groves (16 cavities/ha) than in continuous forest (1.2 cavities/ha) at our study sites (Aitken and Martin 2008). One explanation could be that cavities last longer in the aspen groves, e.g., because cavities were in aspen of greater dbh. However, this does not seem to be true, because we found shorter cavity persistence in aspen groves than in continuous forest. Although trees in aspen groves had larger mean dbh, they were also closer to the edge and had more advanced decay, which were predictors of low cavity persistence. Thus, the high cavity densities in aspen groves occurred in spite of lower cavity persistence and were probably a result of higher excavation rates. These higher excavation rates are likely to occur because the preferred tree for excavators is more common (i.e., aspen; 46% in groves vs. 11% in continuous forest), or the excavator species prefer the more open habitats for foraging and nesting, so their breeding densities are greater there (Martin and Eadie 1999). The comparatively low excavation rates in continuous forest indicate that long-lived cavities are particularly important in maintaining the availability of usable cavities.

Interestingly, we did not detect differences in persistence for cavities created by weak excavators and Northern Flickers, the keystone excavator in our system. Cavities formed by strong excavators had the longest median life spans, whereas cavities formed by Northern Flickers and by weak excavators (including Downy Woodpeckers) had similar shorter median life spans. Strong excavators prefer to excavate cavities in live, unhealthy trees, which may offer greater protection from predators (Nilsson 1984), better thermoregulation (Wiebe 2001), and reduced likelihood of blowdown compared with more decayed trees. Because of their weaker excavation ability, weak excavators must select softer, more decayed trees than strong excavators select (Aitken and Martin 2004). However, weak excavators also tend to select dead trees with broken tops away from the forest edge, which may be relatively resistant to the effects of wind. Apparently the various factors contributing to mortality of Northern Flicker cavities and weak excavator cavities balanced each other so that, overall, the persistence of cavities created by these two

TABLE 5. Cavity characteristics (mean ± SE) for 1196 aspen tree cavities formed by three excavator groups and by natural decay agents in interior British Columbia.

Cavity characteristic	Excavator groups				
	Northern Flicker ($n = 583$)	Strong excavator ($n = 433$)	Weak excavator ($n = 180$)	*F*	*P*
Tree dbh (cm)	33.1 ± 1.4	31.2 ± 0.4	22.9 ± 0.6	141.6	<0.0001
Decay class	3.0 ± 0.2	2.2 ± 0.05	3.3 ± 0.08	105.5	<0.0001
Distance to edge (m)	12.0 ± 2.5	49.2 ± 3.0	54.7 ± 4.6	57.9	<0.0001

excavator groups did not differ, whereas the factors contributing to the mortality of cavities created by strong excavators resulted in longer persistence.

The fact that weak excavators created cavities that tended to last as long as those created by Northern Flickers, and thus contributed equally to cavity supply, is a novel result. In Poland, there were strong differences in cavity longevity across eight woodpecker species: Black Woodpeckers (*Denrocopus martius*) excavated holes in living trees that lasted 18 years, whereas Lesser Spotted Woodpeckers (*Dendrocopus minor*) and White-backed Woodpeckers (*Dendrocopus leucotos*) excavated holes in dead wood that lasted 4 years (Wesolowski 2011). In many studies of cavity-nester habitat suitability, the number of existing cavities is often considered in assessing habitat suitability. However, the decay class and cavity formation agents are also critical data, that need to be included in such habitat assessment exercises. Knowing the life span and availability of cavities created by certain species of excavators may be important in those cases in which a secondary cavity-nesting species depends solely on holes created by a certain excavator (e.g., because the secondary nester requires holes of a specific size).

To ensure conservation of long-lived tree cavities in managed forests, the focus should be on retaining living, unhealthy, and large-dbh trees. This is especially important in continuous forest habitats, where cavity density is low and persistent cavities are necessary to maintain a stable level of cavity availability. In the past, the focus has been to retain dead, decayed snags as wildlife trees in managed forests (e.g., Bull and Partridge 1986, Garber et al. 2005), but our results indicate that cavities in live trees persist the longest. Thus, in our northern temperate mixed forest, the best way to maintain a high density of usable cavities over a period of several decades is to retain a range of live trees with decay, as well as dead trees, and to implement plans for the continuous recruitment of trees that would be suitable for excavation of new tree cavities. The patterns that we found in cavity persistence confirm that persistence is a key trait to study in forest wildlife communities because, in general, survival of nesting and roosting cavities will have a potentially large effect on cavity-nesting community structure and function.

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