

SURVIVAL OF TREE CAVITIES: A CRITICAL RESOURCE FOR CAVITY-NESTING COMMUNITIES

by

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B.Sc., Trinity Western University, 2008

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Forest Sciences)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

October 2011

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ABSTRACT

Tree cavities are a multi-annual resource used by cavity-nesting vertebrates for nesting and roosting, and the abundance of this resource is influenced by the rates at which cavities are created and destroyed. Tree cavities are vulnerable to forest harvesting and retention of long-lived cavity trees is an important strategy in maintaining the richness and abundance of forest species. My objectives were to: 1) investigate factors influencing longevity of cavities in nesting trees; and 2) assess the effect of harvesting on the risk of loss to cavities in retained trees.

To examine factors influencing cavity persistence, I modeled survival of more than 1300 nesting cavities over 16 years (1995-2010) for temperate forests of interior British Columbia, Canada. Sources of loss were tree stem blowdown and breakage (90%), chamber decay (7%), and cavity entrance healing over (3%). Cavities in live trees lasted 2.7 times longer than those in dead trees with advanced decay. There were also differences in cavity longevity across forest types and formation agents, which will affect cavity availability for some populations.

Comparison of hazard of loss for cavities in two partial-harvest treatments and unharvested stands revealed that hazard of loss increased by 70% for cavities in the partial harvest treatment (44–95% removal of basal area) compared with those in uncut forest, while cavities in wildlife reserves (retention patches; ~ 1 ha) had a 48% increase in hazard of loss relative to uncut forest. Rates of loss were highest in the five years following harvest, and after 8 years declined to pre-harvest levels.

My results showed that cavities in live trees lasted longer than cavities in dead trees, cavities in continuous forest stands lasted longer than those in aspen groves within grassland areas, and cavities created by strong excavators lasted longer than those created by weak excavators, or the keystone excavator at my study sites, the northern flicker. Additionally, cavities in trees retained after harvesting had an increased risk of loss across all decay classes, but this effect was somewhat mitigated by retaining cavities embedded in wildlife reserves.

PREFACE

Chapters 2 and 3 of this thesis were written as independent manuscripts and will be submitted in a similar form except that I moved the description of the study area to Chapter 1 and the general conclusions to Chapter 4. This study was designed in collaboration with Dr. Kathy Martin (UBC) and Dr. Karen Wiebe (USASK). I collected data in the field (2007-2010), performed all analyses and prepared the manuscript with input from my co-authors.

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ACKNOWLEDGEMENTS

Thanks to my supervisors Dr. Kathy Martin and Karen Wiebe for their mentorship in ecology and scientific writing. My supervisory committee, Drs. Peter Arcese, Val LeMay provided helpful input in the analysis and revision of my thesis. Dr. Jake Goheen provided early discussion and ideas for statistical analysis. Thanks to the excellent field crews I worked with at Riske Creek, in particular, Haley Kenyon, Matt Huntley, Amanda Adams, and Amy Koch. Thanks to lab members including Andrea Norris, Kristina Cockle, Mark Drever, and Tomas Ibarra for discussion of statistical analysis, ideas, and writing. Lastly, I am grateful for the support and encouragement of my family.

CHAPTER 1: GENERAL INTRODUCTION AND THESIS OVERVIEW

GENERAL INTRODUCTION

More than 40 species of cavity-nesting birds and mammals, or about 30% of forest vertebrates in interior British Columbia (BC), Canada require tree cavities for nesting or roosting. Therefore, the availability and quality of cavities strongly influences the structure and function of cavity nesting vertebrate communities (Martin & Eadie 1999, Aitken & Martin 2008). Cavities are a dynamic resource that changes in abundance as they are created and destroyed, and their characteristics are modified by excavators, predators, and decay processes (Blanc and Walters 2008). In order to maintain a stable supply of this resource in forest communities, a long-term balance in rates of cavity creation is necessary to offset cavity destruction (Sedgwick & Knopf 2002). My research investigates factors influencing cavity persistence and abundance.

Cavities are created in trees with compromised health by excavating species such as woodpeckers and through decay processes such as fungal decay and tree breakage. The relative importance of various cavity-creating agents seems to vary from continent to continent, with vertebrate excavators being predominant in North American forests (Cockle et al. 2011a). Most excavating species create one or more new holes each year for nesting and roosting (Wiebe et al. 2007), but some weak excavators reuse cavities frequently. By definition, secondary cavity-nesters always reuse existing cavities and are dependent on suitable excavated holes and decay-formed cavities for nesting. There is little evidence that nest site availability limits population sizes of birds in mature forests (Wesolowski 2007, Wiebe 2011), although small scale increases in density have been observed in a handful of box addition experiments (e.g. Aitken and Martin 2008). However, there is good evidence of cavity limitation in landscapes altered by human activities such as agriculture and forestry (review in Newton 1994). Furthermore, our lack of knowledge about what cavity traits (e.g. height or depth) a particular species requires or prefers may often bias our estimate of cavity availability on the landscape for the species.

The longevity of tree cavities is an important factor in cavity abundance. Cockle et al. (2011a) demonstrated that persistence of decay-formed vs. excavated cavities

helped to determine the reuse rates of these cavity types across continents. In South America, decay-formed cavities were more persistent than excavated cavities, and were more abundant and stable over time, resulting in a greater use by vertebrates of decay-formed cavities compared to excavated cavities. In temperate forests of North America, excavated and decay-formed cavities had similar longevity and were used in proportion to their availability (Cockle et al. 2011a, Aitken and Martin 2007). Long-term studies of cavity dynamics in Australia and Europe show that cavity longevity is influenced by characteristics of a tree and its context in the landscape. Lindenmayer and Wood (2010) found that decay-formed cavities in Eucalypts were most persistent in large diameter trees and that probability of loss increased with the decay of the cavity tree. Wesolowski (2011) tracked 719 cavities in protected primaeval temperate forest in Poland and found that median lifespans of cavities in four different trees species ranged from 4 to 22 years. In addition to tree species, cavity survival differed across live and dead trees, the location of the cavity on the tree, the excavator species, and the forest type.

To my knowledge, there have been no long-term studies of cavity dynamics in North America, where we have a unique, woodpecker-dominated system of cavity excavation and community structure (Martin and Eadie 1999). In managed forest systems, tree cavities are vulnerable to forest harvesting. Retention of cavity-bearing trees as single stems in clearcuts or embedded in wildlife reserves is one strategy employed to maintain forest species richness; however, there is concern that increased exposure to wind may reduce the longevity of these retained cavity resources (Scott and Mitchell 2005).

My objectives were to: 1) investigate rates of cavity loss in three tree species as well as to determine factors influencing longevity of cavities in aspen (*Populus tremuloides* Michx.) trees; and 2) assess the effect of harvesting on the risk of loss to cavities in retained trees in harvested stands.

STUDY AREA

Cavities were tracked during 16 years (1995–2010) at 27 study sites and the surrounding area within 50 km of Williams Lake (51° 51'N, 122° 21'W) in interior BC

(Wiebe and Swift 2001, Martin et al. 2004). The study included two temperate forest types: continuous mixed coniferous species forests (hereafter termed continuous mixed forest in this thesis) and aspen groves. Continuous forest sites were dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex. Loud.; 42% by stem count) and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco; 28%), and contained hybrid spruce (*Picea engelmannii* x. *glauca*; 18%) and trembling aspen (*Populus tremuloides*; 12%). Aspen groves contained 54–100% aspen, with lodgepole pine and interior Douglas-fir making up the remainder. They were surrounded by grasslands and shallow ponds. Continuous mixed forest patches ranged from 7 to 32 ha, while aspen groves ranged from about 0.2-5 ha. All sites were in the Interior Douglas-fir (IDF) biogeoclimatic ecological zone, which is characterized by a continental climate with warm, dry summers and cool winters (Meidinger and Pojar 1991). The mean annual temperature for the IDF zone is 1.6-9.5°C and the mean annual precipitation ranges from 300 to 750 mm (Meidinger and Pojar 1991).

THESIS OVERVIEW

In Chapter 2, I quantified rates and sources of cavity loss in trembling aspen, lodgepole pine, and hybrid spruce. I then modeled the factors influencing cavity persistence in aspen trees, the most common cavity trees used at my sites (96% of nests), using Cox-proportional hazards models and Kaplan-Meier survival estimates. I analyzed the effect of tree decay class, diameter, and distance to edge in two forest types and across excavator groups. These results indicate that live, large trees were strong contributors to cavity abundance and that cavity longevity is an ecological trait to study in relation to cavity resource availability. Lastly I reviewed the findings of previous studies of cavity dynamics and discuss my results in light of these studies.

In Chapter 3, I tested for reduced cavity persistence in clearcuts and wildlife reserves compared with those in mature, unharvested forest stands. I used a Cox proportional-hazards model to assess the hazard rates to: 1) cavities retained in isolated trees surrounded by clearcuts (hereafter termed cavities in clearcuts or harvested stands); 2) cavities retained in trees embedded in wildlife reserves (retention patches ~ 1 ha); and 3) cavities in unharvested forests. I also examined the pattern of

loss rates with time since harvest. There was a 48% increase in loss rates in wildlife reserves and a 70% increase in trees retained as individuals in clear-cuts compared with baseline loss rates in unharvested forest. Loss rates were highest in the five years following harvest and after eight years declined below baseline levels. I conclude that wildlife reserves provide increased protection from windthrow to retained cavity trees and that cavity trees that survive initially high loss rates will provide long-lived nesting resources for the cavity-nester community.

Chapter 4 summarizes my research and discusses implications for tree cavity management.

CHAPTER 2. SURVIVAL ANALYSIS OF A CRITICAL RESOURCE FOR CAVITY-NESTING COMMUNITIES: PATTERNS OF TREE CAVITY LONGEVITY

INTRODUCTION

Structural elements of habitat, or non-consumable 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 and mammal species could not breed without access to tree cavities for nesting (Martin and Eadie 1999). 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 temperate forests of interior British Columbia (BC), Canada, more than 40 species or about 30% of forest vertebrates use tree holes (Bunnell and Krebs 1990). Thus, cavity availability and quality strongly influence the structure and function of cavity-nesting communities (Martin & Eadie 1999, Aitken & Martin 2008).

Cavities are formed either by excavators such as woodpeckers or by 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). 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 close 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 cavity destruction (Sedgwick & Knopf 2002, Cockle et al. 2011b). 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, I 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.

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. Since tree blow down seems to be the main cause of cavity disappearance (e.g. Sedgwick and Knopf 2002), I predicted that cavities in the stems of large, living aspen trees would survive longest in the system, while cavities located higher above the ground, or those closer to forest edges would be more susceptible to destruction or breakage from the wind. In Australia, Lindenmayer and Wood (2010) found that cavities in mountain ash (*Eucalyptus regnans*) lasted longer if they were in larger, less decayed trees. Cockle et al. (2011b) found cavities excavated by birds had shorter lifespans than non-excavated cavities in temperate forests of Poland and Atlantic forests of Argentina, but a similar time in temperate forests of BC, Canada. Studies that investigated the survival of live and dead trees, regardless of whether they support cavities, consistently found effects of decay stage and tree diameter in a variety of forest systems. Lee (1998) found that the survival of trembling aspen (*Populus tremuloides* Michx.) snags (dead tree stems) in the mixed boreal forests in Alberta increased with tree diameter and with stand maturity. Similarly, dead pine (*Pinus* spp.) and fir trees (*Abies* spp.) with a larger diameter lasted longer in lower montane coniferous forests in the Sierra Nevada of California, United States (US; Raphael and Morrison 1987, Russell et al. 2006). Decay state of the tree was also negatively correlated with survival in a number of tree species such as interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) and ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) in western Idaho, US (Russell et al. 2006). These studies of tree survival did not directly address the survival of nesting cavities and did 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 BC; Martin et al. 2004), 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., less than 10 years) to track most cavities throughout their entire life spans.

Furthermore, the longevity of tree cavities may also influence the availability of cavities in different forest types or in different tree size classes created by different excavators. To my knowledge, these questions have never been investigated. Different

forest types can show strong variation in cavity availability (Aitken 2002, Koch et al. 2008) and experimental studies have found that cavity-nester abundance increases with cavity availability (Aitken and Martin 2008, Cockle et al. 2010). In temperate forests of interior BC, cavity abundance was much higher in aspen groves (16 cavities/ha) than in continuous mixed forests (1.2 cavities/ha; Aitken and Martin 2008). However, predicting relative cavity survival between these two habitats is complicated by the fact that aspen surrounded by grasslands are closer to edges, where nest trees tend to have low taper (short with large diameters) compared to aspen growing in continuous forest stands.

Patterns in cavity longevity across excavator species are easier to predict as 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). If weaker excavators select nest tree characteristics that result in high risk of loss, their cavities may be more ephemeral than those of stronger excavators. Such differences in cavity longevity across excavators potentially impacts 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, my goal was to assess rates of cavity loss in four tree species (trembling aspen, lodgepole pine [*Pinus contorta* var. *latifolia*], hybrid spruce (*Picea engelmannii* x. *glauca*), and interior Douglas-fir) and to model factors influencing cavity persistence in trembling aspen, the tree species that contains 95% of all active cavity nests found in interior BC (Aitken and Martin 2007). I 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. I used failure time analysis techniques to track survival of individual cavities across time for an entire cavity-nesting community to evaluate these questions.

METHODS

Study area

The fates of 1714 tree cavities were monitored during 16 years (1995–2010) on 27 study sites in continuous mixed forests and aspen groves of interior BC, Canada (Wiebe and Swift 2001, Martin et al. 2004; see Chapter 1 for study area details).

Eight excavating species were common on my sites: downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), pileated woodpecker (*Drycopus pileatus*), red-naped sapsucker (*Sphyrapicus nuchalis*), northern flickers (*Colaptes auratus*), red-breasted nuthatch (*Sitta Canadensis*), and black-capped chickadee (*Poecile atricapillus*). Cavity formation agents were grouped into four categories: 1) strong excavators which prefer living wood (i.e., pileated woodpecker, red-naped sapsucker, American three-toed, hairy woodpecker); 2) northern flickers, strong excavators which use a range of decay classes including many dead stems, and given their abundance and cavity type are considered keystone excavators in interior British Columbia (Martin et al. 2004); 3) smaller, weak excavators which typically use decayed, soft wood (downy woodpecker, red-breasted nuthatch, and black-capped chickadee; and 4) cavities formed naturally through decay which tended to be in both live, unhealthy trees and recently dead trees.

Cavity location and monitoring

From May-July, 1995-2010, sites were systematically searched for nests in tree cavities by listening for fresh excavations and following birds, and all cavities occupied in previous years were checked to determine if the trees were still standing and if the cavities were useable. A cavity was considered freshly excavated if a bird was observed excavating or there were many fresh woodchips 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, flashlights and, from 2005, cavities up to 15 m high were inspected using a video camera system on an extendable pole (TreeTop Peeper, Sandpiper Systems, Manteca, Calif.). 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 (contained at least one egg or nestling), it was considered a suitable nest

cavity and was monitored 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; or 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 after a site was dropped or during the last season of the study (2010) were censored. Thus, I could determine the year the cavity was first excavated (new, known age) or first found occupied (minimum age) and its subsequent survival.

A total of 798 cavities were found in the year they were first excavated (fresh), but I 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 (Cox proportional-hazards model run in the “survival” package, R version 2.7.0; likelihood ratio test = 0.2, $df = 1$, $p = 0.66$; Fig. 1). Because the lifespans of known age and minimum age cavities did not differ (probably because cavities were found within the first few years after they were created), I used year of first occupancy as the start date for subsequent analyses of all cavities pooled ($n = 1635$). An earlier study calculated overall cavity lifespan using some of these data for a shorter time series on a subset of the study area that I include here (Cockle et al. 2011b, 818 cavities over 13 years).

Cavity characteristic measurements

I measured survival in relation to cavity characteristics including the diameter at breast height (1.3 m above ground; DBH) of the cavity tree, distance to 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. 2.2). For the analyses, I 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 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 estimated probability of cavity loss at time t (cavity age) for an individual cavity (i) is modeled as:

$$h_i(t) = h_o(t) \exp(\beta_1 x_{i1} + \beta_2 x_{ik} + \dots + \beta_k x_{ik})$$

where $h_o(t)$ is the unspecified baseline hazard function; the x 's are covariates with associated β parameters, which modify the baseline hazard. This formula can also be written as:

$$\ln[h_i(t)/h_o(t)] = \beta_1 x_{i1} + \beta_2 x_{ik} + \dots + \beta_k x_{ik}$$

where $h_i(t)/h_o(t)$ is the hazard ratio, and the coefficients β_1 to β_k are estimated by Cox regression. For a class variable, $\exp(\beta)$ represents the relative risk of loss compared to the baseline hazard level, which is one of the levels the class variable, given the other variables are equal. For continuous variables, $\exp(\beta)$ represents the relative risk of loss associated with an increase of one unit of that variable. Tied cavity loss times were dealt with using the Efron approximation (Efron 1977).

I tested for differences in mean values of DBH and distance to edge across forest types and cavity formation agents using analysis of variance and I tested for a difference in median decay class (a categorical variable) across these same groups using the Kruskal-Wallis rank sum test ("stats" package in R version 2.7.0; R Core Development Team 2010).

To determine which explanatory variables (decay class, DBH, distance to edge) were important predictors of cavity longevity, I used Akaike's Information Criterion (AIC)

to rank all possible subsets of a global model which included my three explanatory variables and all 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. Models that had a ΔAIC value less than 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, for which the properties of cavity trees that can potentially be managed. After investigating which characteristics of the tree itself were important predictors of longevity, I 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 lifespans were calculated as the age when survival reached 50%. Survival analyses were done using the `survfit` and `coxph` functions from the "survival" package in the statistical program R, version 2.7.0 (Therneau and Lumley 2009; R Core Development Team 2010).

RESULTS

At my sites, 95.3% of cavities used for nesting were in aspen trees, 2.8% were in lodgepole pine, 1.3% were in interior Douglas-fir, and 0.5% were in hybrid spruce. At the five-year mark, cavities in aspen trees had the highest survival (0.78), followed by cavities in pine trees (0.65; Table 2.1). After 10 years, aspen tree cavity survival declined to 0.59, while survival of cavities in pine trees did not change. Sample sizes for interior Douglas-fir and hybrid spruce were too small to obtain reliable survival estimates. 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 where the entrance hole grew shut were restricted to cavities excavated in living trees. Because the main sources of mortality were windthrow and chamber decay, I next modeled in detail factors affecting these sources of cavity loss (97%) in aspen trees for which I had the largest sample.

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

Three of the seventeen models I fit to predict hazard of cavity loss received considerable support ($\Delta AIC < 2$; Table 2.2). I used these three models to produce an average model that included decay class, DBH, distance to edge, an interaction of DBH and distance to edge (Table 2.3). Decay class was the most important variable and had the largest effect sizes with lower survival rates at more advanced stages of decay (Fig. 2.3). Live trees were the most persistent and their hazard rates were used as “baseline” rates in comparison to higher decay stages (Table 2.3). The predicted median longevity for cavities in live trees was greater than 15 yrs (predicted survival rate after 15 years = 0.56; Fig. 2.3). Cavities in recently dead trees were 2.70 times more likely to be destroyed in a year than live trees and had a median longevity of 9 years (95% CI = 7-11 years), conditional on average values of the other variables (Table 2.3, Fig. 2.3). Cavities in dead trees with advanced decay were the least persistent with a risk of loss 3.56 times greater than cavities in live trees and their median longevity was only 7 years (95% CI = 6-9 years; Table 2.3, Fig. 2.3). Investigation of the DBH \times distance to edge interaction showed that trees with larger DBH persisted longer than trees with smaller DBH when in the interior of the forest, but there was no effect at the forest edge (Fig. 2.4).

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 2.4). Correspondingly, cavities in aspen habitat were at 52% higher risk of loss than in continuous forest habitat (median lifespan in aspen groves was 12 years, while after 15 years, survival in continuous forest was 64%; Fig. 2.5).

All predictors of cavity longevity (decay class, DBH, and distance to edge) differed significantly across excavators (Table 2.5). Weak excavators created cavities in dead trees with small diameters and advanced decay (82% in dead trees), while strong excavators used the highest proportion of live trees (80%). The majority of cavities excavated by northern flickers were in live trees (52%), but northern flickers 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, while northern flickers excavated near the edge (Table 2.5). Cavities formed by strong excavators lasted the longest (lower 95% CI = 15 yrs) 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 (50% survival) after 12 years (Fig. 2.6). Cavities formed by northern flickers were the least persistent with loss rates 2.17 times greater than cavities formed by strong excavators and their median longevity was 12 yrs (CI = 10–13 yrs). Multiple comparisons amongst 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, $p=0.64$). I did not include decay-formed cavities in this analysis because of their small sample size. Because decay-formed 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.

DISCUSSION

My model of lifespan of aspen tree cavities in two habitat types in interior British Columbia helps to explain the dynamics of cavity resources and to predict the longevity of tree cavities based on characteristics of the tree and its context. 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. 2011a). Long-lived cavities make substantial contributions to the pool of cavity resources available for nesting, especially where they are relatively abundant. 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, while a cavity that survives a single year can only be used once or twice. Cockle et al. (2011b) found that cavity longevity was a strong determinant of the relative importance of excavated vs. decay-formed cavities globally. In tropical forests of Argentina and in

temperate European forests, loss rates of excavated cavities were much higher than loss rates of decay-formed cavities (12.7 and 2 times higher, respectively), and thus were a less available resource for secondary cavity-nesters. In temperate forests of BC, both decay-formed 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 more abundant than cavities formed by decay (Cockle et al. 2011b). My detailed analysis of excavated aspen tree cavities in these North American temperate forests 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 idea that dead trees in advanced stages of decay are the best contributors to wildlife nesting tree resources, I 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 indicator of susceptibility to windthrow, 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 or cavity height. Raphael and White (1984) found that in coniferous forests, excavators select dead trees and prefer advanced stages of decay; however, in systems where aspen is the dominant nest tree (95% of nests at my study sites) or where non-excavated cavities predominate (83% of cavities in the Atlantic forest of Argentina; Cockle et al., 2011b), live cavity trees provide the critical wildlife habitat for nesting and roosting. For example, the heart rot fungus *Phellinus tremulae* infects live aspen trees creating a soft core surrounded by hard sapwood which enables woodpeckers to create structurally sound cavities (Jackson and Jackson 2004). At my sites, live, unhealthy aspen trees represented 45% of the trees chosen by excavators while these trees represented only 15% of the trees at my sites (for details, see 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.

My large sample size also enabled me to detect other potentially important predictors of cavity lifespan in addition to decay class. 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 larger tree height and crown that are associated with larger DBHs are liabilities (Scott and Mitchell 2005). Past studies found that large DBH trees last longer than small DBH trees (Garber et al. 2005, Yamasaki and Leak 2006, Nielsen et al. 2007, Lindenmayer and Wood 2010). Moorman et al. (1999) and Lee (1998) were exceptions, finding that DBH is independent of snag longevity in mixed forest of South Carolina Piedmont, US and Alberta, Canada mixed forests, respectively. These differing results may be due to the large degree of variability in study systems, including tree decay stages, forest types, and forest contexts. By including both live and dead trees as well as a spectrum of edge and interior forest habitats, I was able to detect complex patterns in cavity longevity, which would be masked in a more limited sample.

Longevity patterns across habitat types and excavator groups

Large differences in cavity density across forest types suggest that some characteristics of the forest either result in greater cavity formation rates or longer persistence (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, experimentally increasing cavity density resulted in increased abundance of some cavity-nesters (Aitken and Martin 2008, Cockle et al. 2010). In interior British Columbia, cavity density was much higher in aspen groves (16/ha) than in continuous forests (1.2/ha) at my 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, but this does not seem to be true; I found shorter cavity persistence in aspen groves than in continuous forest. Though 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 likely a result of higher excavation rates. These higher excavation rates could occur because the preferred substrate for excavators is more common (i.e. aspen; 46% in groves vs. 11% in continuous forest), and/or the excavator species prefer the more open habitats for foraging and nesting and so their breeding densities are greater there (Martin and Eadie 1999). The comparatively low excavation rates in continuous forests indicate that long-lived cavities are particularly important in maintaining the availability of usable cavities.

Interestingly, I did not detect differences in persistence for cavities created by weak excavators and northern flickers, the keystone excavators in interior BC. Cavities formed by strong-excavators had the longest median lifespans, while cavities formed by northern flickers and by weak excavators (including downy woodpecker) had similar shorter median lifespans. 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 (Aitken and Martin 2004), but 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 species did not differ, while 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 contribute equally to cavity supply, is a novel result. In temperate forests of Poland, there were strong differences in cavity longevity across eight woodpecker species: black woodpeckers (*Dendrocopus martius*) excavated holes in living trees which lasted 18 years whereas lesser spotted woodpeckers (*Dendrocopus minor*) and white-backed woodpeckers (*Dendrocopus*

leucotos) excavated holes in dead wood which 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 important variables, which need to be included in such habitat assessment exercises. Knowing the lifespan and availability of cavities created by certain species of excavators may be important in those cases where 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).

In summary, I found that decay class of the nest tree had the strongest effect on cavity lifespan, accounting for a median difference in survival of more than 5 years between the highest and lowest decay classes. The patterns I 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.

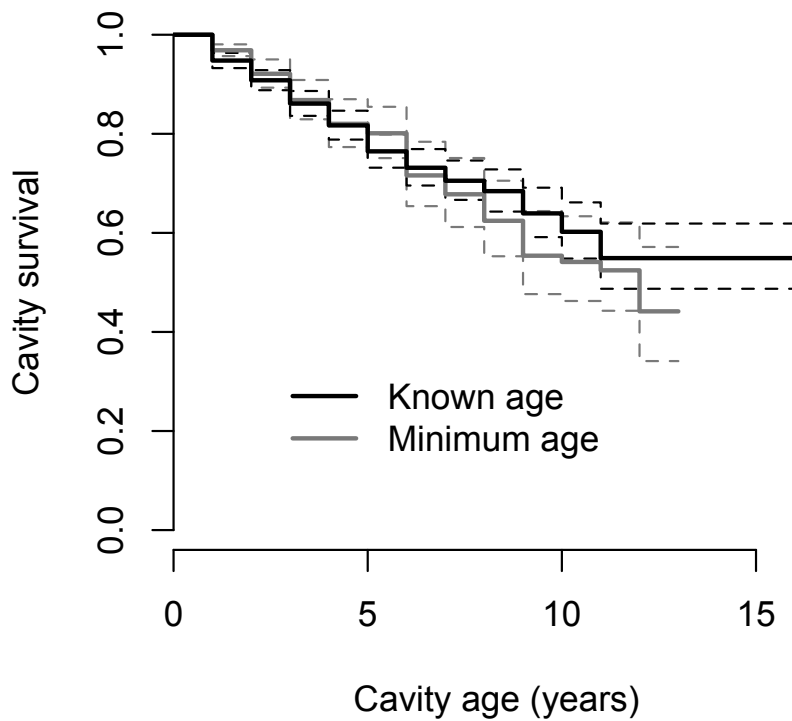


Figure 2.1. Kaplan-Meier survival curves (solid lines) and 95% confidence intervals (dashed lines) for aspen tree cavities in interior British Columbia. Black lines represent cavities of known age (found freshly excavated, N=798) and grey lines represent cavities for which the excavation date is unknown (found used; age is a minimum estimate, N=837).







 			  		
1	2	3	4	5	6
Alive		Recently dead	Advanced decay		

Figure 2.2. Aspen decay classes based on Backhouse and Louiser (1991). The “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).

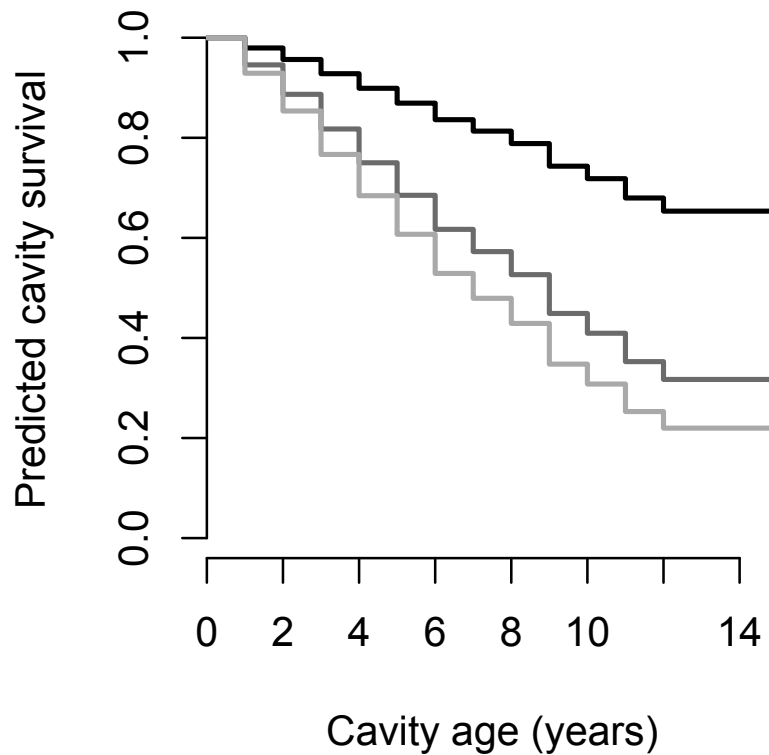


Figure 2.3. Cox proportional-hazards predicted survival curves across three decay stages at average values of DBH and distance to edge for aspen tree cavities in interior British Columbia. Black lines represent cavities in live trees (decay classes 1 and 2; median survival > 15 yrs), medium grey lines represent cavities in recently dead trees (decay class 3; median survival = 9 yrs), and light grey lines represent cavities in snags with advanced decay (decay classes 4, 5, and 6; median survival = 7 yrs).

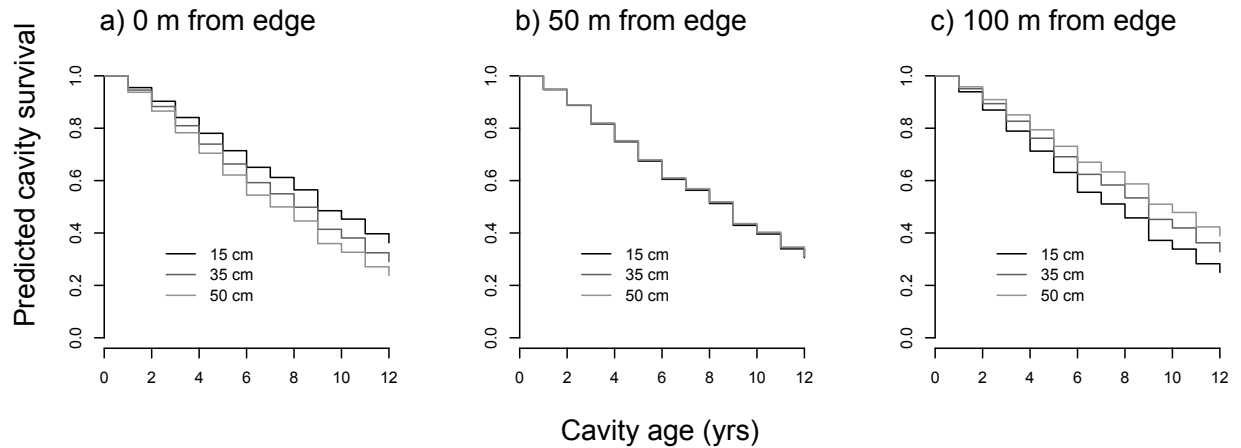


Figure 2.4. Predicted survival curves, based on a Cox proportional-hazards model, showing the effect of DBH and distance to edge (graphs A through C) for aspen tree cavities in interior British Columbia. These graphs show predictions for cavities in recently dead aspen trees (decay class 3), but the pattern of increasing survival for large DBH trees with increasing distance to the edge was consistent across decay classes.

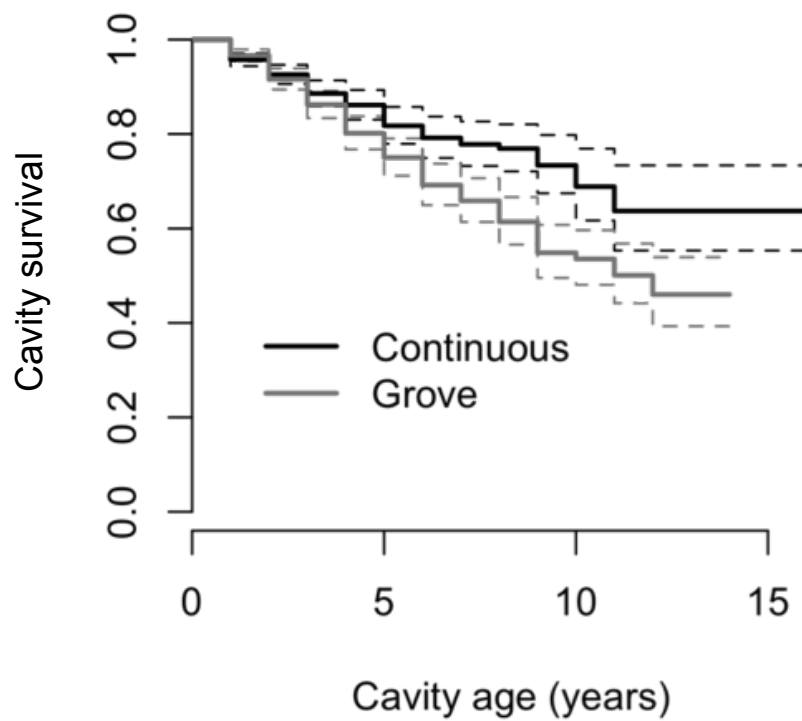


Figure 2.5. Kaplan-Meier survival curves (solid lines) and 95% confidence intervals (dashed lines) across forest habitat types for tree cavities in interior British Columbia. Black lines represent aspen grove habitat (N=771 cavities) and grey lines represent continuous mixed forest habitat (N=864 cavities).

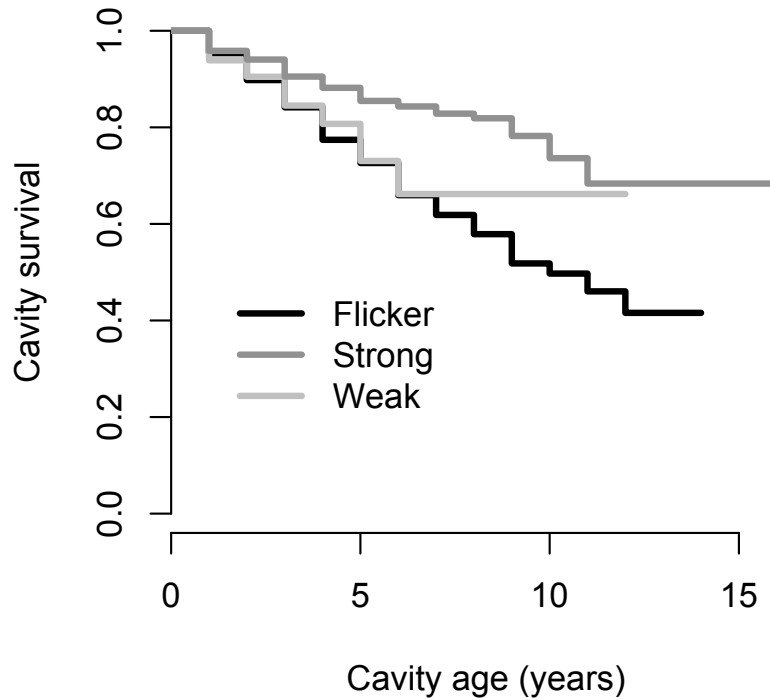


Figure 2.6. Kaplan-Meier survival curves across excavator groups for aspen tree cavities in interior British Columbia. The solid black line represents cavities formed by northern flicker (N=583), the dashed dark grey line represents cavities formed by strong excavators (N=433), and the dashed light grey line represents cavities formed by weak excavators (N=180).

Table 2.1. Survival of cavities in two tree species (trembling aspen, *Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex. Loud.) in interior British Columbia based on Kaplan-Meier estimates. Number of cavities at risk represents the number of usable cavities monitored up to a given age and the number of events gives the number of cavities that were lost. Censored cavities were still standing at the end of the study, after a site was no longer monitored, or were lost through human causes (e.g. prescribed burns, logging).

Tree species	Age (yrs)	# cavities at risk	# censored	# lost	Survival rate
Trembling aspen					
	1	1631	605	63	0.96
	2	963	110	41	0.92
	3	812	111	42	0.87
	4	659	96	35	0.82
	5	528	78	31	0.78
	6	419	71	25	0.73
	7	323	60	12	0.70
	8	251	51	12	0.67
	9	188	39	16	0.61
	10	133	25	5	0.59
	11	103	33	7	0.55
	12	63	21	3	0.52
	13	39	27	0	0.52
	14	12	5	0	0.52
	15	7	6	1	0.45
Lodgepole pine					
	1	45	15	2	0.96
	2	28	5	2	0.89
	3	21	4	3	0.76

Tree species	Age (yrs)	# cavities at risk	# censored	# lost	Survival rate
Lodgepole pine					
	4	14	0	1	0.71
	5	13	1	1	0.65
	6	11	4	0	0.65
	7	7	2	0	0.65
	8	5	1	0	0.65
	9	4	0	0	0.65
	10	4	1	0	0.65

Table 2.2. 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 included here had a $\Delta AIC < 2$ and are ranked from most plausible to least plausible. For each model we give the number of parameters (k), the maximum log(likelihood), the Akaike's Information Criterion (AIC), the difference in AIC compared to the model with the least AIC value ΔAIC , and the weight of the model.

Parameters	k	Log(L)	AIC	ΔAIC	weight
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

Table 2.3. Effect of tree DBH, decay stage, and nearest edge variables on the lifespan of an aspen tree cavity based on averaged Cox proportional-hazards models for 1635 cavities from 1995-2010 in Riske Creek, British Columbia.

	Estimated coefficient	Standard error	Hazards ratio ^a	95% CI for the HR ^b
DBH (0.1 m)	0.027	0.08	1.03	0.89–1.19
Decay=live ^c	-	-	-	-
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	-0.02	0.02	0.98	0.96–0.99

^a The hazards ratio is equal to $\exp(\text{estimated coefficient})$ and represents the change in hazard per unit for continuous variables (DBH = 0.1m, nearest edge=10m), and compared to a “control” for categorical variables (decay stage). A hazards ratio of 1 means that there was no change in hazard, a HR above 1 indicates an increase in hazard (shorter lifespan), and below 1 indicates a decrease (longer lifespan).

^b When the 95% CI for the hazards ratio does not include zero the coefficients differ significantly from 1 at the 5% level, designated bold font.

^c The live tree decay stage was used as the baseline which with the other two decay stages were compared; coefficients for other decay classes represent the change in log hazard ratio relative to live tree decay stage.

Table 2.4. Mean \pm SE cavity characteristics for 1635 aspen tree cavities in two types of forest habitats (aspen grove and continuous forest) in interior British Columbia.

Cavity characteristic	Mean \pm SE		<i>F</i>	<i>p</i>
	Aspen grove (n=771)	Continuous forest (n=864)		
Tree DBH (cm)	32.5 \pm 0.3	28.5 \pm 0.3	80.5	<0.001
Decay class	2.85 \pm 0.04	2.67 \pm 0.04	9.7 ^a	0.008
Distance to edge (m)	13.4 \pm 2.1	52.3 \pm 2.2	162.8	<0.001

^aThis is a Kruskal-Wallis chi-squared value rather than an *F* value because decay class is a categorical variable.

Table 2.5. Mean \pm SE cavity characteristics for 1196 aspen tree cavities formed by three excavator groups and by natural decay agents in interior British Columbia.

Cavity characteristic	Mean \pm SE			<i>F</i>	<i>p</i>
	Northern				
	flicker (N=583)	Strong (N=433)	Weak (N=180)		
Tree DBH (cm)	33.1 \pm 1.4	31.2 \pm 0.4	22.9 \pm 0.6	141.6	<0.001
Decay class	3.0 \pm 0.2	2.2 \pm 0.05	3.3 \pm 0.08	115.5 ^a	<0.001
Distance to edge (m)	12.0 \pm 2.5	49.2 \pm 3.0	54.7 \pm 4.6	57.9	<0.001

^aThis is a Kruskal-Wallis chi-squared value rather than an *F* value because decay class is a categorical variable.

CHAPTER 3: HAZARDS AND LOSS-RATES OF CAVITY TREES IN PARTIALLY HARVESTED FORESTS OF BRITISH COLUMBIA, CANADA

INTRODUCTION

Wildlife conservation in the context of managed and partially harvested forests is a central challenge in forest management. Lindenmayer et al. (2006) suggested that widely applicable guiding principles to forest biodiversity conservation should include retention of structural complexity and should mimic natural disturbances as much as possible. Tews et al. (2004) also emphasized the importance of structural complexity and introduced the concept of keystone structures, which are persistent resources that have a disproportionate impact on ecosystem functioning. For example, the availability of tree cavities used for nesting and roosting helps to determine composition of cavity-nesting vertebrate communities (Martin et al. 2004). Maintenance of structural complexity mimics the patchy effects of regular disturbance events, and when these structural habitat components are used by a wide range of species, retention of structural complexity may have large positive impacts on biodiversity conservation in the context of forest harvesting.

Here, I focus on tree cavities as a structural resource that can be retained in harvested stands. Tree cavities for nesting and roosting are a vital multi-annual resource that are created by woodpeckers and other excavators and may be reused many times by secondary cavity-nesters that require existing holes to breed (Martin and Eadie 1999). In interior British Columbia (BC), Canada, more than 40 species, or about 30% of forest vertebrates, use cavities for nesting and shelter (Bunnell and Kremsater 1990, Martin et al. 2004). Experimental studies in managed forests show that cavity-nester abundance increases when nest boxes are added and thus some cavity-nesting species appear to be limited by nest hole availability in these forests (Newton 1994, Holt and Martin 1997, Aitken and Martin 2008, in press, Cockle et al. 2010). The density of nest cavities is determined both by rates of excavation and by subsequent persistence of cavities (Cockle et al. 2011). In temperate forests of BC, Canada, long-lived cavities created by woodpeckers are the primary source of cavities for secondary cavity nesters, used for 94% of nests (Aitken and Martin 2007), while in the Atlantic forest of Argentina, rapid degradation and loss of excavated cavities means they are used less frequently

and the longer-lived decay-formed cavities are the primary source of nest sites used by secondary cavity nesting birds (Cockle et al. 2011b). Thus, the abundance and longevity of tree cavities has a strong influence on cavity nest-site availability for cavity-nesting communities. Long-lived tree cavities provide an important habitat attribute and should be a focus for forest management strategies.

Partial retention harvesting techniques have been applied to improve wildlife conservation by retaining cavity trees and other potential wildlife trees (Lance and Phinney 2001). At my sites in interior BC, trembling aspen (*Populus tremuloides* Michx.), which are not harvested commercially, and veteran interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) were retained, both as isolated individuals in clearcuts and within wildlife reserve patches. In general, the results of partial retention are positive for wildlife; species richness in partially harvested stands is frequently higher than in clearcuts, mainly due to increases in edge species (e.g. Lance and Phinney 2001). Drever et al. (2008) found that both woodpecker richness and general forest bird richness increased in harvested sites with retention of trembling aspen and veteran interior Douglas-fir. Despite these initial positive results, there is concern that trees retained in clearcuts may have a high risk of loss from windthrow, resulting in longer-term declines in cavity abundance. Studies of tree and snag dynamics following harvest show that loss rates of trees in mixed temperate forests are high following harvest (Huggard et al. 1999, Garber et al. 2005, Russell et al. 2006, Thorpe et al. 2008). Scott and Mitchell (2005) found that windthrow loss was negatively correlated with local post-harvest stand density in Pacific coastal forests of BC.

In addition to hazard of loss across the lifespan of a cavity, patterns of loss rates with time since harvest influence cavity availability in the long-term. If high loss rates are sustained, then cavity availability will continue to decline to the point where only the most windfirm trees persist and freshly excavated cavities are lost rapidly. Tree loss rates across time since harvest vary between forest systems. Thorpe et al. (2008) found that windthrow risk was highest during the first year following harvest (2.7% loss/yr) and then declined exponentially to 0.12%/yr after seven to eight years in black spruce (*Picea mariana* (Mill.) B.S.P.) forests of northern Ontario, while Scott and Mitchell

(2005) found no trend in post-harvest loss rates in forests within the Coastal Western Hemlock biogeoclimatic zone of BC.

Past studies have examined risk to all retained trees or snags in harvested stands, but few have examined the risk to cavity trees, which may have different loss dynamics; Gibbons et al. (2008) found that cavity-bearing trees were at 2.6 times higher risk of collapse than trees without cavities in harvested eucalypt forests of south-eastern Australia. I used a 16-year record of cavity creation and longevity in both harvested and unharvested forest stands in interior BC and addressed the following questions: 1) Does harvesting reduce the longevity of retained cavities compared with those in uncut forest? 2) What cavity tree characteristics affect risk of loss after harvesting? and 3) What is the pattern of cavity loss with time since harvest? I predicted that rates of loss would be highest in the years immediately following harvest when cavities in the most susceptible trees would be lost more quickly, followed by a decline in loss rates and eventual stabilizing as only the most windfirm cavity-trees remain (Fig. 2.1).

METHODS

Study area

The persistence of individual cavities were monitored for up to 16 years between 1995 and 2010 at 22 study sites in interior BC. Because all harvested sites were in continuous forest, and there was a difference in cavity longevity between continuous forest and aspen grove forest types (chapter 2), I included only continuous forest sites in this analysis. The study area is described in detail in Chapter 1.

Eleven of my sites were harvested between 1998 and 2005, which involved removal of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex. Loud.) and/or hybrid spruce (*Picea engelmannii* x. *glauca*), with retention of most trembling aspen and veteran interior Douglas-fir, either as part of reserves or individual trees throughout the sites. Eight of these sites were clear-cut with reserves, which involved removal of 44–95% of basal area, and three sites were partially harvested with 15–30% basal area removal in restricted areas of the site (Table 3.1). For the purpose of this analysis, I divided these partially harvested sites into cut and uncut sections and considered any retained forest patch within 100 m of a harvested area to be a reserve. Most additional

retention patches at my harvested stands were ~ 1 ha in size and were situated around natural features, such as riparian areas, wetlands, or rock outcrops.

The remaining 11 sites were not harvested, except for two sites where selective removal of large interior Douglas-fir occurred 60 to 80 years ago and one site which had a 4 ha section logged using horses in 1998.

Data collection

To locate active cavity nests, the study sites were systematically searched for signs of fresh excavation and existing cavities. Nests up to 5.2 m high were visually monitored using ladders, mirrors and flashlights, and starting in 2006 video cameras on extendable poles were used to inspect cavities up to 15 m high. A nest was considered active when there was at least one egg or nestling present. Nest cavities were monitored in subsequent years until they were no longer usable (when the section of tree containing the cavity broke off or fell over, the cavity chamber decayed, or the entrance grew over). The primary source of cavity loss at my sites was windthrow or stem breakage (90%; chapter 2).

Tree decay class was measured during the first year a cavity was found active using the scale developed by Backhouse and Louiser (1990; Figure 2.2). For this analysis, decay classes 1 and 2 were grouped into an “alive” category, decay class 3 was “recently dead”, and decay classes 4 through 6 were “dead with advanced decay” because they had similar patterns of loss. All nest trees were in decay classes 1 through 6.

Statistical analysis

I used Cox proportional-hazards regression to model the hazard of cavity loss throughout their lifespan in relation to harvest treatment (unharvested, cavities retained as isolated trees in clearcuts, and cavities retained within wildlife reserves) and decay stage (alive, recently dead, and dead with advanced decay). The hazard ratios produced by Cox proportional-hazards models represent the proportional risk of cavity loss compared with the baseline hazard level (Fox 2002), which were unharvested stands and alive decay class in my analysis. All models were fit using the “survival”

package in the statistical program R, version 2.7.0 (Therneau and Lumley 2009, R Core Development Team 2010).

I fit three alternative models to predict the hazard of cavity loss that included the following factors: Model 1) harvest treatment; Model 2) harvest treatment and decay stage; and Model 3) harvest treatment, decay stage, and an interaction of harvest treatment and decay stage (Table 3.2). Harvest treatment was included as a time-dependent covariate, which allows a covariate value to change part-way through the lifespan of a cavity (e.g. when forest surrounding an existing cavity was harvested). The model including an interaction term of harvest treatment and decay stage allowed me to test whether cavities in more decayed trees were more susceptible to loss after harvest than those in less decayed trees.

To estimate baseline annual cavity loss rates, I divided the number of cavities lost across all unharvested study sites in a year by the total number of cavities available for loss in the previous year (excluding right-censored individuals). I then averaged these annual loss rates to give a mean annual loss rate in unharvested forest, weighted by the number of cavities at risk. Post-harvest annual loss rates were calculated from data aggregated across harvested sites by the number of years since harvest.

To assess the pattern of cavity loss rates with time since harvest, I fit three candidate models, excluding the unharvested forest data: 1) an intercept only model; 2) a linear decline; and 3) a nonlinear, reverse sigmoidal curve (Figure 3.1). The reverse sigmoid curve was a generalized form of the logistic function, which modelled rate of loss (R) with the number of years since harvest (t) as follows:

$$R(t) = A + \frac{K - A}{1 + e^{(t-M)}}$$

where K is the maximum loss rate, A is the minimum loss rate, and M is the time at which loss rates are at their median value. All models were weighted by the sample size of cavities that were at risk in a particular time period. I assessed the relative goodness of fit of my three candidate models and ranked them using Akaike's Information criterion

(Burnham and Anderson 2002). Loss rate models were fit using the “stats” package in the statistical program R, 2.7.0 (R Core Development Team 2010).

RESULTS

The fates of 1319 cavities in 985 trees were monitored for up to 16 years in total and up to 12 years after harvesting. Most cavities were in trembling aspen (1257), and the remainder were in lodgepole pine (25), interior Douglas-fir (24), hybrid spruce (10) and birch (*Betula* spp.; 1). Of these cavities, 587 were in isolated trees surrounded by a clear-cut, 46 were embedded in wildlife reserves, and 748 were in unharvested forest. Sixty-two cavities (5%) were represented in more than one harvest treatment (ie. uncut, then cut and retained as an isolated tree or within a wildlife reserve) during their lifespan. Most, but not all, cavities in harvested stands were either excavated or first located after harvesting occurred as all harvested stands were monitored for 2 to 9 years before harvest.

Of the 1319 cavities monitored, 767 were found in the year that they were freshly excavated, while 552 were found after the year they were excavated, allowing me to assign a minimum age, but not an exact age. I tested for a difference in lifespan between these cavity types using a Cox proportional hazards model and found none (likelihood ratio test = 1.84, df = 1, $p = 0.18$), thus I included both groups in my analyses.

Harvest treatment and decay class, but not an interaction of the two, were important predictors of hazard rate in the top model (Table 3.2). Cavity trees in unharvested forest had the lowest hazard of loss (13% annual loss) and were used to represent baseline hazard levels. Isolated cavity trees retained in clearcuts had the highest rates of loss (22% annual loss, 70% higher than baseline rates), while cavity trees in wildlife reserves experienced an intermediate risk of loss (19.5% annual loss; 48% higher than baseline rates), given the equivalent levels of decay (Table 3.3). Although there was a clear trend of higher hazard rates across harvest treatments, only

the hazard rates for cavities in unharvested stands and in isolated trees in clearcuts had non-overlapping confidence intervals (Table 3.3).

The average annual rate of cavity loss prior to harvesting and at unharvested sites was 13% (95% CI = 11–15%) and ranged from 5 to 19% per year (Figure 3.2). The nonlinear, reverse sigmoid curve best fit the pattern of loss rates with time since harvest (Table 3.4). Annual loss rates nearly doubled following harvest to their maximum value (K) of 23%, and remained high for six years, after which they declined rapidly, reaching a median value (M) after 7.5 years, and stabilized after 11 years at a minimum value (A) of 8% (Figure 3.2). Post-harvest loss rates remained higher than pre-harvest loss rates for eight years following harvest.

DISCUSSION

My study of persistence of tree cavities builds on past studies of snag longevity after harvesting and the general dynamics of cavity loss to directly address the effects of harvesting on cavity longevity. I found that there was a 70% reduction in survival for cavities in harvested sites compared with unharvested sites, and a 48% reduction in reserves. Furthermore, loss rates were initially high following harvest but then declined below pre-harvest levels. Most of the aspen trees (key tree supporting nesting cavities) were retained on the study plots. Because such live trees survive longer than dead and decayed trees, cavity loss rates would have been significantly higher if only dead trees (snags) were retained in harvested plots. Thus, it is important to retain live trees as well as dead “wildlife” trees and to have the dead trees in group retention patches.

Increased risk of loss for retained wildlife trees and the potential for windthrow at newly created edges is a well-documented phenomenon; trees at newly created edges are exposed to higher levels of wind but may not have the root or stem structure to withstand the wind (Scott and Mitchell 2005). Studies of cavity persistence with respect to tree and forest stand factors are more limited, but results show that factors related to wind and stability, such as distance to edge, tree diameter, and tree decay stage strongly affect loss rates of cavity trees (Lindenmayer and Wood 2010, Chapter 2). In the southern interior of BC, loss rates of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) increased by a factor of 2.4 in harvested sites compared with unharvested stands and

Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) loss rates were 20 times greater in harvested forest (Huggard et al. 1999). The high variation in rates of loss of retained trees or patches suggest that forest systems may vary in factors such as topography, climate, soil composition, and tree species which have been shown to affect windthrow susceptibility (Scott and Mitchell 2005). Many of the cavities at my sites were in live aspen trees, but a cavity-nesting community that relies on more quickly decaying dead trees might suffer a more rapid decrease of available nesting substrates in partially harvested stands. Tree loss rates are typically highest in stands where high percentages of basal area are removed and for tall, narrow tree forms (Scott and Mitchell 2005). My results support these findings in that cavities were at the highest risk of loss when retained as isolated trees, followed by cavities in wildlife reserves which presumably received some protection from the wind, but still experience increased wind velocities due to removal of surrounding forests. Cavities in unharvested forests were at the lowest risk of loss and even lower in unharvested aspen groves in a grassland matrix (Chapter 2). Therefore, I suggest that including reserves as part of an overall tree retention plan will be very beneficial to extend the lifespan of available nest cavities. Our sites are only moderately influenced by wind disturbance events and forest ecosystems with wind as a key disturbance would have an even greater hazard of loss of cavity trees.

Interestingly, loss rates were initially high and then declined to levels below the baseline levels of loss based on pre-harvest and unharvested control sites. Either most of the highly susceptible trees were lost soon after harvest, leaving the more stable, wind-resistant after these first few years, and/or after 5 years the remaining trees had acquired a higher wind firmness (e.g. by losing major branches or by growing larger root systems). Assuming that baseline rates of cavity loss are near equilibrium, the drop in loss rates after 8 years to below equilibrium levels suggests that cavity abundance levels will reach a new equilibrium. At my sites, woodpecker populations increased after cutting and excavated in new trees, enabling the maintenance or increase of cavity nester populations in harvested sites that retained significant levels of aspen and large interior Douglas-fir (Drever et al. 2008). Trees that were selected by woodpeckers for new excavation three to four years after cutting likely were relatively more windfirm than

cavity trees that remained after harvest, and thus woodpeckers may have been selecting for the more robust trees for excavation in harvested stands. The increase in woodpecker populations in partially harvested stands would also increase the number of cavities for nesting. However, it is uncertain how cavity recruitment rates change at time-scales longer than eight years. If sites become poorer habitat for woodpeckers, or few suitable nest trees remain, low rates of loss may not balance low cavity recruitment rates.

In conclusion, I found that harvest had a negative impact on cavity survival that was greater for cavities retained in clearcuts than in wildlife reserves. Loss rates were highest in the first five years following harvest and then declined to below pre-harvest levels after eight years, suggesting that cavities that survive the initial period of high loss, or are created after harvesting in trees that survive this period, are relatively hardy and contribute to long-term tree cavity resource supply. Although harvesting does decrease cavity lifespan and causes direct loss when machines knock trees down, my results indicate that this effect is not catastrophic and it is certainly worthwhile to retain aspen cavity trees as well as potential cavity trees in partially harvested forests. The loss of cavity trees from harvesting is also mitigated by increases in woodpecker populations that excavate a new supply of cavities. Wildlife patches appear to provide some protection from windthrow to embedded cavity trees and also provide more complex habitat and so it is important to retain cavity trees in reserves wherever possible. Retention of these nesting resources will provide habitat for a diverse community of cavity-nesting birds and mammals, and help to conserve forest biodiversity in managed landscapes.

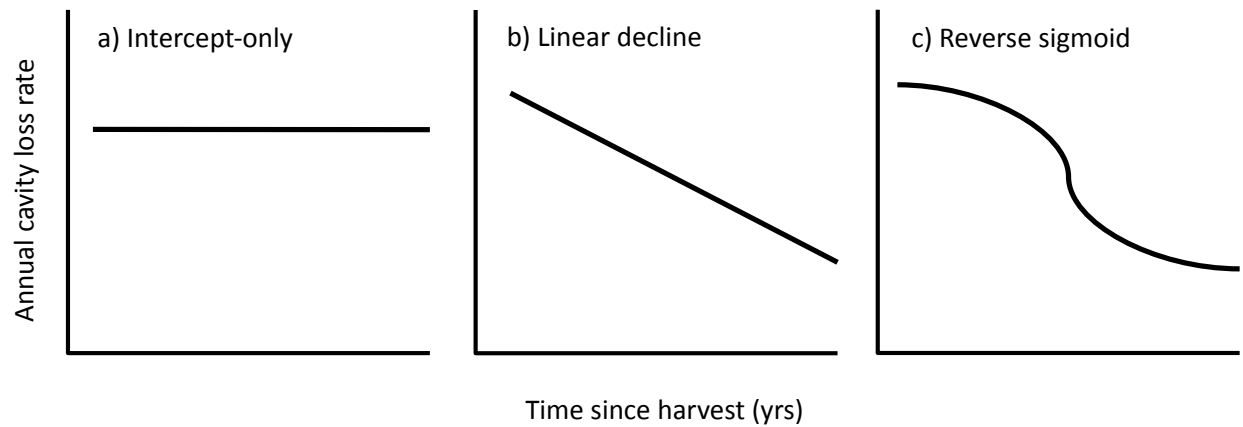


Figure 3.1. Schematic of three scenarios for how loss rates of retained cavity trees may change with time since harvest. Labels indicate the model used to describe each alternative.

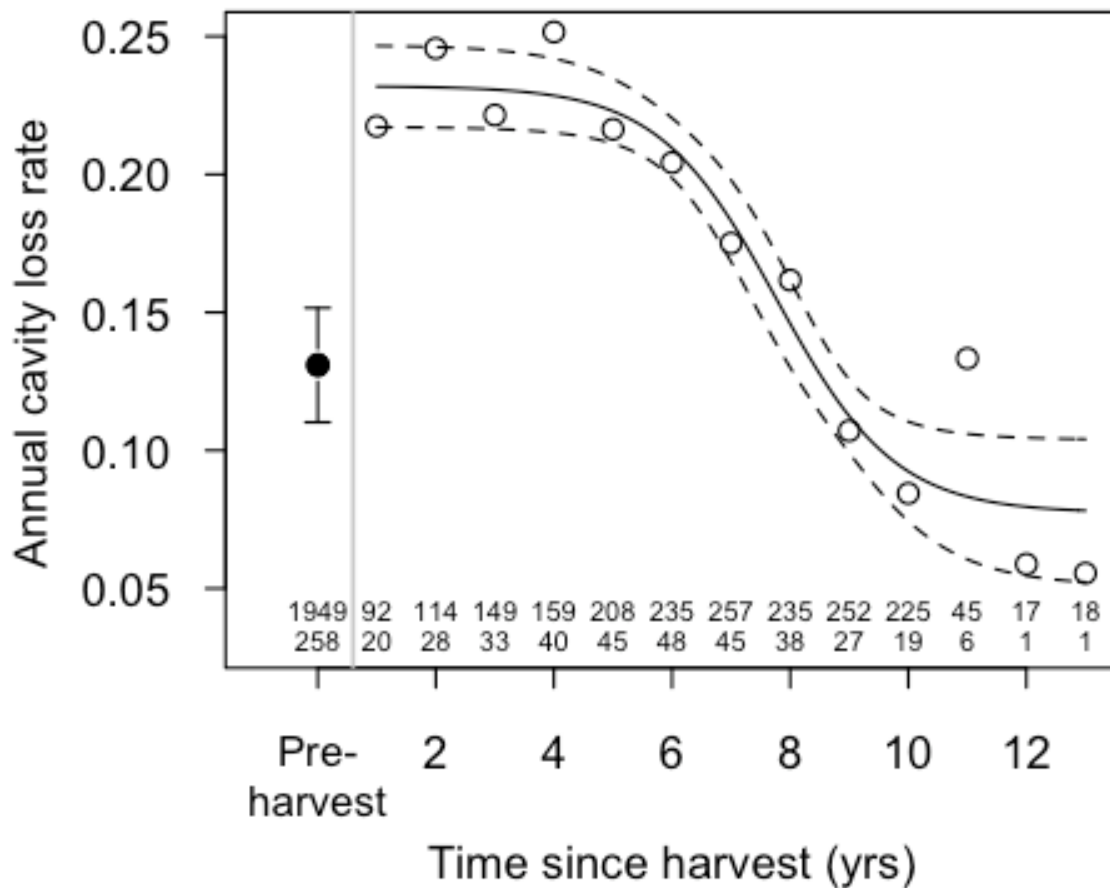


Figure 3.2. Mean annual loss rate prior to harvesting (error bars=95% CI) and cavity loss rates across years since harvesting (dashed lines=95% CI) for 1319 cavities at 22 study sites, 1995 to 2010, in interior British Columbia, Canada. The vertical grey line divides the pre-harvest and post-harvest time periods. Sample sizes are given for the total number of cavities in standing trees in the previous year (cavities at risk; top line) and the number of cavities lost (bottom line). There were only three sites with data for more than 10 yrs since harvest and thus sample sizes are lower for 11 to 13 years post harvest (see Table 3.1).

Table 3.1. Summary of harvest treatment and basal area removal for all trees and aspen trees at 22 sites in interior British Columbia, Canada.

Site	Years monitored	Year(s) harvested	% total basal area removed	% aspen basal area retained
Unharvested sites				
Solitary Woods	1995-2010	NA	NA	NA
Tongue	1995-2010	NA	NA	NA
Y	1995-2010	NA	NA	NA
Rock Lake	1995-2010	NA	NA	NA
South Hawks Control	1996-2010	NA	NA	NA
Little Till 2	1998-2010	NA	NA	NA
Mailbox Control	1997-2010	NA	NA	NA
Military Gate	1995-2010	NA	NA	NA
7 Mile	1997-2010	NA	NA	NA
MLF	1995-2001	NA	NA	NA
Doc English	1995-2001	NA	NA	NA
Harvested sites				
Sword Pine	1997-2006	2005	0.22	0.68
Dingwall 2	1997-2010	2001	0.29	0.96
Dingwall 1	1997-2010	2000	0.30	0.86
Hermit Hill	2002-2010	2004	0.44	1.00
Missed Moose	1997-2010	2001	0.57	0.89
Little Till 1	1998-2010	2002	0.74	0.77
Coldstream triangle	1996-2010	2001	0.77	0.06
Fork	1996-2010	2001	0.79	1.00
Mailbox Cut	1996-2010	2002, 05 ^a	0.61, 0.83 ^b	0.98, 0.76 ^b
South Hawks Clearcut	1996-2010	1998	0.83	1.00
Knife	1996-2010	2001	0.95	0.42

^aSections of site were clear-cut with reserves in both 2002 and 2005.

^bBoth proportions given are relative to pre-harvest basal area.

Table 3.2. Results of model selection based on Cox proportional-hazards models of loss in relation to harvest treatment and decay stage for 1319 cavities in interior British Columbia, Canada (1995-2010). Models are ranked from most plausible to least plausible and k is the number of parameters.

Predictor variables	ln(L)	k	AIC	Δ AIC
Harvest treatment, decay stage	-1031.4	5	2072.8	0
Harvest treatment, decay stage, harvest treatment x decay stage	-1028.2	9	2074.4	1.6
Harvest treatment	-1104.2	3	2214.4	141.6

Table 3.3. Model parameters for Cox proportional hazards model predicting hazard rate in relation to harvest treatment and decay class for 1319 cavities in interior British Columbia, Canada (1995-2010)

Variable	Coefficient	se(coeff)	Hazards ratio ^a	95% CI for the hazards ratio ^b
Unharvested ^c	-	-	-	-
reserve	0.39	0.38	1.48	0.71-3.11
clearcut	0.53	0.16	1.7	1.23-2.34
decay A ^c	-	-	-	-
decay B	1.16	0.18	3.2	2.27-4.51
decay C	0.69	0.22	1.99	1.30-3.04

^a The hazards ratio is equal to $\exp(\text{estimated coefficient})$ and represents the change in hazard compared to a “control” for categorical variables (harvest treatment and decay stage). A hazards ratio of 1 means that there was no change in hazard, a hazards ratio above 1 indicates an increase in hazard (shorter lifespan), and below 1 indicates a decrease (longer lifespan).

^b When the 95% CI for the hazards ratio does not include zero the coefficients differ significantly from 1 at the 5% level, designated bold font.

^c The unharvested treatment and live tree decay stage were used as the baseline to which the other levels of each of these factors were compared.

Table 3.4. Results of model selection for three models of cavity loss rate in relation to time since harvest. Sample size is 1319 cavities in interior British Columbia, Canada (1995-2010). Models are ranked from most plausible to least plausible.

Model	$\log(L)^a$	k^a	AIC ^a	ΔAIC
Reverse sigmoid	373.095	4	-738.19	0
Linear	29.45	3	-52.9	685.29
Intercept-only	16.7	2	-29.4	708.79

^a k is the number of fixed- and random-parameters; $\log(L)$ is the log Likelihood; AIC is Aikake's Information Criterion.

CHAPTER 4. GENERAL DISCUSSION AND MANAGEMENT RECOMMENDATIONS

GENERAL DISCUSSION

Tree cavities are a vital nesting resource for cavity-nesting communities, and their abundance can limit the populations of some species, especially in managed forests (Newton 1994, Aitken and Martin 2008, Cockle et al. 2010). Persistent cavities are used many times across their lifespans by a range of species that rely on existing nest cavities in order to breed (Sedgewick 1997). Long-lived cavities are an important structural resource and their conservation in harvested landscapes will help to maintain forest biodiversity (Lance and Phinney 2001, Lindenmayer et al. 2006). Tree forms and conditions, forest types, and formation agents will also affect the availability of suitable nest cavities for individual species of secondary cavity-nesters because such factors influence cavity persistence. My major results for temperate forests of interior BC showed that cavities in live trees lasted longer than cavities in dead trees, cavities in continuous forest stands lasted longer than those in aspen groves, and cavities created by strong excavators lasted longer than those created by weak excavators, or the keystone excavator at my study sites, the northern flicker. Additionally, cavities in trees retained after harvesting had an increased risk of loss across all decay classes, but this effect was somewhat mitigated by retaining cavities embedded in wildlife reserves.

The few previous studies of factors influencing cavity loss also reported similar effects for tree form and stand context. For example, Lindenmayer and Wood (2010) found that cavities in mountain ash (*Eucalyptus regnans*) forests of Australia were increasingly susceptible to loss with increasing levels of tree decay and smaller tree diameters. Wesolowski (2011) also found a strong effect of decay class on survival, as well as differences in cavity longevity across tree species in Poland. The latter study also found that cavity persistence was associated with the species of woodpecker which created them, as a result of the decay classes and tree species selected by different excavators; weaker excavators selected trees that were softer, with more advanced decay than strong excavators. My study confirmed that cavity longevity is strongly influenced by factors that relate to risk of windthrow in aspen trees. I also showed that longevity depended on formation agent and forest type where underlying tree and context variables differed.

Past studies of tree retention in clearcuts generally showed increased risk of windthrow to these trees, especially trees with small diameter-to-height ratios, and high exposure to the wind (e.g. Scott and Mitchell 2005). However, I have not found any studies that directly quantify loss rates of cavities retained in harvested stands compared with those in unharvested stands. I found that partial harvest had a negative impact on cavity survival that was greater for nest cavity trees retained in clearcuts than in wildlife reserves. Loss rates were highest in the first five years following harvest and then declined to below pre-harvest levels after eight years, suggesting that cavities that survive the initial period of high loss, or are created after harvesting in trees that survive this period, are relatively hardy and contribute to long-term cavity resources.

SUGGESTIONS FOR FUTURE RESEARCH

To complete the picture of cavity availability dynamics, it is necessary to quantify formation rates and to examine cavity quality across a range of forest types. Cavities are modified over time as they are enlarged by secondary users and decay processes, or filled in by debris (Blanc and Walters 2008). Additionally, changes in the patch and forest context may alter the quality of a cavity (Norris and Martin 2008). Investigation of cavity reuse across the lifespan of a cavity and with changing cavity characteristics would help to determine the actual contributions of long-lived cavities to nesting resources.

MANAGEMENT APPLICATIONS

In order to ensure conservation of long-lived tree cavities in managed forests, the focus should be on retaining trees which are living, unhealthy, and of large diameter based on my research in temperate forests. 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 in western Canada and US has been to retain dead, decayed snags as wildlife trees in managed forests (e.g. Bull and Partridge 1986, Garber et al. 2005), but my results indicate that cavities in live trees persist the longest. Thus, in northern temperate mixed forests, 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 plan on the continuous recruitment of trees that would be suitable for excavation of new tree cavities.

Although partial harvesting does decrease the lifespan of retained trees supporting cavities, my results indicate that this effect is not catastrophic and it is certainly worthwhile to retain aspen (*Populus tremuloides* Michx.) cavity trees as well as potential cavity trees in harvested forest. Wildlife patches appear to provide some protection from windthrow for cavity trees embedded in retention patches and these also provide more complex habitat; thus, it is important to retain cavity trees in reserves in addition to isolated individuals in clearcuts. Retention of these nesting resources will provide habitat for a diverse community of cavity-nesting birds and mammals, and help to conserve forest biodiversity in managed landscapes.

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