Cavity Availability, Characteristics and Use by Over-wintering Birds and Mammals in Southern Yukon

by

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Abstract

Cavity using birds and mammals are significant components of boreal forest communities, and the availability of tree cavities suitable for roosting and resting may be critical for supporting these communities. Furthermore, cavity availability and habitat suitability may limit populations of over-wintering northern species that use tree cavities as a strategy for coping with extreme cold. However, research investigating the potential cavity, tree or habitat requirements of over-wintering, northern boreal species is limited. Therefore, the objectives of this study were 1) to examine winter cavity-use by birds and mammals in relation to their availability in southern Yukon, and 2) to examine the influence of cavity microclimate on winter cavity selection.

Four study areas were established throughout southern Yukon, each containing white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), mixedwood (white spruce/trembling aspen (*Populus tremuloides*)), and spruce bark beetle (*Dendroctonus rufipennis*) affected spruce forest sites. Tree-cavities were located within each site and surveyed during the day and night to observe cavity use by birds and mammals. Cavity, tree and habitat characteristics were recorded for comparisons among forest types, between healthy and beetle-affected forests, and between used and unused cavities. Densities and proportions of natural and excavated cavities were not significantly different among forest types; however, some cavity characteristics differed among spruce, mixedwood and pine forests (i.e. cavity height, entrance shape and tree appearance), and between healthy and beetle-affected forests (i.e. cavity height, entrance area and tree appearance). Cavity volume, height and live conifer cover best predicted cavity-use for all bird species; however, only live conifer cover was a predictor of cavity-use for American three-toed woodpeckers (*Picoides dorsalis*). Three-toed woodpeckers preferred to roost in relatively healthy spruce forests, while boreal chickadees (*Poecile hudsonicus*), and hairy woodpeckers (*Dryobates villosus*) preferred to roost in pine forests. All species avoided beetle-affected spruce forests. Overall, birds preferred smaller, deeper, east-oriented cavities with relatively small entrances, located within forests with high live conifer cover. Low, shallow cavities in small-diameter trees were avoided. Surprisingly, mammals were not observed resting in tree-cavities; however, red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys sabrinus*) did use cavities for caching food and appeared to prey on or scavenge cavity-roosting birds.

The importance of cavity microclimate to roost-site selection was examined by determining which cavity, tree and habitat characteristics affected cavity temperatures, and by exploring the relationships between cavity-site temperatures and cavity use. Average sunset temperature increment (*air temperature – cavity temperature*), along with cavity height, depth, and volume, were predictors of cavity-use for three-toed woodpeckers. Furthermore, cavities used by three-toed woodpeckers were marginally warmer at sunset than unused cavities. Neither nightly nor sunset temperatures were predictors of cavity-use when all species were combined, which suggests that microclimate was a less important consideration in cavity selection by species other than three-toed woodpeckers. Though not a predictor of cavity-use, diameter-at-cavity-height had a significant positive effect on cavity temperatures. Entrance orientation had a significant negative effect on nightly cavity temperatures, with south-facing entrances having marginally lower average nightly temperatures, likely due to wind effects. Smaller and deeper cavities were warmer and were preferred by roosting birds, and both variables were also predictors of cavity-use. Live conifer density had a significant positive effect on external air temperatures, and a marginal positive effect on internal cavity temperatures, but was not a predictor of cavity-use when temperatures were included in analyses.

Beetle-affected forests contained more potential roost-sites than did other forest types but were avoided by cavity-users. Though salvage-logging in beetle-affected forests may not affect winter cavity use by birds, more research is needed to fully understand the importance of these forests to resident cavity-using bird and mammal populations. Dense, mature conifer forests containing beetle-killed and infested trees were important winter-roost habitat for most cavity-users; therefore, these forests should be conserved to maintain the integrity of the cavity-using boreal forest community.

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Chapter 1:
General Introduction and Thesis Overview

Cavity using birds and mammals are significant components of boreal forest communities, and the availability of tree cavities for roosting and nesting is thought to be critical for supporting these communities (Newton 1994; Aitken and Martin 2012). Furthermore, winter resource availability and habitat suitability are thought to be limiting factors in the populations of non-migratory bird species (Sherry and Holmes 1995). This may be especially true of over-wintering, northern species that use cavities to withstand extreme cold weather conditions. For many bird species, cavity-roosting reduces the energy requirements for thermoregulation, thus, reducing the risk of starvation and allowing for the reallocation of energy to other vital processes (Wolf and Walsberg 1996; Mainwaring 2011; Gruebler et al. 2014). Therefore, the thermal qualities of available roost sites are likely critical for roosting birds that need to conserve energy during long, cold nights. In southern Yukon Territory, Canada, many resident bird and mammal species are known to depend on tree-cavities for nesting and roosting. These species include: Boreal chickadee (*Poecile hudsonicus*), black-capped chickadee (*Poecile atricapillus*), mountain chickadee (*Poecile gambeli*), red-breasted nuthatch (*Sitta canadensis*), downy woodpecker (*Dryobates pubescens*), hairy woodpecker (*Dryobates villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), boreal owl (*Aegolius funereus*), American marten (*Martes americana*), red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*) (Buskirk and Powell 1994; Sinclair, et al. 2003; Naughton 2012; Patterson 2012).

Few studies have quantified cavity availability and characteristics in the boreal forests of North America (e.g. Paragi 2010) or in Eurasian boreal forests (e.g. Pulliainen and Saari 2002;

Bai et al. 2003; Andersson 2018). Research in the unmanaged forests of the boreal forests of Mongolia (Bai et al. 2003) found higher densities of cavities in mixed forests than in conifer forests, which was attributed to there being fewer naturally-formed broken branch cavities in conifer forests. Furthermore, research in the northwestern boreal forests of Alaska (Paragi 2010) examined differences in cavity characteristics among various tree types and found that cavity entrance size, height above ground, and cavity tree diameter were greater for deciduous trees than for conifers.

Many studies have explored cavity and nest habitat use by birds and mammals for breeding (Rothwell 1979; Rendell and Robertson 1989; Steeger and Hitchcock 1998; Wiebe 2001; Aitken and Martin 2004; Hough and Dieter 2009), but relatively few studies have examined winter cavity use. Furthermore, most of the published research on winter cavity use has focused on species and populations within southern and sub-boreal forest regions. Research has explored winter rest-site use and selection red squirrels (Rothwell 1979), and northern flying squirrels (Cotton and Parker 2000) and winter roost-site use by woodpeckers (Covert-Bratland et al. 2007; Gentry and Vierling 2008), but as these studies focused on southern and sub-boreal forest regions, the results may not be representative of cavity use by boreal forest populations. Trudeau et al. (2011) studied winter cavity use by northern flying squirrels in the Canadian boreal forest and found that they tended to select rest-sites in ground burrows and external nests, suggesting that availability of tree-cavities may not limit flying squirrel populations. This may also be true of Eurasian pine marten (*Martes martes*) as research in Scandinavian boreal forests showed that marten use ground burrows more often during colder temperatures (Brainerd et al. 1995). The percent of live conifer cover at roost sites is thought to be important for protection against weather and predation for American three-toed woodpeckers (Zapisocki et al. 2000) but little else is known of winter cavity use by this species. Research on nest cavity use by Eurasian three-toed woodpeckers (*Picoides tridactylus*) in northern Finland (Pakkala et al. 2018) showed that they tended to use cavities in moderately large-diameter trees, and with relatively low heights above ground, as many cavities were in dead, broken trees. They also tended to use dead or decaying trees, for reasons likely related to ease of cavity excavation.

Few studies have investigated the influence of cavity-site characteristics on cavity microclimate. Paclik and Weidinger (2007) and Pinowski et al. (2006) examined the relationships between various characteristics and cavity temperatures during winter nights and found that smaller entrances reduced internal cavity heat loss, cavities in living trees were warmer than those in dead trees, and temperatures decreased with an increase in volume. Results from northern flicker (*Colaptes auratus*) nest-cavity research in interior British Columbia (Wiebe 2001) showed that cavity temperatures increased with tree health and diameter, and that south-oriented cavities were warmer, possibly due to the influence of the sun. However, entrance orientation may also be important for reasons related to wind exposure. Though much research has examined the winter microclimates of potential cavity roost-sites and discussed the implications for cavity-roosting birds (McComb and Noble 1981; Pinowski 2006; Paclik and Weidinger 2007; Coombs et al. 2010; Gruebler and Widmer 2014), few studies have investigated the relationship between cavity microclimate and winter roost-site selection by birds. Velky et al. (2010) compared the microclimates of winter roost-cavities to unused cavity-sites and found that European great tits (*Parus major*) selected cavities that were warmer at sunset. However, this was a controlled experiment which used artificial cavities (nest boxes), and therefore, the results may not represent tree-cavity selection in natural environments. No known studies have compared the winter microclimates of used and unused tree-cavities in natural conditions.

The goal of this research was to better understand the extent to which birds and mammals depend on tree-cavities in winter, and to identify cavity-site characteristics that predict cavity-use and thermal quality. In Chapter 2, I examined winter cavity use in relation to cavity availability to determine the winter roost and rest-site requirements of birds and mammals in southern Yukon by: 1) comparing cavity and cavity-bearing tree densities and characteristics among forest types, 2) performing statistical comparisons of the characteristics of used and unused cavity-sites, 3) determining which cavity, tree and habitat characteristics best predicted cavity use, and 4) calculating selection indices to identify significant selection preferences. In Chapter 3, I examined the importance of cavity microclimate to winter cavity selection by birds in southern Yukon by: 1) determining which cavity, tree and habitat characteristics affected cavity temperatures, 2) exploring the relationships between cavity-site temperatures and cavity use, and 3) determining whether cavity temperatures, in combination with other cavity-site characteristics, were predictors of cavity use.

If conservation and forest management practices are to be well informed, more information is needed about winter cavity use by North American boreal bird and mammal species and the availability of cavities suitable for withstanding northern winters. The results of this study provide information that can be used in the conservation and management of cavity-using birds and mammals in northern boreal forest communities. Specifically, this information can help guide forest use and management practices such as firewood cutting and salvage logging of beetle-killed stands in northern boreal forests, ensuring that winter roost-sites with preferred characteristics are retained on the landscape.

Chapter 2:
Cavity availability and use by over-wintering birds and mammals in southern Yukon

Introduction

Cavity using birds and mammals are significant components of boreal forest communities, and the availability of suitable tree cavities for roosting and nesting may be critical for supporting these communities (Newton 1994; Aitken and Martin 2012). Furthermore, winter resource availability and habitat suitability are thought to be limiting factors in the populations of non-migratory bird species (Sherry and Holmes 1995). This may be especially true of over-wintering, northern boreal species that use tree cavities as a strategy for coping with extreme cold. Cavity densities tend to be lower in northern forests, relative to more southern regions (Remm and Lohmus 2011), and therefore, the availability of cavities suitable for winter roosting may be particularly critical to maintaining viable populations of northern species.

Few studies have quantified cavity availability and characteristics in the boreal forests of North America (e.g. Paragi 2010) or in Eurasian boreal forests (e.g. Pulliainen and Saari 2002; Bai et al. 2003; Andersson 2018). Research in the unmanaged boreal forests of Mongolia (Bai et al. 2003) found higher densities of cavities in mixed forests than in conifer forests, which was attributed to there being fewer naturally-formed broken branch cavities in conifer forests. Research in the northwestern boreal forests of Alaska (Paragi 2010) examined differences in cavity characteristics among various tree types and found that cavity entrance size, height above ground, and cavity tree diameter were greater for deciduous trees than for conifers. Other research has explored habitat use by cavity-roosting birds in the boreal forests of North America (Imbeau and Desrochers 2002; Hadley and Desrochers 2008; Thompson et al. 2016), and have suggested that dense, mature forests are preferred winter habitat, but cavity availability was not included as a factor in habitat selection.

Many studies have explored cavity and nest habitat use by birds and mammals for breeding (Rothwell 1979; Rendell and Robertson 1989; Steeger and Hitchcock 1998; Wiebe 2001; Aitken and Martin 2004; Hough and Dieter 2009), but relatively few studies have examined winter cavity use. Furthermore, most of the published research on winter cavity use has focused on species and populations within southern and sub-boreal forest regions. For example, research has explored winter rest-site use and selection by red squirrels (Rothwell 1979) and northern flying squirrels (Cotton and Parker 2000), and winter roost-site use by woodpeckers (Covert-Bratland et al. 2007; Gentry and Vierling 2008), but as these studies focused on southern and sub-boreal forest regions, the results may not be representative of cavity use by boreal forest populations. Trudeau et al. (2011) studied winter cavity use by northern flying squirrels in the boreal forests of eastern Canada and found that, though flying squirrels used tree-cavities for diurnal resting, they tended to select rest-sites in ground burrows and external nests, suggesting that availability of tree-cavities may not limit flying squirrel populations. This may also be true of Eurasian pine marten (*Martes martes*) as research in Scandinavian boreal forests showed that they use ground burrows more often during colder temperatures (Brainerd et al. 1995). For American three-toed woodpeckers, the percent of live conifer cover at roost sites is thought to be important for protection against weather and predation (Zapisocki et al. 2000) but little else is known of winter cavity use by this species. Research on nest cavity use by Eurasian three-toed woodpeckers in northern Finland (Pakkala et al. 2018) showed that they tended to use cavities in moderately large-diameter trees, and with relatively low heights above ground, as many cavities were in dead, broken trees. They also tended to use dead or decaying trees, for reasons likely related to ease of cavity excavation. The winter roost site requirements of three-toed woodpeckers and other resident boreal bird species are little understood. Overall, little is known about the availability of suitable roost-cavities and winter cavity use in the northern boreal forests of North America as a combination of remoteness, limited access, and harsh winter conditions may have constrained winter research in this region. If conservation and forest management practices are to be well informed, more information is needed about winter cavity use by northern boreal bird and mammal species and the availability of cavities suitable for withstanding northern winters.

The purpose of this study was to examine winter cavity use in relation to cavity availability in southern Yukon to determine the winter roost and rest-site requirements of birds and mammals in a northern boreal forest. Winter cavity use and availability was examined by: 1) comparing cavity and cavity-bearing tree densities and characteristics among forest types, 2) comparing the characteristics of used and unused cavity-sites, 3) determining which cavity, tree and habitat characteristics best predicted cavity use (backward step-wise logistic regression), and 4) calculating selection indices to identify significant selection preferences (i.e. cavity use in relation to availability). I predicted that cavity densities would be greater in mixedwood forests than pine and healthy spruce forests, due to more broken branch holes in deciduous trees (Bai et al. 2003). However, I also predicted that cavity densities would be greatest in beetle-affected sites, as these forests would have higher proportions of dead-standing trees that would be easier for cavity producers to excavate. As entrance areas are larger and cavity heights higher in deciduous trees than in conifers (Paragi 2010), I predicted that these variables would have higher values in forests with higher proportions of deciduous trees (mixedwood or pine). As dead-broken trees are likely to be more abundant in forests with higher proportions of dead trees, and as strong and weak excavators tend to take advantage of decayed, broken tree-tops when choosing a cavity-site (Bunnell 2013), I predicted that beetle-affected spruce forests would contain greater proportions of dead-broken cavity trees compared to other forest types. I also predicted that three-toed woodpeckers would show a preference for roost sites with more live conifer cover as these trees are likely to provide protection from weather and predators (Zapisocki et al. 2000), and that cavities used by three-toed woodpeckers would have larger diameter-at-cavity-heights and would be lower to the ground due to a preference for dead-broken trees (Pakkala et al. 2018). Preferences for smaller cavities, smaller entrances, and for south-oriented entrances were predicted for reasons related to the thermal quality of roost-sites. Finally, I predicted that very few flying squirrels and marten would be observed resting in tree cavities as they tend to use ground burrows for withstanding cold temperatures (Brainerd et al. 1995; Trudeau et al. 2011).

Methods

Study area and design

Four study areas were established throughout southern Yukon, each containing three 40-hectare sites representing the forest types within each area (Figure 2.1). The Mendenhall study area contained white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*) and mixedwood (white spruce/trembling aspen (*Populus tremuloides*)) forest sites, all in the vicinity of Mendenhall Subdivision and the Mendenhall River wetland complex. The Mendenhall pine forest site was also located within Kusawa Territorial Park. The Ibex study area contained white spruce, lodgepole pine, and mixedwood forest sites, all within or near the Ibex Mountain and Takhini River Valley. The Chadburn study area contained the same three forest types, and all were located within Chadburn Lake Park, near the city of Whitehorse. Finally, the Kluane study area consisted of 3 spruce bark beetle (*Dendroctonus rufipennis*) affected white spruce forest sites, all within 15 kilometers of the village of Haines Junction. Two of the Kluane sites were also located within Kluane Wildlife Sanctuary. The beetle-affected sites were established for the comparison of cavity availability and use to the three "healthy" spruce forest sites in the other study areas. Though each site was largely representative of a broad forest type, other tree species and small stand types were also present, permitting the determination of whether birds and mammals selected cavity sites with certain characteristics, in preference to others available on the landscape. Study areas were spread across a large area to account for ecological and geographical variation across southern Yukon, and to capture potential behavioral variation among populations of cavity-using species. Forest sites were spaced at a minimum distance of 2 kilometers, to ensure that individuals were not detected in more than one site, which was determined to be an adequate spacing for research on the winter ecology of American three-toed woodpeckers (Imbeau and Desrochers 2002).

Mixedwood forest sites were composed of between 35–50% deciduous trees, the majority of which were aspen. The remaining trees were either spruce or a mix of spruce and pine. Spruce forest sites were composed of between 75–90% spruce trees, with most of the remaining trees being willow (*Salix* spp.*)* and aspen. The pine forest sites chosen for this study were composed of 53–60% lodgepole pine trees, with most of the remaining trees being spruce, willow and aspen (Figure 2.2). Though the general criteria for a forest to be considered "dominated" by a species is a proportion of $\geq 75\%$, all scouted pine-dominated forests were young and lacked trees of adequate size (>10 cm) for cavity excavation; therefore, a lower limit criterion of 50% pine cover was chosen for these sites. A minimum tree diameter-at-breast-height criterion of 10 cm was based on the minimum diameter of red-breasted nuthatch cavity trees observed by Thomas et al.

(1979), which is the smallest resident cavity-using bird species in Yukon. Beetle-affected spruce sites were generally composed of 80% white spruce, 45% of which were dead and showed evidence of spruce beetle infestation. In contrast, only 12% of the spruce trees in the healthy spruce forests were affected by spruce beetles (Figure 2.2).

The Kluane study area was located within the Ruby Ranges ecoregion, which is characterized by a cooler and drier climate relative to other regions across southern Yukon, and by a white spruce-dominated landscape (Smith et al. 2004). Mean annual temperatures range from -3 to -7°C and mean January minimum temperatures range from -30 to -35°C (Smith et al. 2004). Sites within this study area were located within forests significantly altered by a 30-year beetle infestation that affected an area of over 350,000 hectares (Garbutt et al. 2007). All other study areas were located within the Southern Lakes ecoregion, which is characterized by a relatively wetter and warmer climate, and a pine-dominated landscape (Smith et al. 2004). Mean annual temperatures for the Southern Lakes ecoregion range from -1 to -4°C and mean January minimum temperatures range from -21 to -25°C (Smith et al. 2004).

Cavity searches

Cavities were located in the fall of 2017 by systematically walking 26 transects, spaced 25 meters apart, across each 632 x 632-meter (40-hectare) study site. Transects were zigzagged, using a GPS, to an approximate distance of 12.5 meters on either side of a central line, which was intersected every 25 meters. This spacing and search method ensured maximum land and tree area coverage (Figure 2.3). Tall and densely-branched trees that may have contained high and hidden cavities were twice circled at approximate distances of 5 and 15 meters, while carefully searching trunks and large branches using binoculars. The effort spent searching for tree cavities was approximately 1 hour per transect (26 hours per site) equaling an estimated total of 312 search hours (approximately 45 days) for all sites. Total distance walked during cavity searches was approximately 470 km (39 km per site). Once a cavity-tree was located, its coded location was recorded on a GPS and marked with flagging tape. Cavity height, tree species, number of cavities in a tree, and tree appearance were also recorded, to aid in their relocation at night. Subsets of 3 transects, within one randomly-selected site belonging to each forest type (total=12), were re-walked in the fall of 2018 to look for newly excavated and missed cavities. Cavity types surveyed in this study included excavated and natural holes in standing trees and broken treetops. However, broken-top cavities were not included in analyses as none were definitively used for roosting, and cavities with vertical depths greater than two meters were not included as the bottoms were not visible or reachable with the cameras.

Cavity surveys

Tree cavities were surveyed during the day and night using two portable camera systems, which consisted of lit cameras attached to a telescopic pole, and wirelessly connected to a monitor. The camera systems were used to detect cavity occupation and to identify the species and number of individuals that occupied a cavity. A Peeper Camera system (IBWO.org, North Little Rock, AR) was used to survey most cavities, but a THZY 1200P Wireless Endoscope system (Warm Electronics LTD, London, UK) was required to search cavities with entrances too small (<3.8 cm horizontal diameter) for the Peeper Camera to access. Eleven rounds of cavity use surveys were conducted during daylight hours to detect roosting/resting nocturnal species (i.e. owls and flying squirrels) and during the night to detect diurnal species (i.e. woodpeckers, chickadees, nuthatches, red squirrels, and marten), representing a total of approximately 460 hours of monitoring survey effort. Winter cavity-use surveys began in November and ended in mid-April, when boreal owls were observed preparing and defending cavities for nesting.

Surveys concluded at this time as owl nest defense behaviors likely prevented other species from selecting their preferred winter-roosting/resting cavities. Two additional rounds of surveys were conducted in early June of 2018 and 2019 to determine whether winter-roosting/resting cavities were also being used for nesting, and whether species not observed using cavities in winter were using them for nesting.

Cavity, tree and habitat measurements

To determine the characteristics of available and used cavities, information on entrance area, vertical cavity depth (lower lip of entrance to cavity floor), cavity volume, cavity height, entrance orientation (four cardinal directions), wood condition (% decay), cavity type (natural or excavated), entrance shape (circular, ovular, irregular) and cavity lining material were collected for each cavity that was low and safe enough to measure. Areas of circular entrances were approximated using entrance-hole diameters and the formula for the area of a circle ($A=\pi r^2$). Areas of ovular entrances were calculated using the maximum vertical and horizontal entrance-hole diameters and the formula for the area of an ellipse ($A=\pi r_1 r_2$), where r_1 is the maximum horizontal diameter and r_2 is the maximum vertical diameter. Irregularly-shaped entrance areas were approximated by dividing them into regular shapes (square, oval and triangle (*1/2 base × height*)), based on proportionate field drawings, and adding the areas of the various shapes. Cavity volume was approximated using cavity length (floor to ceiling), horizontal cavity depth (inner edge of lower lip of entrance to the back wall of the cavity), and the formula for the area of an ellipsoid ($V = 4/3\ \pi \times 1/2\ length \times 1/2\ horizontal\ depth \times 1/2\ cavity\ width$), assuming that cavity width is equal to horizontal cavity depth. Wood condition (percent of wood decay) was approximated by estimating the proportion of soft wood to hard wood within a cavity and recorded as less than or greater than 50%. Wood was considered soft if it could be easily flaked off by hand. Cavity volume measurement and calculation methods were based on those used by Andersson et al. (2018). Wood condition classification methods followed those used by British Columbia's Ministry of Forestry and Range and Ministry of Environment, in the "Field Manual for Describing Terrestrial Ecosystems, 2nd edition" (2010). Other cavity measurement and calculation methods used in this study followed those used by Martin and Eadie (1999) and Aitken and Martin (2004).

Tree characteristics recorded included species, diameter-at-cavity-height (DCH), bark retention (% of bark remaining within 1 meter of cavity entrance) and tree appearance (living, unhealthy, dead-whole, dead-broken). Bark retention and tree appearance classification and measurement methods followed those from the "Field Manual for Describing Terrestrial Ecosystems, 2nd edition" (2010). For habitat context, forest and stand characteristics such as tree species composition, canopy density (%), cavity density, tree density (ha^{-}), and live conifer cover (%) were recorded at each cavity location. Canopy densities were estimated for each cavity-site based the average of four measurements made with a spherical densiometer, at points 5 meters from the cavity tree, in each of the cardinal directions. Tree density calculations were based on the number of trees counted within four 100 m^2 (25m x 4m) rectangular plots running lengthwise in each cardinal direction (total area = 400 m^2), each beginning 2 meters from the center of each cavity tree to prevent the double-counting of trees. The total number of trees within both plots were multiplied by 25 to estimate cavity-site tree densities, per hectare. The percent of live conifer trees at each cavity site was estimated based on the percent of live conifers counted within the tree density plots.

Statistical analyses

Comparisons of cavity and cavity-tree characteristics, and regression and selection index analyses were based on those that were measured and surveyed over both winters. Statistical analyses were performed with RStudio version 1.2.1335 (RStudio Team 2018) and the package Companion to Applied Regression (car) version 3.0-3 (Weisberg 2019), using significance levels of $\alpha = 0.05$. Shapiro-Wilks tests were used to test the normality of continuous variables, using a 95% confidence level.

i) Cavity and cavity-tree densities and proportions of natural and excavated cavities

As the numbers of available cavities and cavity-bearing trees differed between the first winter and the second winter, densities were calculated separately for statistical comparisons. Densities of cavities and cavity-bearing trees were calculated as *number of available cavities or cavity-trees / 40 ha*, for each 40-hectare site. Proportions of natural and excavated cavities were also calculated separately for each site and survey year as *number of cavity type in site / number of cavities in site.* Mean cavity and cavity-tree densities were grouped by forest class (Mixedwood, Pine, Spruce, and Beetle-affected spruce) for comparisons. However, beetle-affected spruce site densities were only compared with those of healthy spruce sites, for the determination of whether there was a difference between the cavity and cavity-tree densities of healthy and unhealthy spruce forests. To test whether cavity and cavity-tree densities differed among mixedwood, pine, and spruce forests, ANOVA comparisons were performed. Density data were log-transformed to meet the assumptions of normality of residuals and homogeneity of variance for comparisons. To test whether cavity and cavity-tree densities differed between beetle-affected and healthy spruce forests, independent samples t-tests were used. To determine whether there was a difference in proportions of natural and excavated cavities among mixedwood, pine and spruce forests, Kruskal-Wallis rank sum tests for non-parametric data were performed as the data did not meet the assumptions of ANOVA. To test whether proportions of natural and excavated cavities differed between beetle-affected and healthy spruce forests, independent samples t-tests were used. Proportions of natural and excavated cavities in beetle-affected spruce sites were only compared with those of healthy spruce sites to determine whether there was a difference in proportions between healthy and unhealthy spruce forests. Furthermore, proportions of natural and excavated cavities were only calculated for those available in the second winter, as cavity type characteristics of those available in the first winter were not recorded.

ii) Comparisons of available cavity and cavity-tree characteristics among forest types

Characteristics of cavities and cavity-trees that were surveyed and available during both winters were compared among forest classes, and between beetle-affected and healthy spruce forests using univariate analyses. To test whether there were differences in cavity characteristics among mixedwood, pine and spruce forests, ANOVA comparisons performed on normally-distributed continuous variables (cavity volume, cavity height, and DCH) and Kruskal-Wallis rank sum tests were performed on non-parametric continuous variables (cavity depth and entrance area). Post-hoc pairwise comparisons using Tukey HSD (honestly significant difference) tests were performed on variables with significantly different ANOVA results (cavity height). To test whether there were differences in cavity characteristics between beetle-affected and healthy spruce forests, independent samples t-tests were performed on normally-distributed continuous variables (volume and DCH) and Wilcoxon rank sum tests were used on variables with non-parametric continuous data (depth, entrance area, and height). To determine whether there were differences in the characteristics of categorical variables (cavity orientation, tree appearance, and cavity shape) among forest types, Pearson's chi-square and Fisher's Exact tests were performed. Post-hoc tests, using the Bonferroni correction for multiple-testing, were performed on variables with significant results (tree appearance). Log-transformations were performed on continuous predictor variables with data that did not meet the assumptions of normality.

iii) Comparisons of used and unused cavity-site characteristics, and roost-site selection analyses

Characteristics of cavities, trees and habitat used by three-toed woodpeckers and by all species combined were compared with the characteristics of those not used. To determine whether there were differences between the characteristics of used and unused cavity-sites, independent samples t-tests were used to compare normally-distributed continuous variables (cavity volume) and Wilcoxon rank sum tests were used for non-normally distributed continuous variables (cavity depth, DCH, cavity height, entrance area, percent of live conifer cover, and tree density). Fisher's exact tests were used for comparisons of categorical variables (cavity orientation and wood condition). Arcsine transformations were performed on continuous predictor variables with proportional data and log-transformations were performed on those with continuous data that did not meet the assumptions of normality. One-tailed tests were performed on comparisons between the height, DCH and live conifer cover of used and unused cavities to test predictions that cavity heights were lower and DCH were greater for used sites. All other comparisons used two-tailed tests.

A backwards step-wise logistic regression using Akaike's Information Criterion (AIC) was used to determine which variables best predicted winter cavity use. Variables included in the step-wise regression were systematically "dropped" based on the lowest resulting AIC score until an increase in score indicated that the remaining variables best predicted cavity-use. No further analyses were performed on the model selected by the step-wise regression. The variables included in the analysis were DCH, cavity depth, cavity volume, cavity height, entrance area, entrance orientation, wood condition, percent bark retention, and percent of live conifer cover. Arcsine and log-transformations were performed on continuous predictor variables with data that did not meet the assumptions of normality. Variance inflation factor (VIF) scores were used to quantify the severity of multicollinearity among continuous variables, with a cutoff value of 4 for inclusion in the model. Chi-square tests were used to quantify multicollinearity among categorical variables. VIF scores < 4 for all continuous variables, and p-values > 0.05 from a chi-square test on all categorical variables, indicated weak collinearity among variables included in the regression.

A Manly's selection index (Manly et al. 1993, Krebs 1999) was used to determine which cavity, tree and habitat characteristics were selected for winter-roosting relative to what was available in all study sites combined. Only cavities and cavity-trees available in the second winter were included in analysis as the characteristics of the additional cavities available in the first year were not recorded. Selection indices were calculated for cavities used by three-toed woodpeckers and for all observed cavity-using species combined. As most used cavities were occupied by three-toed woodpeckers, the numbers of other cavity-using species were too low for independent analyses. Selection coefficients (w_i) for each variable category were calculated as $w_i = o_i / p_i$, where o_i was the ratio of the number of cavities occupied in category i to the total number of cavities occupied, and p_i was the ratio of the total number of cavities in category i to the total number of cavities. Standard errors for each selection coefficient were calculated as $SE(w_i) = \sqrt{} [(o_i (1 - o_i)) / Up_i]$, U being the total number of occupied cavities. Bonferroni corrected 95% confidence intervals were calculated for each selection coefficient, as $w_i \pm z_{a/I}\ SE(w_i)$ where I was the number of variable categories, and $z_{a/I}$ was the standard normal table value corresponding to an upper tail probability of $_{a\,/\,I}$ (Krebs 1999). A lower 95% confidence interval limit >1 indicated a significant preference and an upper limit <1 indicated significant avoidance. Variables included in the analysis were tree species, DCH, cavity depth, cavity volume, cavity height, entrance area, wood condition, cavity orientation, canopy density, and percent of live conifer cover.

Results

The number of cavities found within all 40-hectare sites totaled 515. However, of these cavities, only 333 (0.69 per hectare) were considered available for roosting during the first winter. Of the 182 cavities that were unavailable, 151 were incomplete as they were either unfinished "test holes" (<1cm in depth; n=106), in broken-top trees with no ceiling (n=20), had incomplete walls due to damage by animals or decay (n=3), or were in hollow trees with no visible floor (n=22). An additional 31 cavities were unavailable for roosting due to either woody debris blockages (n=2), squirrel debris (grass and moss; n=21), or ant debris (wood dust, needles and cone scales; n=8; Figure 2.4). In the second winter, only 304 cavities (0.63 per hectare) were available for roosting as an additional 10 cavities were filled with squirrel debris, 4 with ant debris, and 11 trees containing a total of 15 cavities had blown over. During the first winter, 283 trees contained available cavities, and there were 262 cavity-bearing trees during the second winter.

No completed new cavities were located during the second round of cavity searches; however, one tree contained two newly-created test-holes (unfinished cavities with no vertical depth). Two cavity-trees had been missed during the initial search, each containing one cavity. However, as the transect subsets were surveyed in the same manner, and by the same surveyor, it was concluded that these cavities were missed due to random sampling error as opposed to a systematic error. The characteristics of the two cavities and cavity-trees missed during the first round of cavity searches were not included in analyses. Of the 302 cavities available and surveyed over both winters, 286 were measurable; the remaining 16 were either too high or too unsafe to reach.

Cavity and cavity-tree densities and proportions of natural and excavated cavities

Cavity densities did not differ significantly among forest types in the first or second winter ($F_{2,6}$=1.537, *P*=0.289; $F_{2,6}$=1.326, *P*=0.334) or between beetle-affected and healthy spruce forests in the first or second winter ($t_{3.999}$=0.477, *P*=0.658; $t_{3.997}$=0.611, *P*=0.574; Table 2.1). Cavity tree densities also did not differ significantly among forest types in the first or second winter ($F_{2,6}$=0.855, *P*=0.471; $F_{2,6}$=0.858, *P*=0.470) or between beetle-affected and healthy spruce forests in the first or second winter ($t_{3.727}$=0.818, *P*=0.462; $t_{3.992}$=0.833, *P*=0.452; Table 2.1). Though not significantly different, cavity and cavity-tree densities were highest in beetle-affected spruce forest and lowest in pine forest in both the first and second year (Figure 2.5). Tree-cavities consisted of either natural cavities in broken branch holes or cracks in trunks (16%, n=50), or those excavated by birds (84%, n=254). The ratio of natural to excavated cavities was highest in mixedwood forest and lowest in spruce forest (Figure 2.6); however, they did not differ significantly among forest types ($\chi^2_{2,286}$=4.267, *P*=0.118), or between beetle-affected and healthy spruce forests ($t_{3.775}$=0.875, *P*=0.434). Though not significantly different ($t_{21.914}$=1.301, *P*=0.207), more natural cavities were found in deciduous trees (63%) than in conifers (Figure

2.7). Cavities were higher above ground in spruce trees ($F_{5,298}$=14.200, P=<0.001), but heights did not differ among other tree species (Figure 2.8).

Comparisons of available cavity and tree characteristics among forest types

Spruce forests had significantly greater cavity heights than did mixedwood and pine forests ($F_{2,181}$=10.480, P<0.001; Table 2.2), but heights did not differ significantly between mixedwood and pine forests (Figure 2.9). Cavity height and entrance area differed between beetle-affected and healthy spruce forests (cavity height: W=8568, P=<0.001; entrance area: W=3202, P=0.002), with mean cavity height being greater in beetle-affected forest and entrance area being greater in healthy spruce forest (Table 2.2, Figure 2.9). Cavity-tree appearance (live, dead-whole, and dead-broken) differed among mixedwood, pine, and spruce forests ($\chi^2_{9,159}$=202.070, P<0.001), with significantly more dead-broken trees in spruce forests than in mixedwood and pine. Tree appearance also differed between healthy and beetle-affected forests ($\chi^2_{6,157}$=192.340, P<0.001), with significantly more dead-broken trees in beetle-affected spruce forest than in healthy spruce forest. Tree appearance did not differ significantly between mixedwood and pine forests (Table 2.2, Figure 2.10). There were significantly more irregular-shaped cavities in mixedwood forests than other forest types ($\chi^2_{6,202}$=85.268, P<0.001), but cavity shape did not differ between healthy and beetle-affected forests (Table 2.2, Figure 2.11). Pine forest sites contained many (n=9; 20%) cavities within fire scars on the lower trunks of pine trees, and no fire-scarring or cavities within fire scars were observed in other forest types.

General cavity use

Over the course of two winter seasons, three bird species were observed using 15 different tree-cavities. These species included American three-toed woodpecker (n = 12), boreal chickadee (n = 2), and hairy woodpecker (n = 1). No mammals were observed resting in tree cavities during the day or night. Of the 302 cavities that were available and surveyed during both winters, 4.6% were used by birds in only the first or second year (n=14), 0.3% were used in both years (n=1), and 95.0% were not occupied in either year (n=287). In the first winter, roosting birds were observed occupying 1.2% of cavities (n=333) over 4 survey rounds, and in the second winter, cavity use was observed in 4.0% of cavities (n=302) over 7 survey rounds. One cavity was used by two different three-toed woodpeckers (one male and one female), on separate nights, throughout the second winter, and this was the same cavity occupied frequently during both winters. Of the 15 cavities used in both years, seven were reused by three-toed woodpeckers (one during both winters) and one was used at least twice by a boreal chickadee. One boreal owl appeared to be taking temporary shelter in a broken-top cavity, while hunting on a windy night, perhaps for protection from wind or for ease of hearing prey.

American three-toed woodpeckers used cavities with vertical depths between 5 and 18.5 cm (mean = 12.8 cm ± 3.6), and those with volumes between 833.5 and 4123.9 cm^3 (mean = 2311.2 cm^3 ± 1201.3; Table 2.3). Ten of twelve three-toed woodpecker roost-cavities were in broken trees with 50-75% decay, one was in a broken tree with >95% decay, and the other was in an unhealthy but intact tree with <25% decay. Nine of twelve three-toed woodpecker roost-cavities were in white spruce, 2 were in aspen, and 1 was in birch. All used cavities had a thick lining of fine wood chips, relative to those not used. Cavities used by three-toed woodpeckers had heights above ground ranging from 1.85 to 8.2 m (mean = 3.57 m ± 1.87), entrance areas from 16.3 to 33.2 cm^2 (mean = 22.3 cm^2 ± 4.1), and DCH from 12.9 to 29.9 cm (mean = 23.0 cm ± 5.0; Table 2.3). Finally, all but 2 three-toed woodpecker roost-cavity trees were in open gaps within dense spruce forest (66.7%) or on the edges of dense forest (33.3%). Both cavities used for winter roosting by boreal chickadees were relatively shallow (mean = 6.9 cm ± 0.2), had smaller volumes (mean = 1645.0 cm^3 ± 1721.3), and had smaller entrance areas (mean = 18.2 cm^2 ± 4.8), when compared to woodpecker roost cavities (Table 2.3). However, both chickadee cavities may have been originally excavated by woodpeckers. Though both chickadee cavities were in pine forest, they were both in white spruce trees. Both chickadee roost-cavity trees were broken with between 25 and 75% decay. Average chickadee cavity heights were nearly twice that three-toed woodpecker cavities (6.16 m ± 2.21). Average DCH of chickadee cavities were somewhat similar to that of three-toed woodpecker cavities (29 cm ± 1.4; Table 2.3). Though both chickadee cavities were lined with layers of fine wood chips, the layers were considerably thinner than those used by three-toed woodpeckers. The habitat characteristics of chickadee roost-sites were similar to those of three-toed woodpeckers. As only one cavity was used by a hairy woodpecker, comparisons could not be made to three-toed woodpeckers and boreal chickadees (Table 2.3).

No mammals were observed resting in tree-cavities during the day or night. However, red squirrels were observed visiting five cavities to cache or eat spruce cones, seeds and berries and/or possibly for temporary shelter. Furthermore, a red squirrel or flying squirrel had cached a mushroom inside a cavity during the summer or fall of 2018, but it had been eaten or removed between survey visits. During a pilot season during which remote cameras were tested as a sampling method for detecting winter cavity use, several red squirrels were observed frequently visiting cavities within a half-hour before and after sunrise, during the same time that three-toed woodpeckers were also observed leaving their roost-cavities. Also, one flying squirrel was captured by camera, entering a cavity at night, during the same pilot study. No other predator species were detected entering tree-cavities.

Two northern flying squirrels and one red squirrel were observed feeding hairless babies in tree-cavities in early June 2018, and one red squirrel appeared to be with young in early May 2019, suggesting that squirrels used tree-cavities for nesting but not for winter-resting, even though they were present or presumed present throughout the winter in all study sites. Boreal owls were also found nesting in tree-cavities but were not observed using them for winter roosting. In the spring of 2018 and 2019, boreal owls were observed nesting in two different tree-cavities. Boreal owls began defending and readying cavity-nests in early April, and hatchlings were fledged between mid-June and early July. Interestingly, no tree-cavities were used by other nesting bird species.

Comparisons of used and unused cavity-site characteristics and roost-site selection

Percent live conifer cover was significantly greater at roost-sites used by both three-toed woodpeckers and all species combined than at unused cavity-sites (W=1034, P=0.015; W=763, P<0.001) and used cavities had a greater height above ground than unused cavities when all species were combined (W=1105, P=0.028; Table 2.4). Cavity-use by all observed species combined was best predicted by cavity volume, cavity height, and percent of live conifer cover, based on the lowest AIC score achieved following backwards stepwise logistic regression (Table 2.5). For American three-toed woodpeckers, over both years, cavity-use was best predicted by percent of live conifer cover (Table 2.5).

Resource selection indices were calculated for cavity-sites used during both winters. Of the 11 variables examined for both three-toed woodpeckers and all observed species combined, all but wood condition was significantly preferred and/or avoided (Table 2.6). Three-toed woodpeckers showed strong preferences for birch trees, cavity height classes between 2–4 and 8–10 m, cavity depths between 10–20 cm, DCH between 30–40 cm, cavity entrance area between 30–40cm², cavity volume between 2500–5000 cm³, tree canopy densities of < 25%, live conifer cover between 50–75%, and an eastern entrance orientation. The preferences of all species combined were similar to those of three-toed woodpeckers, except that there was only a preference for cavity height between 8–10 m, and not for a height between 2–4 m, and there was no entrance area preference. Three-toed woodpeckers avoided cavity heights < 2 m, cavity depths < 10 cm, and live conifer covers of < 50%. With all species combined, there was no cavity depth class avoidance but diameter-at-breast-heights between 20–30 cm were avoided. Finally, when all species were combined, there was a significant preference for roost-cavities in pine forest and an avoidance of beetle-affected forest. Notably, all boreal chickadee roost-cavities and the only hairy woodpecker cavity were in pine forest. For three-toed woodpeckers, there was a significant preference for roost-cavities in healthy spruce forest and all species avoided beetle-affected forest.

Discussion

Cavity and cavity-tree densities and proportions of natural and excavated cavities

Cavity and cavity-tree densities did not differ among mixedwood, pine and spruce forests, which is contrary to what was predicted for this study and to the findings of other cavity availability research in the boreal forests of Mongolia (Bai et al. 2003). However, this is a similar result to research in the northeastern United States (Clugston 1999) that found no significant difference in cavity and cavity-tree densities among forest type classes, defined solely by species composition. It is likely that densities of cavities likely related more to the structural characteristics of a forest. For example, natural or unmanaged forests with higher densities of large trees, dead-standing trees and greater structural complexity have been shown to contain higher densities of cavities than logged and urban forests (LaMontagne et al. 2015; Andersson et al. 2018), and Paragi (2010) found that densities were higher in mature forests that contained abundant dead-standing trees. These findings support the results predicted in this study that showed that cavity densities were greatest in beetle-affected forests, where there were greater proportions of larger, dead-standing trees. It is possible that relatively high densities of excavated cavities in beetle-affected spruce forests are due to the historic abundance of primary excavators, such as American three-toed and black-backed woodpeckers, that took advantage of an abundance of beetle larva. Populations of three-toed woodpeckers and densities of their nesting cavities are known to increase where there is an abundance of bark beetle larva (Murphy and Lehnhausen 1998; Kelly et al. 2019; Saab 2019). Though there were not as many trees affected by spruce beetles in healthy spruce forest sites (12%) as there were in beetle-affected sites (45%), higher cavity densities in healthy spruce sites relative to mixedwood and pine sites may also be explained by a greater abundance of food for three-toed woodpeckers. Though mountain pine beetles (*Dendroctonus ponderosae*) are abundant in pine forests throughout most of western North America, they do not occur in Yukon, which likely explains greater cavity densities in the pine forests of other regions. Natural cavities did not occur with greater frequency in mixedwood forests, contrary to other research (Bai et al. 2003) that found that there were more naturally-formed broken branch cavities in mixed forests than conifer forests. However, 63% of natural cavities were found within deciduous trees, such as aspen and willow.

Total cavity densities during the first and second winter (0.69/ha and 0.63/ha, respectively) were relatively lower than densities observed in the more southern forests of interior British Columbia (Aitken 2002) where densities ranged from 0.95 to 2.86/ha in natural conifer and mixed forests. Lower cavity densities in northern forests have been shown to relate to lower amounts of annual precipitation in northern regions with continental climates and, thus, a lower incidence of trees with fungal heart-rot (Remm and Lohmus 2011). As both weak and strong excavators often take advantage of the softer heartwood in decayed trees (Bunnell 2013) fewer available trees with heart-rot may explain why cavity densities were higher in southern forests. It is also possible that cooler climates in northern forests reduce decay rates and, thus, the densities of cavities (Remm and Lohmus 2011). However, cavity densities in the unmanaged boreal forests of Sweden (Andersson et al. 2018) and eastern Canada (Ouellet-LaPointe et al. 2012) were also relatively higher than what was observed in this study, with cavity densities averaging 2.4/ha and 9.8/ha, respectively. Though it is unclear why cavity densities were greater in in the boreal forests of Sweden, it may relate to climate, the abundances of cavity excavators, or the abundances of trees of suitable size for excavation. Substantially greater densities of cavities in eastern Canadian forests was likely largely due to the study sites consisting only of deciduous forests, and because natural cavities are more abundant in deciduous trees than conifer trees (Bai et al. 2003).

Comparisons of available cavity and tree characteristics among forest types

Contrary to what was predicted, cavities were significantly higher above ground in spruce forests than in mixedwood and pine forests, despite there being significantly more dead-broken cavity trees in spruce forests. Cavities being higher in spruce forests was largely due to mixedwood forests containing a much larger proportion of aspen cavities (74%; Figure 2.12) than spruce forests (7%) and mean aspen cavity height being nearly half that of spruce cavities (Figure 2.8). However, this is somewhat contrary to what was observed in the Alaskan boreal forest (Paragi 2010) where cavities were significantly higher in deciduous trees. Lower aspen cavity heights observed in this study may have been due to the many cavities that had naturally formed in lower broken-branch holes of stunted trees. However, another possible explanation for cavities being higher above ground in spruce forests is that spruce sites may have had a greater proportion of large trees capable of housing higher cavities. Pine forest sites also contained many low naturally-made cavities in aspen and willow trees, but there were also many excavated cavities (n=9; 20%) within fire scars on the lower trunks of pine trees, which likely explains why cavities were lower in pine forests than in spruce forests. Fire scars are a common feature of mature pine forests and are created when low-intensity surface fires burn a tree's bark and cambium, exposing the surface of the sapwood and making it more vulnerable to fungal rot (McBride 1983). Both strong and weak excavators likely took advantage of the exposed and rotting wood when choosing a cavity-site within the pine forests. Also contrary to what was predicted, mean cavity height was greater in beetle-affected spruce forests, relative to healthy spruce forests, despite there being more dead-broken trees in beetle-affected sites. Greater cavity height in beetle-affected spruce forests may be due to there being more large-diameter trees that allowed for the excavation of higher cavities. Spruce-beetles typically infect older, larger trees (Hard 1983), so it is possible that the higher proportion of beetle-killed trees in the beetle-affected sites could reflect a higher proportion of large trees. Cavities in tall, large-diameter trees are known to be disproportionate to their availability, and woodpeckers tend to make cavities higher in large-diameter trees, likely for reasons related to predator avoidance (Bunnell 2013). Therefore, it is possible that higher cavities in beetle-affected forests could be explained by higher numbers of tall, large-diameter trees that contained three-toed woodpecker-excavated cavities. Significantly higher numbers of cavities in broken trees in healthy spruce forests than in mixedwood and pine forests was likely related to the relatively high proportion of spruce beetle-killed trees that had been weakened by rot and broken by wind. Furthermore, as predicted, there was a greater proportion of dead-broken cavity-trees in beetle-affected forests than in healthy spruce forests, likely due to there being a greater proportion of beetle-killed trees susceptible to wind blowdown, and because both strong and weak excavators often take advantage of the rotted, broken tree-tops when choosing a cavity-site (Bunnell 2013).

It was predicted that entrance area would be greater in forests that contained higher numbers of deciduous trees based on the findings of cavity availability research in Alaska (Paragi 2010); however, there were no differences in entrance area among mixedwood, pine and spruce forests. Entrance area was, however, found to be greater in healthy spruce forest than in beetle-affected forests, which may be explained by there being potentially more cavities made by weak excavators (e.g. chickadees) in the healthy spruce sites. Cavity entrances of weak excavators are usually irregularly shaped and, as they are often made in soft wood, are easily and often enlarged by weather and by other excavators over time (Andersson et al. 2018). Therefore, proportionately more irregularly shaped weak excavator cavities in healthy spruce sites than in beetle-affected sites (Figure 2.11) may explain some of the difference in entrance area.

Comparisons of used and unused cavity-site characteristics and roost-site selection

As predicted, three-toed woodpecker roost-sites had greater live conifer cover than unused cavity sites. This supports other research that suggests the importance of trees that retain leaves (i.e. needles) over winter to roosting three-toed woodpeckers for protection against weather and predation (Zapisocki et al. 2000). All three-toed woodpecker roost-sites were in spruce forest, pine forest, or spruce-dominated patches within mixedwood forest, which adds further support for the importance of live conifer cover to winter roosting birds. The results of this study also showed that live conifer cover at roost-sites was greater when boreal chickadees and hairy woodpeckers were included in analyses; however, this is likely due to 80% of used cavities being used by three-toed woodpeckers. Selection indices showed that both three-toed woodpeckers and all species combined preferred live conifer cover between 50 and 75% and avoided cover less than 50%. Furthermore, the results of the step-wise regression analysis showed that live conifer cover was a predictor of winter cavity use for all species and was the sole predictor of cavity-use by three-toed woodpeckers. It is possible that higher cover improves the microclimates of roost-sites (see Chapter 3) and provides more foraging opportunities, both of which may be important considerations in winter. As three-toed woodpeckers are bark beetle specialists and are known to excavate their cavities close to an abundant food source (Murphy and Lehnhausen 1998), it is possible that food that naturally occurs in dense coniferous forest influences the selection of roost-sites. Research on three-toed woodpecker winter foraging ecology (Imbeau and DesRochers 2002) and seasonal habitat use by hairy woodpeckers (Conner 1981; Covert-Bratland et al. 2006) suggested that population abundance within winter habitat is related to the abundance of wood-boring beetles and beetle-suitable trees, and this was shown to be true in Arizona pine forests (Covert-Bratland et al. 2007) even though canopy cover was greatly reduced by high-severity forest fires. All but one of the three-toed woodpecker roost-cavities in this study were in spruce forest where 12 to 45% of the spruce trees showed signs of beetle-infestation; therefore, food availability appears to be a factor in the selection of sites with greater live conifer cover. Boreal chickadees are highly associated with conifer forests during the winter and breeding season (Whitaker and Montevecchi 1997; Hadley and DesRochers 2008) so they would be expected to select roost-sites with greater live conifer cover. However, it is unclear how much of this selection is influenced by thermal factors, protection from predators, or food availability. Three-toed woodpeckers preferred roost-sites in healthy spruce forest, possibly because of the relatively high proportion of live conifers in spruce forests, and for reasons related to the thermal quality of roost-sites and food availability. Though cavities were most abundant in beetle-affected forests, both three-toed woodpeckers and all species combined avoided this forest type, possibly due to lower live conifer covers resulting in increased predation risk and a reduction in the thermal quality of roost-sites.

Contrary to what was predicted, used three-toed woodpecker cavities were not significantly lower to the ground than those not used; however, regression results showed that cavity height above ground was a predictor of cavity-use and selection indices showed a three-toed woodpecker preference for relatively low cavities. Three-toed woodpeckers preferred cavities between 2 and 4 meters, which was a similar result to other three-toed woodpecker research in the boreal forests of Finland (Pakkala et al. 2018) where the median cavity height was 4 meters. This height preference may be due to lower cavities having a greater DCH, and to the strong positive effect that DCH has on cavity temperatures (Wiebe 2001; Coombs et al. 2010). However, results also indicated a three-toed woodpecker preference for heights between eight and ten meters, but this result was due to one of only ten available cavities within this height range being occupied. Selection indices indicated that all observed species avoided cavities lower than two meters, which is a similar result to what Camprodon et al. (2008) found for cavity selection by birds in the northern Iberian Peninsula, and has been attributed to lower cavities being more accessible to predators (Mazgajski 2002; Camprodon et al. 2008). When all species were combined, used cavities were higher above ground than unused cavities. Furthermore, selection indices indicated a preference for heights between eight and ten meters, but not for heights between two and four meters, which may reflect a stronger preference for higher cavities by boreal chickadees and hairy woodpeckers (average = 6.16 m and 6.68 m, respectively) relative to three-toed woodpeckers (average = 3.57 m). Though cavities may be more exposed to wind at greater heights, predation risks may be lower, which is perhaps a worthy trade-off for chickadees who may not be as capable of fending off predators as are woodpeckers.

A nest cavity DCH range between 37.0 and 42.4 cm, observed by Carlson et al. (1998) and a mean DCH of 26.2 cm observed by Pakkala et al. (2018) is similar to the selection preference observed in this study for both three-toed woodpeckers and all species combined. All species preferred to roost in trees with a DCH between 30 and 40 cm, and there was an avoidance of trees with a DCH less than 30 cm only when all species were included in analyses. As predicted, cavity trees used by three-toed woodpeckers had a greater DCH than those not used, possibly for reasons related to radiative and conductive heat loss. For example, this diameter may be large enough to house a cavity with an ideal volume, while maintaining a wall thickness that minimizes heat loss by thermal conductance. Results from a study on northern flicker (*Colaptes auratus*) nest microclimates (Wiebe 2001) showed that trees with larger diameters were generally warmer, and that DCH was positively correlated with cavity volume.

Cavity volume was a predictor of winter cavity-use for three-toed woodpeckers and all species combined, and selection indices indicated strong volume preferences, suggesting that it is an important factor in winter cavity selection. Cavities with volumes between 2500 and 5000 cm^3 were preferred for roosting and no cavities with greater volumes were used, which confirms what was predicted for three-toed woodpeckers and is a similar finding to nest-cavity research that showed that used cavities were significantly smaller (Carlson et al. 1998). As most cavities were used by three-toed woodpeckers, this cavity volume range is likely best suited for their body size. Research has shown that smaller cavities are warmer (Andreev 1980; see Chapter 3), and that cavities with smaller volumes and thicker lining materials can increase internal temperatures and reduce energy expenditure in roosting birds by minimizing radiative and conductive heat loss (Pinowski et al. 2006). As all used cavities had a thick lining of fine wood chips, relative to those not used, it is possible that cavity volume was correlated with lining thickness; however, lining thickness was not quantified in this study. Minimizing heat loss and, thus, energy expenditure is likely of great importance to winter-roosting birds in northern boreal forests.

Though entrance areas of used cavities were not significantly smaller than those of unused cavities, three-toed woodpeckers showed a preference for an entrance area between 30 and 40 cm^2 over smaller and larger entrances; an area likely best suited to their body size. This confirms the prediction that smaller entrances are preferred as they minimize predation (Moeed and Dawson 1979; Nilson 1984; Martin et al. 2004) and can minimize convective heat loss due to wind (Pinowski et al. 2006). Many studies have illustrated the benefits of small cavity entrances (for example, Peterson and Gauthier 1985; Carlson et al. 1998; Bai et al. 2005; Camprodon et al. 2008), but the influence of entrance area on cavity microclimate and winter cavity-use is poorly understood.

Contrary to what was predicted, an east-oriented cavity entrance was preferred over south-oriented entrances by all species, which was also the preference observed for many species of nesting woodpeckers in Central Ontario (Lawrence 1967). Many studies have shown that entrance orientation can influence cavity temperatures (Haggerty 1995; Hooge et al. 1999; Wiebe 2001; see Chapter 3). For example, in more southerly latitudes, east-oriented cavities were shown to have higher average internal temperatures due to increased sun exposure (Hooge et al. 1999), which is contrary to Wiebe (2001) who found that south-facing cavities were warmer, likely due to the lower angle of the sun in more northerly latitudes. As the winter sun angle is very low in southern Yukon, the preference for an eastern orientation may be due to other factors such as wind exposure. Winter winds tend to come from the southwest in southern Yukon (Government of Canada 2019), so an east-facing cavity would often be on the leeward side of the tree. Haggerty (1995) found that breeding birds selected nests with entrances on the leeward sides of trees for protection from strong prevailing winds. Notably, no south-facing cavities were used for roosting; therefore, it can be suggested that birds preferred east-facing cavities as they were sheltered from prevailing southwest winds. The effect of entrance orientation on cavity temperatures is discussed in Chapter 3.

Though tree species, cavity depth, canopy density, and forest type were not selected in the step-wise regression models as predictors of cavity use, selection indices showed that categories within these variables were preferred or avoided. An apparent strong preference for cavities in birch trees is due to the only birch cavity being occupied by a three-toed woodpecker, though 11 of 15 roost-cavities were in spruce trees. As cavity volume may be dependent on the depth of a cavity, it is possible that preferences for cavities less than 20 cm in depth is also related to the thermal quality of a cavity. And as with cavity volume, three-toed woodpecker preference for cavities between 10 and 20 cm in depth, and avoidance of cavities less than 10 cm deep, may reflect the suitability of the cavities to their size. Average occupied cavity depths between 13.8 and 20.0 cm observed by Carlson et al. (1998) and avoidance of cavities with greater mean depths adds further support for a selection preference for this depth range. A preference by all species for a canopy density of less than 25% is the result of 1 of 9 roost-sites with this density being used, though 14 of 15 roost-sites had canopy densities of over 50%, 8 of which were over 75%. But as all used cavity-sites were either in open forest gaps within dense forest, or on the edges of dense forest, perhaps dense forests were preferred for roosting, while open flyways were also important for reasons related to predator evasion. Notably, when woodpeckers were flushed from cavities during night surveys, they were sometimes entangled in branches which delayed their escape and, perhaps, caused injury and excessive stress. Finally, though 11 of 15 cavities used by all species were in spruce forest or spruce-dominated patches within mixed forest, pine forests were preferred for roosting in proportion to their availability, particularly by boreal chickadees and hairy woodpeckers which only roosted in pine forest. Little is known of the winter ecology of boreal chickadees and hairy woodpeckers. Thompson et al. (2016) noted boreal chickadees using pine forests for winter-foraging in a sub-boreal forest region of eastern Canada, and Conner (1981) noticed an increase in pine tree use by hairy woodpeckers for foraging in southeastern Virginia. However, it cannot be concluded that a preference for roost-cavities in pine forests by woodpeckers was related to food availability as pine beetles are not known to occur in Yukon.

General cavity use

Most of the used cavities (80%) were occupied by American three-toed woodpeckers, which is not surprising as they are the most abundant resident woodpecker species in southern Yukon (Sinclair et al. 2003), and they likely roost only in tree-cavities. It was surprising that only two boreal chickadees and no black-capped chickadees were observed roosting in cavities given that they are very common throughout southern Yukon; however, it is possible that they were not solely roosting in tree-cavities. On rare occasions, black-capped and mountain chickadees have been observed roosting in ground or snow burrows (Smith 1997; Olson and Grubb 2007), which implies that they are not limited to roosts in tree-cavities. However, it is not known whether boreal chickadees share this behavior. One boreal owl appeared to be taking temporary shelter in a broken-top cavity while hunting on a windy night, perhaps for protection from wind or for ease of hearing prey. However, no boreal owls were observed day-roosting in tree cavities, which is not surprising as they are known to roost on branches and only use tree-cavities for nesting (Hayward et al. 1993). Other cavity-roosting bird species were uncommon or absent in most sites which likely accounts for why they were not observed using tree-cavities.

Though red squirrels did not appear to rest in tree-cavities at night, they were observed visiting five cavities during the day to cache and eat spruce cones, seeds and berries, or perhaps for temporary shelter. A sixth cavity temporarily contained a large mushroom that was likely cached by a red squirrel or flying squirrel. Red squirrels typically use external tree nests during the non-breeding season, in branches and in the crotches of forked branches (Rothwell 1979), so it is not surprising that they were not observed resting in tree-cavities. Furthermore, red squirrels typically use ground middens, not tree-cavities, to cache food (Vahle and Patton 1983; Gurnell 1984; Donald and Boutin 2011), so it is possible that some were using the cavities for warmth or protection from predators while they ate food retrieved from middens. However, as a spruce cone and a mushroom had been cached in tree-cavities, likely by red squirrels, they may also use them for caching food in southern Yukon. Red squirrels were observed feeding young in two tree-cavities not used for resting, so it appears as though they use cavities for nesting but not resting in southern Yukon.

Other mammal species were not observed using tree-cavities during the non-breeding season, and this could be due to low species abundance or to their natural histories. It was predicted that flying squirrels would use tree cavities less in winter than bird species as, though they are known to use tree-cavities for resting, they tend to select rest-sites in ground burrows and external nests (Trudeau 2011). As flying squirrels were observed feeding young in tree-cavities not used for resting, it is likely that ground burrows and grass nests are preferred for winter-resting in southern Yukon. As predicted, marten were not observed resting in tree cavities, likely due to their known tendency for using ground den-sites during winter (Brainerd et al. 1995).

Notably, the remains of two three-toed woodpeckers were found in their roost-cavities, and as only wings, feathers and bones remained, it is evident that they had been eaten. Remote camera captures of cavity visits by red squirrels in early morning, and flying squirrel visits at night, suggest that it is possible that both species may scavenge or hunt roosting birds. Though this is not evidence of squirrels resting in tree-cavities, it is evidence of cavity-use.

Conclusion

Cavity densities and proportions of natural and excavated cavities were not significantly different among forest types. However, cavity shape, height, entrance area, and cavity-tree appearance differed among forest types. The differences in cavity characteristics among forest types were likely the result of a combination of disturbance history (i.e. insect and fire) and the natural histories of the cavity-excavating species that inhabit the forests. Surprisingly, mammals were not observed resting in tree-cavities, which raises many questions related to how mammals cope with northern winters, such as where they rest and whether there are thermal and energetic benefits to resting in ground burrows or external nests. Cavity volume, height and live conifer cover best predicted cavity-use for all bird species; however, only live conifer cover was a predictor of cavity-use for three-toed woodpeckers. Three-toed woodpeckers preferred to roost in healthy spruce forests, and boreal chickadees and hairy woodpeckers preferred to roost in pine forests; however, all species avoided beetle-affected spruce forests suggesting that they are less important for roosting than for nesting and foraging. All cavity-site characteristics preferred and avoided by birds, and all characteristics that predicted cavity-use, are likely attributed to reasons related to predator avoidance, food availability, and microclimate. The microclimates of tree-cavities are likely important considerations in roost-site selection, particularly for non-migratory species that reside in regions with cold climates. The following chapter explores the influence of microclimate on winter cavity-use.

Table 2.1. Comparisons of cavity and cavity-tree densities among forest types and between beetle-affected and healthy spruce forests for year one and year two.

	Spruce, Mixedwood, and Pine forest			Beetle-affected and healthy spruce forest		
			Year 1			
	df	*Test statistic*	*P*	*df*	*Test statistic*	*P*
Cavity	2	1.537	0.289	3.999	0.477	0.658
Cavity-tree	2	0.855	0.471	3.727	0.818	0.462
			Year 2			
	df	*Test statistic*	*P*	*df*	*Test statistic*	*P*
Cavity	2	1.326	0.334	3.997	0.611	0.574
Cavity-tree	2	0.858	0.470	3.992	0.833	0.452

Data were log-transformed to meet the assumptions of normality for ANOVA comparisons. Significance levels of $\alpha = 0.05$ were used. There were no significant ANOVA or t-test results.

Table 2.2. Comparisons of available cavity and cavity-tree characteristics among forest types and between beetle-affected and healthy spruce forests.

	Spruce, Mixedwood, and Pine forest				Beetle-affected and healthy spruce forest			
	Test statistic	*df*	*P-value*	*Post hoc comparisons*	*Test statistic*	*df*	*P-value*	*Post hoc comparisons*
Continuous variables								
Cavity depth	5.139	2	0.077	S = M = P	4146	-	0.706	B = H
Cavity volume	2.189	2	0.115	S = M = P	-0.424	176.55	0.672	B = H
DCH	0.471	2	0.625	S = M = P	1.114	172.30	0.267	B = H
Entrance area	0.928	2	0.629	S = M = P	3202	-	0.002*	B < H
Height	10.480	2	< 0.001*	S > M = P	8568	-	< 0.001*	B > H
Categorical variables								
Cavity orientation	9.708	9	0.375	-	3.137	3	0.371	-
Tree appearance	202.070	9	< 0.001*	-	192.340	6	< 0.001*	-
Cavity shape	85.268	6	<0.001*	-	1.082	1	0.298	-

* indicates a significant difference. ANOVA and t-tests were used for normally distributed continuous variables; Kruskal-Wallis and Wilcoxon Rank Sum tests were used for non-normally distributed continuous variables. Chi-square tests were used for all categorical comparisons. Significance levels of $\alpha = 0.05$ were used for continuous variables, and $\alpha = 0.01$ for categorical variables due to small sample sizes.

Note: Using height as an example, "S > M = P" means that height was significantly greater in spruce forest than in mixedwood and pine forest but heights in mixedwood and pine forests were equal, and "B > H" means that height was greater in beetle-affected forest than in healthy spruce forest. Results of post-hoc tests on tree appearance and cavity shape are summarized in Figures 2.10 and 2.11.

Table 2.3. Means and standard deviations of characteristics of cavities used by American three-toed woodpeckers, boreal chickadees and hairy woodpeckers, during both winters.

Species	**Wood decay** (%)	**Bark retention** (%)	**DCH** (cm)	**Cavity height** (m)	**Entrance area** (cm²)	**Cavity depth** (cm)	**Cavity volume** (cm³)
ATTW (n=12)	58.3 ±17.0	75.0 ±25.0	23.0 ±5.0	3.57 ±1.87	22.3 ±4.1	12.8 ±3.6	2311.2 ±1201.3
BOCH (n=2)	50.0 ±17.7	87.5 ±0.0	29.0 ±1.4	6.16 ±2.21	18.2 ±4.8	6.9 ±0.2	1645.0 ±1721.3
HAWO (n=1)	62.5 N/A	87.5 N/A	24.4 N/A	6.68 N/A	35.3 N/A	14.5 N/A	3759.4 N/A

Table 2.4. a) Means and standard deviations of characteristics of cavity-sites not used, and of those used by American three-toed woodpeckers and all species combined, and b) comparisons of the characteristics of cavity-sites used by American three-toed woodpeckers and all species combined to unused cavity-sites.

	All species	**ATTW**	**Not occupied**	**ATTW vs not used**		**All species vs not used**	
	a)			b)			
Characteristics	Mean ± SD (n)	Mean ± SD (n)	Mean ± SD (n)	*Test statistic*	*P-value*	*Test statistic*	*P-value*
Continuous variables							
Cavity volume (cm^3)	2438.03 ± 1264.40 (12)	2467.44 ± 1204.75 (9)	2494.22 ± 3071.43 (274)	- 0.908	0.365	- 0.959	0.338
Cavity depth (cm)	12.23 ± 4.21 (12)	13.17 ± 3.94 (9)	13.84 ± 10.61 (274)	1480	0.559	1601	0.878
DCH (cm)	23.18 ± 5.02 (12)	21.74 ± 4.85 (9)	23.34 ± 6.82 (274)	1561	0.384	1525	0.336
Entrance area (cm^2)	22.80 ± 6.00 (12)	22.42 ± 4.65 (9)	22.09 ± 8.12 (274)	1383	0.352	1419	0.422
Height (m)	4.10 ± 2.30 (12)	3.35 ± 2.03 (9)	2.90 ± 1.79 (292)	1259	0.085	1105	0.028*
Live conifer cover (%)	69.15 ± 13.49 (12)	67.11 ± 13.90 (9)	48.87 ± 24.47 (248)	1034	0.015*	763	<0.001*
Tree density (ha^{-})	3254.17 ± 868.77 (12)	3272.22 ± 862.09 (9)	3127.01 ± 1633.31 (248)	1606	0.892	1427	0.439
Categorical variables							
Cavity orientation	-	-	-	-	0.529	-	0.143
Wood condition	-	-	-	-	0.656	-	0.545

* indicates a significant difference. Independent-samples t-tests were used for normally distributed continuous variables (cavity volume), Wilcoxon Rank Sum tests were used for non-normally distributed continuous variables (all other continuous variables), and Fisher's Exact tests were used for continuous variables. One-tailed tests were performed on DCH, height and live conifer cover, and two-tailed tests were performed on all other variables.

Table 2.5. Global and best model selection results from a backwards step-wise logistic regression using Akaike's Information Criterion.

All observed species				**American three-toed woodpecker**			
Global model							
Variable	***Df***	***Deviance***	***AIC***	***Variable***	***Df***	***Deviance***	***AIC***
DCH	1	101.19	119.19	Cavity depth	1	90.95	108.95
Cavity depth	1	101.24	119.24	Entrance area	1	90.95	108.95
Wood condition	1	101.26	119.26	Bark retention	1	90.96	108.96
Entrance area	1	101.30	119.30	DCH	1	91.07	109.07
Bark retention	1	101.37	119.37	Wood condition	1	91.32	109.32
Entrance orientation	1	101.78	119.78	Entrance orientation	1	91.51	109.50
Cavity volume	1	102.92	120.92	Cavity volume	1	92.27	110.27
<none>		101.19	121.19	Cavity height	1	92.48	110.48
Cavity height	1	107.06	125.06	<none>	1	90.90	110.90
Percent live conifer	1	107.35	125.35	Percent live conifer	1	94.35	112.35
Best model							
Variable	***Df***	***Deviance***	***AIC***	***Variable***	***Df***	***Deviance***	***AIC***
<none>		102.27	110.27	<none>		95.77	99.77
- Cavity volume	1	104.48	110.48	- Percent Live Conifer	1	99.6	101.6
- Percent Live Conifer	1	109.16	115.16				
- Cavity Height	1	109.22	115.22				

AIC scores determined the best model for predicting winter cavity use. The AIC scores associated with "<none>" are the result when no variables are dropped, and those associated with other variables are the resulting scores when a variable is individually dropped.

Table 2.6. Selection coefficients and 95% confidence intervals for cavity-site use by American three-toed woodpeckers and all observed species combined during both winters.

Cavity-site characteristics	**All observed species**		**American three-toed woodpecker**	
	coefficient	***confidence interval***	***coefficient***	***confidence interval***
Tree species				
Aspen	0.62	0.16-1.06	0.77	0.22-1.32
Birch	19.07*	16.46-21.67	23.83*	20.60-27.06
Pine	0.62	0.15-1.08	-	-
Spruce	1.18	.83-1.52	1.21	0.83-1.58
Wood condition				
Unhealthy live	1.04	.60-1.49	0.98	0.49-1.46
Dead	0.98	0.73-1.24	1.01	0.72-1.29
Height (m)				
0 - 2	0.18*	-0.07-0.43	0.23*	-0.08-0.53
2 - 4	1.45	0.92-1.98	1.81*	1.23-2.40
4 - 6	1.27	0.70-1.86	1.20	0.56-1.83
6 - 8	0.96	0.39-1.52	-	-
8 - 10	4.03*	2.90-5.15	2.52*	1.50-3.54
Cavity depth (cm)				
0 - 10	0.66	0.23-1.09	0.41*	0.01-0.82
10 - 20	1.72*	1.30-2.14	1.95*	1.56-2.35
> 30	-	-	-	-
Diameter-at-cavity-height (cm)				
20 - 30	0.45*	0.07-0.82	0.56	0.10-1.02
30 - 40	1.41*	1.09-1.73	1.47*	1.14-1.80
40 - 50	0.60	0.15-1.04	-	-
Entrance Area (cm²)				
20 - 30	0.62	0.20-1.03	0.58	0.12-1.03
30 - 40	1.43	0.96-1.90	1.59*	1.09-2.09
40 - 50	1.19	0.56-1.82	0.74	0.17-1.32
Cavity volume (cm³)				
0 - 2500	0.75	0.40-1.11	0.82	0.43-1.21
2500 - 5000	2.57*	1.86-3.27	2.29*	1.52-3.07
Entrance orientation				
North	1.13	0.63-1.64	0.57	0.12-1.01
East	1.68*	1.10-2.26	2.10*	1.44-2.77
South	-	-	-	-
West	1.03	0.53-1.53	1.29	0.69-1.89
Canopy density (%)				
0 - 25	2.12*	1.30-2.93	2.65*	1.64-3.66
25 - 50	-	-	-	-
50 - 75	0.85	0.43-1.26	1.06	0.59-1.53
75 - 100	1.25	0.81-1.69	0.98	0.49-1.47
Live conifer cover (%)				
0 - 25	0.38*	0.04-0.73	0.48*	0.05-0.90
25 - 50	0.24*	-0.03-0.51	0.30*	-0.04-0.64
50 - 75	1.59*	1.13-2.05	1.77*	1.27-2.27
75 - 100	1.59	0.96-2.21	0.99	0.40-1.58
Forest type				
Mixedwood	0.67	0.23-1.11	0.84	0.30-1.38
Pine	1.66*	1.01-2.30	0.52	0.07-0.96
Healthy spruce	1.50	0.98-2.02	1.87*	1.30-2.45
Beetle-affected spruce	0.34*	0.03-0.65	0.43*	0.04-0.81

Coefficients represent the ratio of cavity use to availability. *A lower 95% confidence interval limit >1 indicates significant preference and an upper limit <1 indicates significant avoidance. A blank value indicates that no cavities were used within a given variable class.

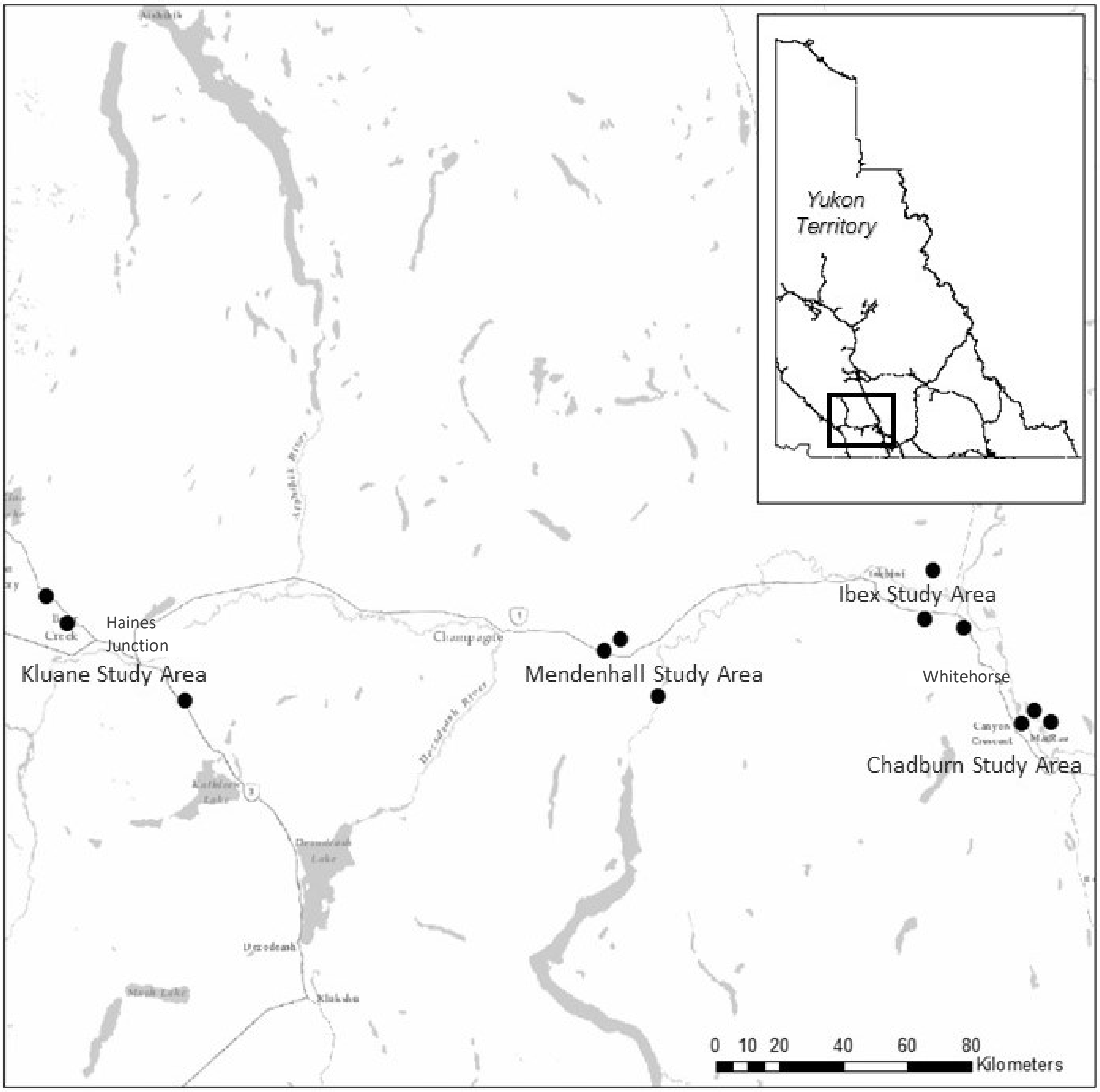


Figure 2.1. Cavity availability and winter use study area and forest site locations in southern Yukon, Canada. The Kluane study area consisted of 3 beetle-affected spruce forest sites, and the Mendenhall, Ibex and Chadburn study areas consisted of a pine, spruce and mixedwood site. All forest sites were 40 hectares in area.

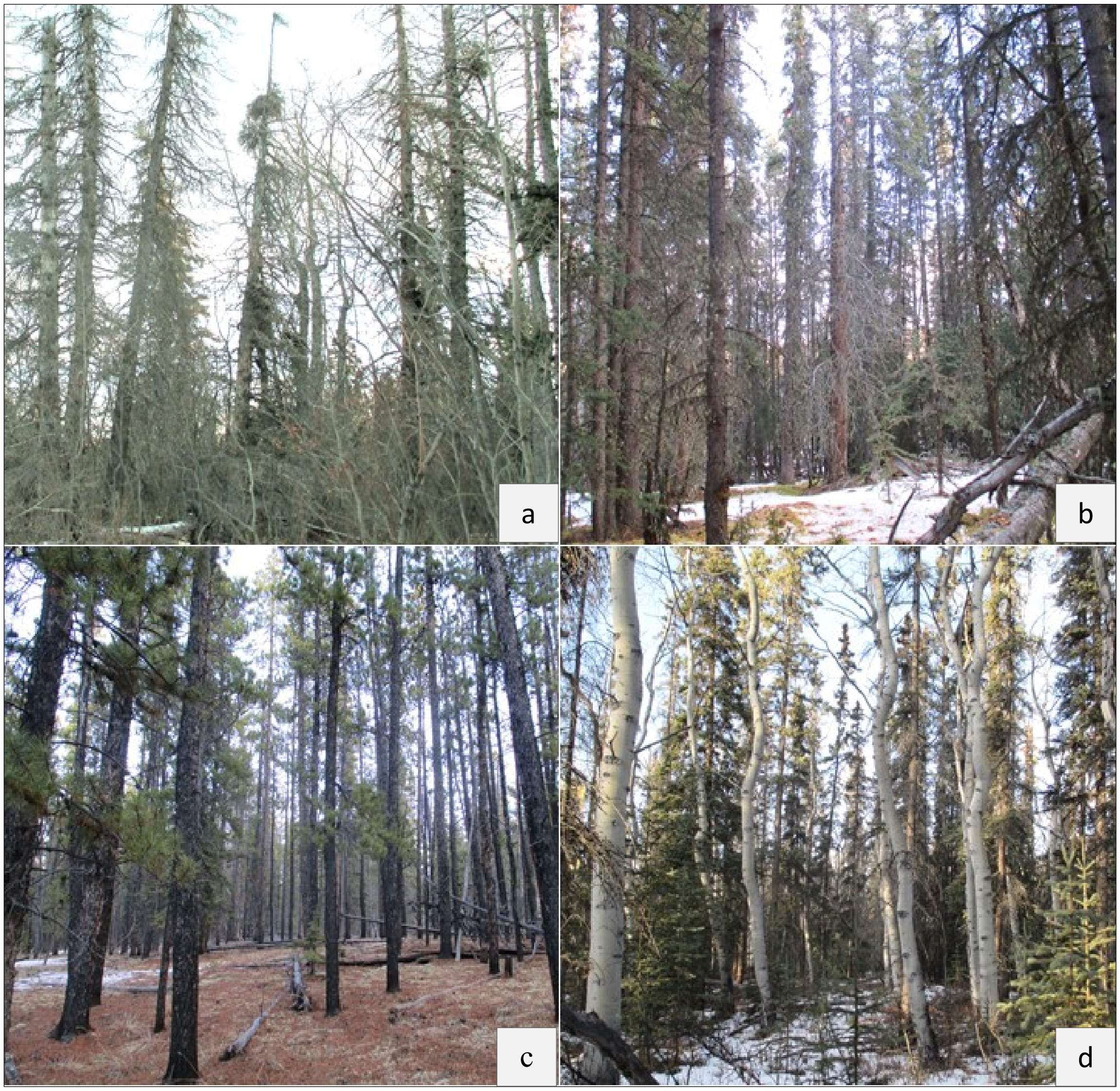


Figure 2.2. Photo comparison of beetle-affected spruce (a), healthy spruce (b), Pine (c), and mixedwood (d) forests. Mixedwood forest sites were composed of between 35–50% aspen and willow trees, the remaining being spruce or a mix of spruce and pine. Healthy spruce forest sites were composed of between 75–90% spruce trees, with an average of 12% showing signs of spruce beetle infestation. Beetle-affected spruce sites were generally composed of 80% white spruce, with an average of 45% showing signs of spruce beetle infestation.

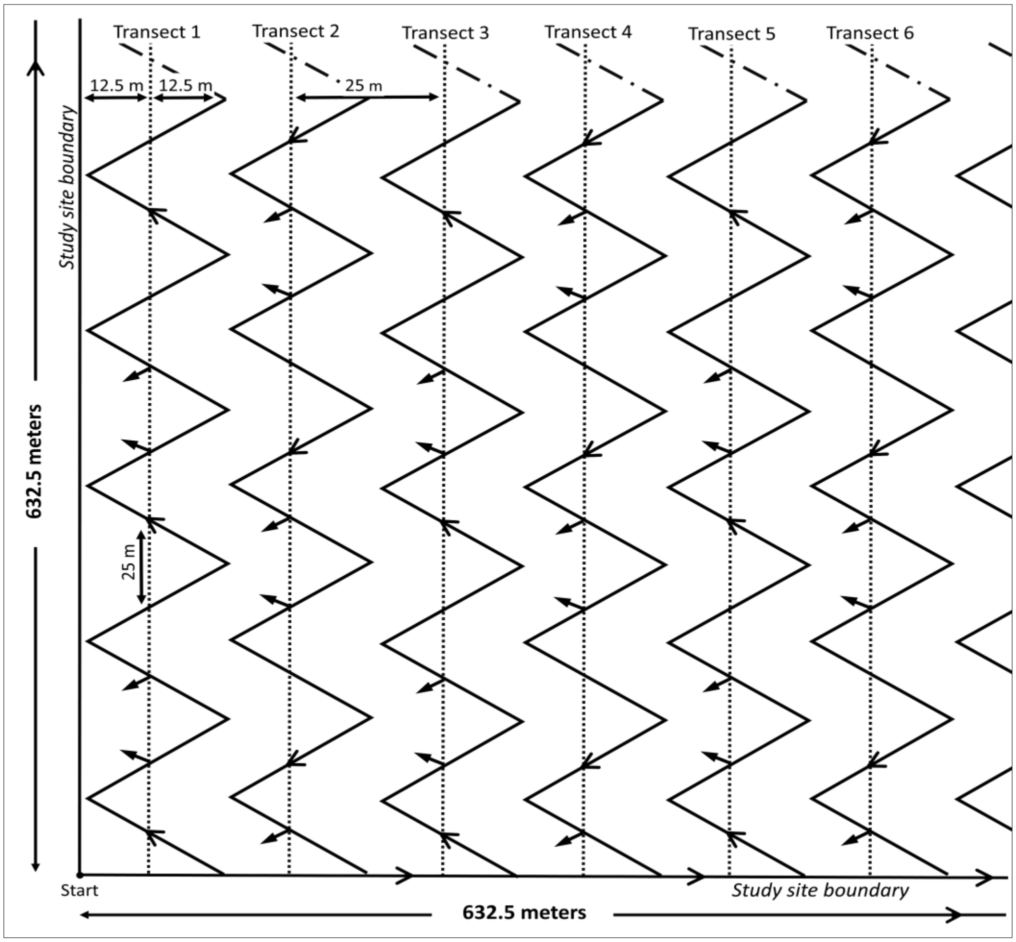


Figure 2.3. Schematic diagram of the standardized procedure used for cavity searches in all 40-hectare (632.5 x 632.5 m) study sites. The dotted lines show 6 of 26 transects that divided each plot, and the zigzagged lines show the paths walked while searching. Transects had a spacing of 25 meters and search paths intersected transects every 25 meters. Tailed arrows show the main direction that the observer focused while searching, though the visible sides of trees on the opposite sides of transects were also scanned for cavities. The chevrons show the direction walked. All sides of trees were scanned using binoculars. Tall and densely-branched trees were twice circled at distances of 5 and 15 meters to ensure that high and hidden cavities were found.

Figure 2.4. Photo examples of cavities containing squirrel material (a) and ant material (b). Squirrel debris generally consisted of grass and moss and ant debris consisted of wood dust, needles and cone scales. Cavities blocked by squirrel or ant material, or those that were filled up to the lower lip of the entrance, were not considered available for roosting or resting and, therefore, were not included in analyses.

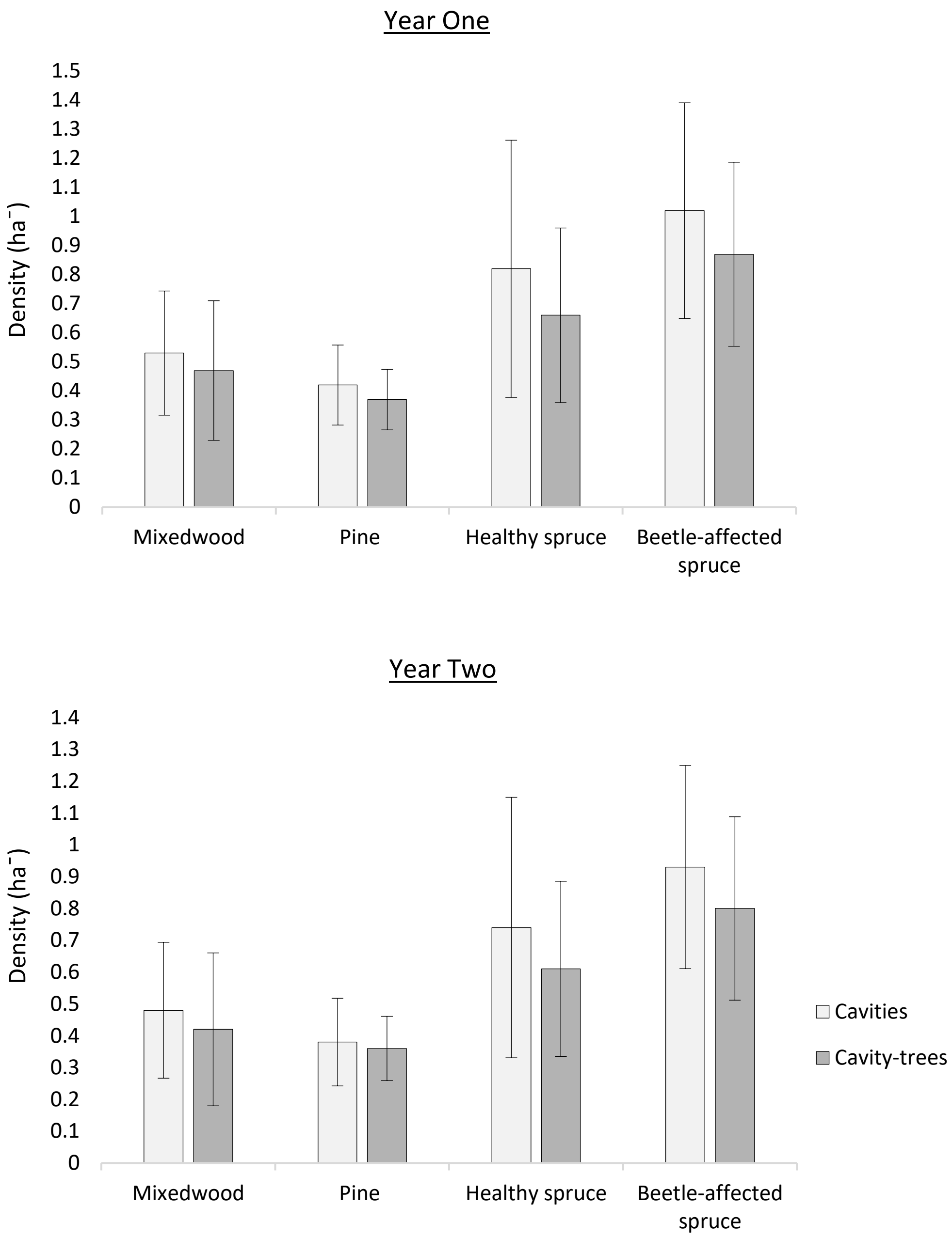


Figure 2.5. Available cavity and cavity-tree densities (per hectare) in 2018 and 2019 (year one and year two, respectively), for forest types surveyed in southwest Yukon, Canada. 333 cavities and 283 cavity-trees were available in year one, and 304 cavities and 262 cavity-trees were available in year two. There were no significant differences in cavity and cavity-tree densities among mixedwood, pine and healthy spruce forests, or between healthy spruce and beetle-affected spruce forests, in both years.

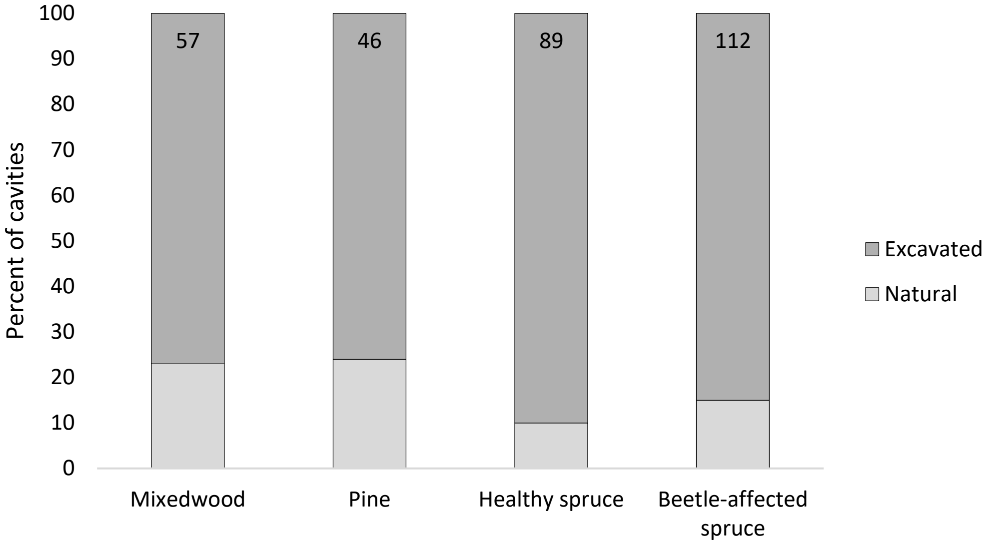


Figure 2.6. Proportions of natural and excavated cavities within forest types surveyed in southwest Yukon, Canada. There were no significant differences in proportions among mixedwood, pine and spruce forests, or between healthy spruce and beetle-affected spruce forests. Numbers at tops of bars show the number trees per forest type.

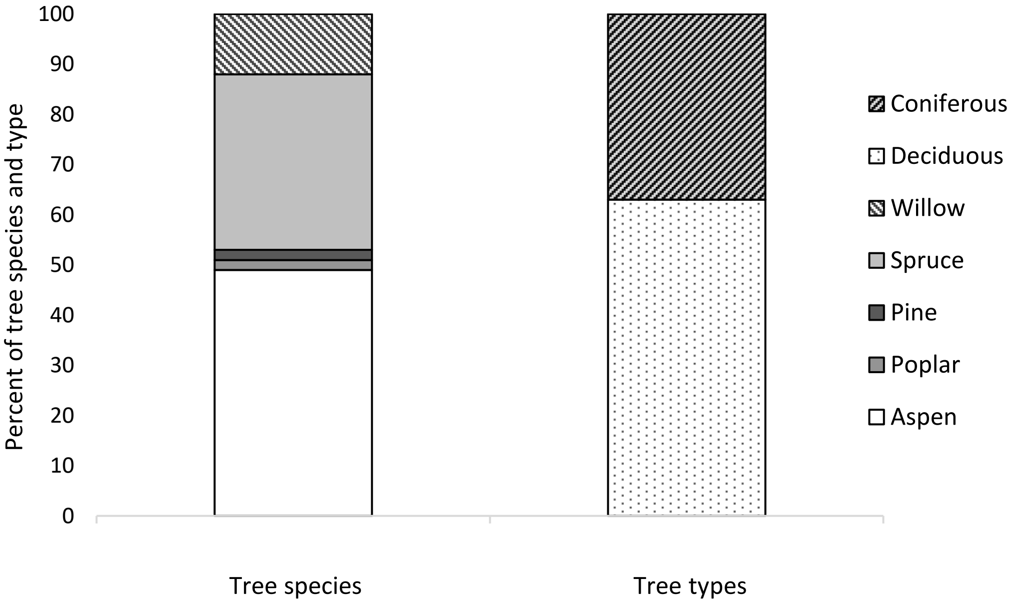


Figure 2.7. Proportions of naturally-made cavities for each cavity-tree species and tree type (deciduous and coniferous; n= 304).

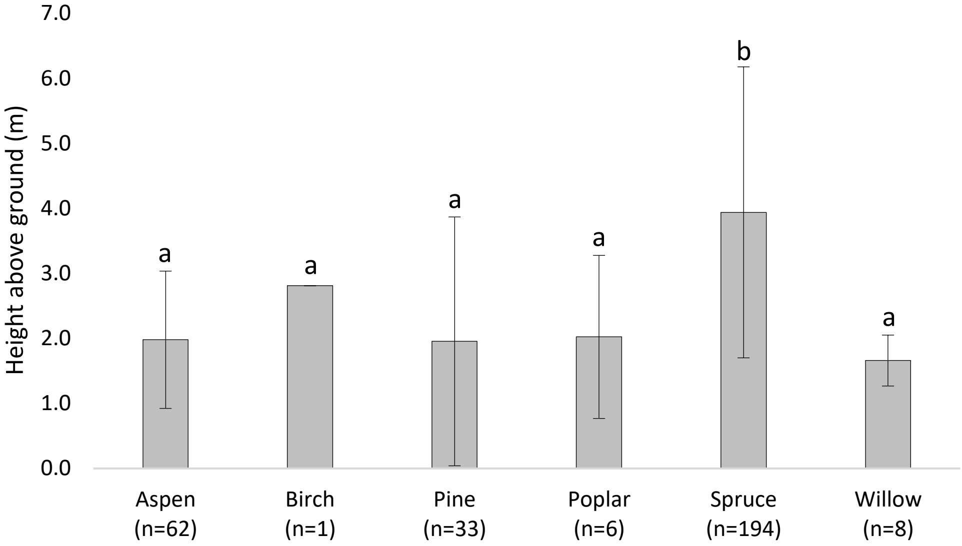


Figure 2.8. Means and standard deviations of cavity heights for each cavity-tree species. Different letters above the boxes indicate significant differences, based on ANOVA and Tukey HSD post-hoc tests.

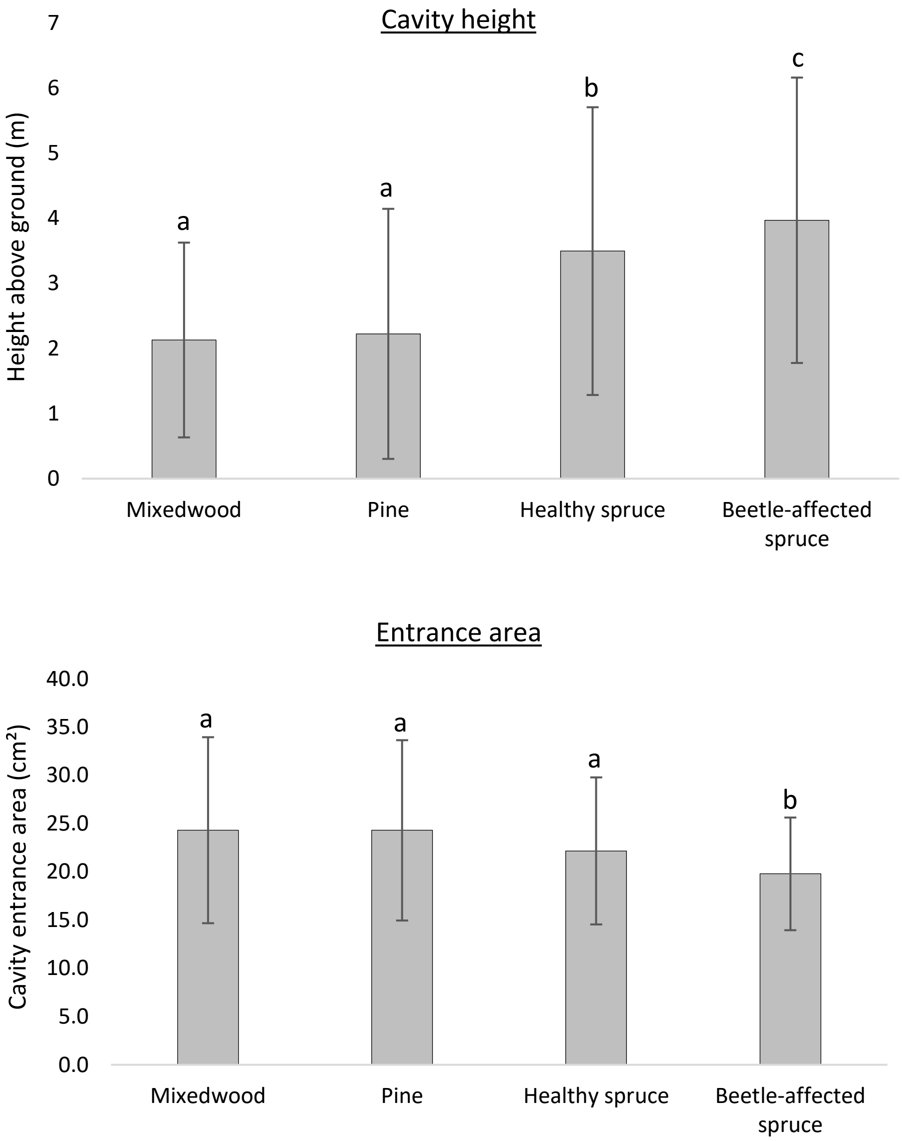


Figure 2.9. Means and standard deviations of cavity heights and entrance areas for each forest type. Different letters above the boxes indicate significant differences, based on ANOVA and Tukey tests (for comparisons among mixedwood, pine, and healthy spruce), and t-tests (for comparisons between healthy and beetle-affected spruce).

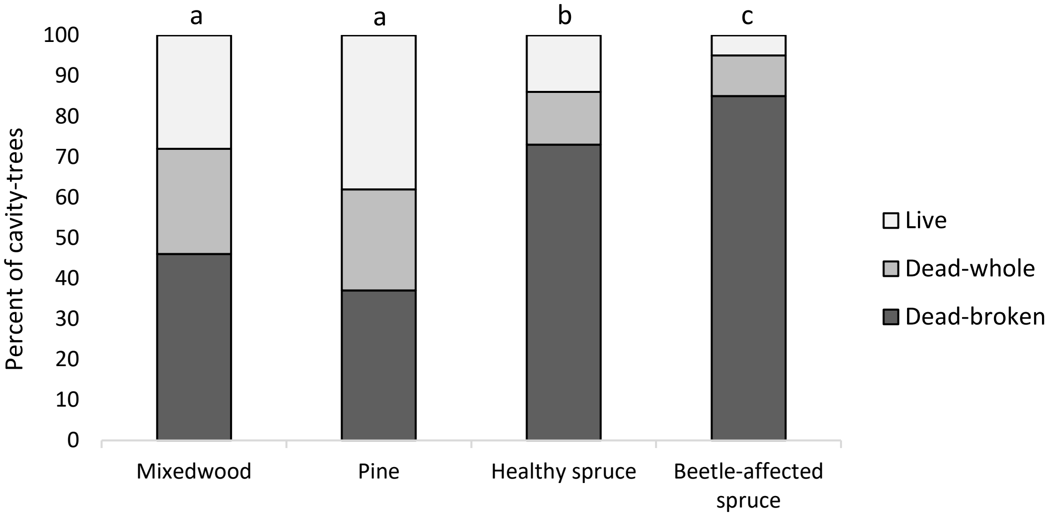


Figure 2.10. Tree appearance class proportions for each forest type. Different letters above the boxes indicate significant differences, based on Chi-square and post-hoc tests (summarized in Table 2.2).

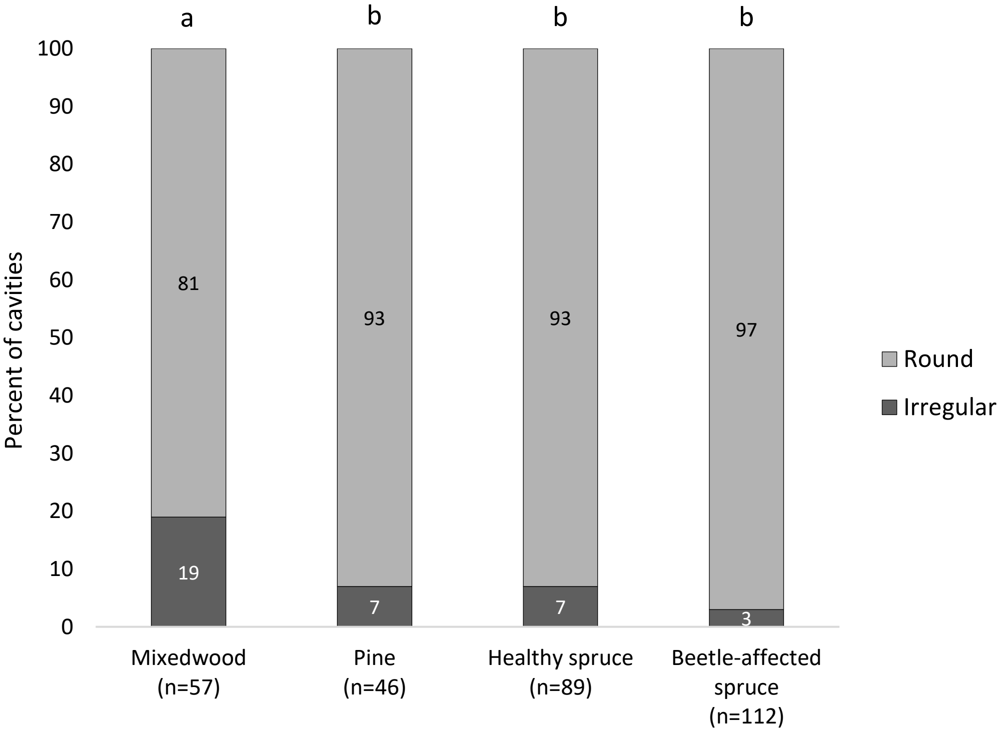


Figure 2.11. Proportions of irregularly shaped excavated cavities within each forest type. Different letters above the boxes indicate significant differences, based on Chi-square and post-hoc tests (summarized in Table 2.2).

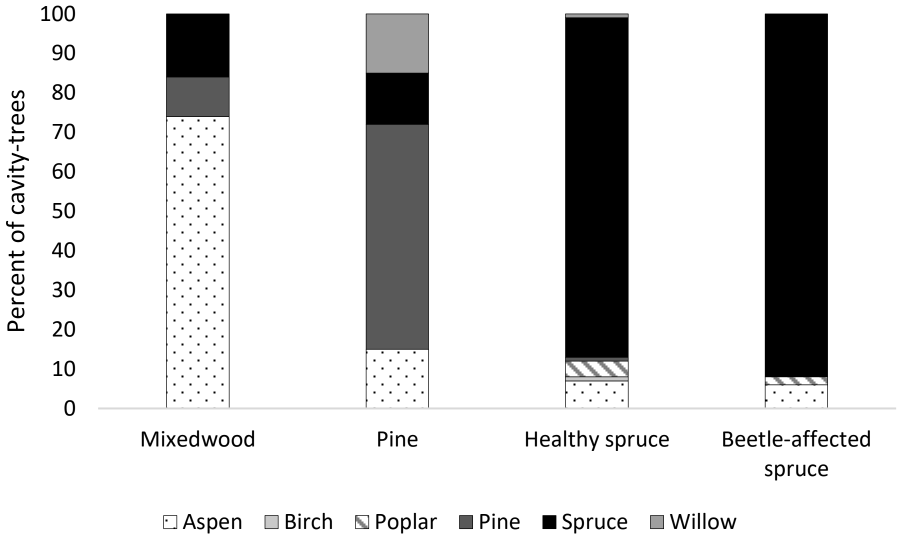


Figure 2.12. Proportions of cavity-tree species for each forest type (n=283).

Chapter 3:
The influence of microclimate on winter roost-site selection by cavity using birds in southern Yukon

Introduction

For many bird species, cavity-roosting reduces the energy requirements for thermoregulation, thus, reducing the risk of starvation and allowing for the reallocation of energy to other vital processes (Wolf and Walsberg 1996; Mainwaring 2011; Gruebler et al. 2014). Therefore, the thermal qualities of available roost sites are likely critical for roosting birds that need to conserve energy during long, cold nights. Furthermore, winter habitat suitability is thought to be a population-limiting factor for non-migratory bird species (Sherry and Holmes 1995), and this may be especially true of over-wintering, northern species. How cavity-site characteristics affect winter cavity temperatures is little understood, and no known research has investigated the effect of forest structure on roost-site microclimate. Understanding these relationships is important because identifying characteristics that predict the thermal quality of a roost-site is necessary for understanding winter cavity selection by birds.

Few studies have investigated the influence of cavity-site characteristics on cavity microclimate. Paclik and Weidinger (2007) and Pinowski et al. (2006) examined the relationships between various characteristics and cavity temperatures during winter nights and found that smaller entrances reduced internal cavity heat loss, cavities in living trees were warmer than those in dead trees, and temperatures decreased with an increase in volume; however, winter cavity use was not examined. Andreev (1980) observed that Siberian tits (*Poecile cinctus*) that roosted in smaller cavities reduced energy expenditure as those sites were warmer than larger cavities. Results from northern flicker nest-cavity research in interior British Columbia (Wiebe 2001) showed that cavity temperatures increased with tree health and diameter, and that south-oriented cavities were warmer, possibly due to the influence of the sun. However, entrance orientation may also be important for reasons related to wind exposure (Haggerty 1995), particularly for nocturnal roosting birds in northern latitudes where winter nights are long.

Though much research has examined the winter microclimates of potential cavity roost-sites and discussed the implications for cavity-roosting birds (McComb and Noble 1981; Pinowski 2006; Paclik and Weidinger 2007; Coombs et al. 2010; Gruebler and Widmer 2014), very few studies have investigated the relationship between cavity microclimate and winter roost-site selection by birds. Velky et al. (2010) compared the microclimates of winter roost-cavities to unused cavity-sites and found that European great tits selected cavities that were warmer at sunset. However, this was a controlled experiment which used artificial cavities (nest boxes), therefore, the results may not represent tree-cavity selection in natural environments. No known studies have compared the winter microclimates of used and unused tree-cavities in natural conditions. Furthermore, most cavity microclimate research was conducted in southern and sub-boreal forest regions, where the thermal qualities of roost-sites may not be as critical to winter survival as in regions with more extreme cold climates, such as the northern boreal forests of southern Yukon.

The purpose of this research was to examine the importance of cavity microclimate to winter cavity selection by northern boreal birds, and to determine whether cavity, tree, and habitat characteristics selected by birds reflect the thermal quality of roost-sites. The results of this study will complement other research on winter cavity use and availability (see Chapter 2). The importance of cavity microclimate to roost-site selection was examined by: 1) determining which cavity, tree and habitat characteristics affected cavity temperatures, 2) exploring the relationships between cavity-site temperatures and cavity use, and 3) determining whether cavity temperatures, in combination with other cavity-site characteristics, were predictors of cavity-use. Based on the results of previous research, I predicted that cavity temperatures would increase with tree diameter and health, and that temperatures would decrease with an increase in cavity volume and entrance size. I also predicted that cavity orientation would influence temperatures due to the exposure to sun and wind. Finally, I predicted that birds would select roost-sites with characteristics that reflect the thermal quality of cavities, and that cavity temperatures would be predictors of roost-site selection.

Methods

Study area and design

Four study areas were established throughout southern Yukon (Figure 2.1), each containing three 40-hectare sites representing the forest types within each area. The Mendenhall, Ibex and Chadburn study areas contained white spruce, lodgepole pine and mixedwood (white spruce/trembling aspen) forest sites, and the Kluane study area contained three beetle-affected spruce forest sites. These sites were established for a previous study that compared cavity availability and use among forest types (see Chapter 2 for additional study area details). In addition to these study sites, a five-hectare site established within the Mendenhall study area during a 2017 pilot season was also included in this study. This site encompassed a mixedwood forest that had been thinned, and where dead-standing and fallen trees had been removed for the suppression of potential wildfires. The Kluane study area was located within the Ruby Ranges ecoregion where mean annual temperatures range from -3 to -7°C and mean January minimum temperatures range from -30 to -35°C (Smith et al. 2004). All other study areas were located within the Southern Lakes ecoregion where mean annual temperatures range from -1 to -4°C and mean January minimum temperatures range from -21 to -25°C (Smith et al. 2004).

Tree-cavities were located and monitored during a two-year winter cavity-use study (see Chapter 2 for additional cavity search details), as well as during a winter pilot season, from January to April 2017. The temperatures and characteristics of cavity-sites that were observed being used over all three winter seasons were measured to understand the effects of cavity, tree, and habitat characteristics on cavity-site microclimate. Also, the temperatures and characteristics of five unused cavities nearest to each used cavity were measured to understand the effect of temperature on winter roost-site selection.

Cavity-site temperature measurements

A combination of HOBO U12 Temperature Data Loggers (Onset Computer Corporation, Bourne, MA) and Thermochron DS 1921G-F5# iButton temperature loggers (Maxim Integrated, San Jose, CA) were used to measure the external air and internal cavity temperatures at used and unused cavity-sites for statistical comparisons. Thermochron loggers recorded temperatures with a resolution of 0.5°C and an accuracy of ± 1.0°C between 70°C and –40°C. HOBO U12 loggers recorded temperatures with a resolution of 0.03°C and an accuracy of ± 0.35°C–0.5°C throughout its recommended operating range (70°C to -20°C). For analyses, temperatures recorded with HOBO U12 loggers were rounded to the nearest 0.5 of a degree Celsius to make the data comparable with those collected using the Thermochron loggers. Temperature loggers were installed at 15 roost-sites as well as at the five unused cavity-sites nearest to each used cavity, for a minimum of 20 nights. HOBO U12 logger units contained two probes and were programmed to simultaneously record the internal and external temperatures at 15-minute intervals. The external probes were placed on the north sides of cavity-trees to shade them from sun during the day and protect them from prevailing southwest winds. The internal cavity probes were suspended inside a small metal spring to keep them from direct contact with the cavity wall and occupants, ensuring that the probes only measured ambient cavity temperatures. The iButton temperature loggers (two separate units per site) were placed in wire mesh baskets and were also suspended on the insides and outsides of cavities and programmed to record temperatures at 15-minute intervals. All internal probes were placed standard distances of one centimeter from cavity floors, to prevent conductive heating by cavity contents and to measure the ambient temperatures where occupants roosted.

From the temperature logger data, temperature increments (*external air temperature – internal cavity temperature*) were calculated for statistical comparisons. Temperature increments are a measure of the thermal quality of a cavity (i.e. a cavity with a greater increment indicates that it is warmer, relative to the external air temperature, than a cavity with a lesser increment). Average nightly temperature increments were calculated using temperature data recorded between one-half hour after sunset to one-half hour before sunrise as this is the time when most cavity-roosting birds occupied a cavity (based on remote camera observations). Average sunset temperature increments were calculated using temperature data recorded between one-half hour before and after sunset as this is the time when most birds tend to scout and select roost-cavities (Velky et al. 2010; personal observations).

Data collected with a combination of temperature loggers, remote cameras (Bushnell Outdoor Products, Overland Park, KS), and ground surveys, were examined to determine whether dataloggers prevented cavity-use. As most used cavities continued to be used after installation, it can be concluded that they did not prevent cavity use. Furthermore, photo captures and ground surveys also confirmed that temperature data could be used to confirm cavity use, though the species or individual could not be confirmed by temperature data alone. However, a cavity was not considered used unless confirmed by remote camera or ground observations. By using the combination of remote cameras and temperature loggers, cavity-use was detected, some occupant species were identified, and temperature increments were measured on nights when cavities were not surveyed on foot.

Cavity, tree and habitat measurements

To identify relationships between cavity-site characteristics and microclimate for used and unused cavities, information on entrance area, vertical cavity depth (lower lip of entrance to cavity floor), cavity volume, cavity height, DCH, entrance orientation (four cardinal directions), bark retention (%), and wood condition (% decay) was collected for statistical analyses. For habitat context, forest characteristics such as canopy density (%), tree density (trees/ha), and live conifer density (live conifers/ha) were measured at each cavity-site. See Chapter 2 for additional information on cavity-site measurement methods.

Statistical analysis

i) The effect of cavity, tree and habitat characteristics on cavity-site microclimate

Multiple linear regressions, with average nightly temperature increments and average sunset temperature increments as response variables and cavity, tree, and habitat characteristics as predictor variables, were performed to determine whether there were relationships between cavity microclimate and the characteristics of cavity-sites. The continuous variables included in the analyses were bark retention, cavity height, DCH, entrance area, cavity depth, cavity volume, canopy density, and live conifer density. Categorical variables consisted of entrance orientation and wood condition. Bark retention and canopy densities were arcsine-transformed to meet the assumptions of normality, and all other continuous variables except for DCH were log-transformed. ANOVA analyses and Tukey tests were performed on cavity entrance orientation and wood condition to determine whether there were differences in temperature increments among variable classes. Finally, separate multiple linear regression analyses were performed using average nightly external air and average nightly internal cavity temperatures as the response variables and live conifer, total tree, and canopy densities as the predictor variables to determine whether structural forest characteristics affected temperatures at cavity-sites. Total tree densities were log-transformed to meet the assumption of normality.

ii) The influence of temperature on winter cavity selection

Logistic regressions were performed on the temperature increment data from used and unused cavities to determine whether there was a relationship between average nightly temperature increment and cavity-use, and between average sunset temperature increment and cavity-use, for three-toed woodpeckers and all species combined. Square root transformations were performed on the continuous predictor variables (average nightly and sunset temperature increments) as the data did not meet the assumptions of normality. Logistic regressions were also performed with nightly and sunset temperature increments included with other cavity-site characteristics to determine whether they were factors in winter roost-site selection by three-toed woodpeckers and all species combined. Finally, backwards step-wise logistic regressions, with average nightly and sunset temperature increments included with other cavity-site characteristics, were performed to determine whether cavity-site temperatures were predictors of cavity selection by three-toed woodpeckers and all species combined. Akaike's Information Criterion (AIC) scores were used in the stepwise regressions to determine which variables best predicted winter cavity use. Variables were systematically "dropped" based on the lowest resulting AIC score until an increase in score indicated that the remaining variables best predicted cavity use. The variables included in the analysis were average nightly temperature increment, average sunset temperature increment, bark retention, cavity height, DCH, entrance area, cavity depth, cavity volume, canopy density, live conifer density, entrance orientation, and wood condition. Arcsine and log-transformations were performed on continuous predictor variables with data that did not meet the assumptions of normality. VIF scores of < 4 indicated no collinearity among the continuous variables, and chi-square test results showed no collinearity between the categorical variables (P>0.05) included in regression analyses.

While hairy and downy woodpeckers, boreal chickadees, and brown creepers (*Certhia americana*) were observed using cavities, their numbers were too low to draw inferences about the influence of microclimate on winter cavity selection for these species. For this reason, cavity use and temperature data for these species were combined with three-toed woodpecker data for analyses. Three-toed woodpecker observations accounted for most of the data and were also analyzed separately. Temperature increment and ambient temperature measurements were made at 15 of the 17 roost-sites used over three winters (three-toed woodpecker = 11, Boreal chickadee = 2, Hairy woodpecker = 1, downy woodpecker/brown creeper = 1), as well as at 45 cavity-sites that were unused over three winters. Statistical analyses were performed with RStudio version 1.2.1335 (RStudio Team 2018) and the package Companion to Applied Regression (car) version 3.0-3 (Weisberg 2019). Shapiro-Wilks tests were used to test the normality of continuous variables, using a 95% confidence level. Results with P-values < 0.05 were considered statistically significant, and those P-values between 0.05 and 0.1 were considered marginally significant.

Results

The effect of cavity, tree and habitat characteristics on cavity-site microclimate

DCH and cavity depth had significant positive effects on average nightly temperature increments (*P*<0.001; *P*=0.005), and cavity volume had a negative effect (*P*=0.002; Table 3.1). There was also a significant relationship between average nightly temperature increment and cavity orientation (*P*=0.039; Table 3.1), with south-facing entrances having marginally smaller average nightly temperature increments (*P*=0.079). There were no significant differences in average nightly temperature increments between wood decay classes (F($_{1,59}$)=0.553, *P*=0.460); however, trees with more than 50% decay had slightly smaller temperature increments than those with less than 50% decay (Figure 3.1). There were no significant sunset temperature increment differences among cavity orientations or decay classes (F($_{3,55}$)=0.098, *P*=0.961; F($_{1,57}$)=0.302, *P*=0.585); however, northerly-facing cavities and trees with more than 50% decay had the smallest sunset increments (Figure 3.2). Tree, canopy, and live conifer densities did not significantly affect internal cavity temperatures (*P*=0.071; *P*=0.338; *P*=0.052). However, there was a significant positive relationship between the densities of live conifer-trees and external air temperatures at cavity-sites (*P*=0.043). Total tree and canopy densities had no significant effect on external air temperatures (*P*=0.062; *P*=0.316; Table 3.2).

The influence of temperature on winter cavity selection

The average nightly temperature increment was slightly higher for cavities used by all species combined (0.64 ± 0.72 °C) than for unused cavities (0.55 ± 0.72 °C); however, there was no relationship between nightly temperature increment and cavity-use (*P*=0.669). Likewise, the average temperature increment at sunset was slightly higher for cavities used by all species (1.01 ± 0.86 °C) than for unused cavities (0.73 ± 0.67 °C), though the difference was not significant

(*P*=0.209; Figure 3.3). For three-toed woodpeckers, the average nightly temperature increment was slightly higher for used cavities (0.60 ± 0.68 °C) than for unused cavities (0.57 ± 0.73 °C), though the difference was not significant (*P*=0.779; Figure 3.3). However, the average temperature increment at sunset was marginally higher for cavities used by three-toed woodpeckers (1.16 ± 0.92 °C) than for unused cavities (0.72 ± 0.66 °C; *P*=0.068).

When the nightly average temperature increments and average increments at sunset were included with other cavity-site characteristics in logistic regression analyses, there were no significant relationships between temperature increments and cavity-use by all species combined. Furthermore, results of the backwards step-wise logistic regression showed that neither average nightly temperature increment or increment at sunset were predictors of cavity-use. However, for three-toed woodpeckers, temperature increment at sunset was positively related to cavity use (*P*=0.040) and was included as a predictor of cavity-use, along with cavity height, depth, and volume. Average nightly temperature was not a predictor of cavity-use by three-toed woodpeckers (Table 3.3).

Discussion

The effect of cavity, tree and habitat characteristics on cavity-site microclimate

As was predicted, cavity-tree DCH had a significant positive effect on average nightly temperature increments. This result supports other research that found that larger diameter trees were warmer (Wiebe 2001; Coombs et al. 2010) but is contrary to Paclik and Weidinger (2007) who found there to be a strong negative relationship between DCH and cavity temperature increments, possibly due to a correlation between diameter and entrance area. The insulative quality and thermal inertia of wood are known to increase with tree diameter (Derby and Gates

1966), which is a likely explanation for the positive relationship observed between DCH and cavity temperature. Also as predicted, cavity volume had a significant negative effect on average nightly temperature increments (i.e. larger-volume cavities were colder). This result supports other research (Paclik and Weidinger 2007) that found that nighttime cavity temperatures decreased with vertical and horizontal depth (both measures of cavity volume), and research on Siberian tits (Andreev 1980) that showed that smaller cavities were warmer. Contrary to what was predicted and to the findings of other research (Paclik and Weidinger 2007), the results of this study showed no negative relationship between temperature increment and entrance area; however, cavity temperatures slightly increased with entrance size, perhaps due to correlations with other cavity variables. As predicted, entrance orientation influenced average nightly temperature increments, as south-oriented cavities were marginally colder (P=0.079), likely for reasons related to wind exposure. Prevailing southern winds likely had some effect on the temperatures of south-facing cavities, making them cooler and less desirable for roosting birds (no south-oriented cavities were used; see Chapter 2). Convective heat loss from wind was shown to increase energy expenditure in cavity-roosting chickadees (Mayer et al. 1982), juniper titmice (*Baeolophus griseus*) and mountain chickadees (Cooper 1999). Inversely, though there was no significant relationship between orientation and sunset temperature increment, south-facing cavities had slightly greater increments at sunset, relative to average nightly increments, and cavities on the leeward side of trees (north and east) were coldest. This is likely due to a stronger heating effect by solar radiation on south-facing cavities prior to sunset, relative to the cooling effect of prevailing southern winds. Similar differences in daytime nest-cavity temperatures were observed between north and south-oriented cavities in other studies (Inouye et al. 1981; Wiebe 2001), which was attributed to sun exposure. Contrary to what was predicted, tree health did not have a significant effect on cavity temperatures. However, cavities in live trees were slightly warmer than those in dead trees. This is likely due to live trees having a higher water content and the stabilizing effect of latent heat on cavity temperatures throughout the night (McComb and Noble 1981).

Cavity depth had a significant positive effect on average nightly temperature increments, which is contrary to other research (Paclik and Weidinger 2007) that observed a negative relationship between cavity depth and cavity temperature. Though larger cavities are typically cooler, the increase in cavity temperatures with depth observed in this study may have been due to a decrease in heat dispersion by wind with an increase in depth. Tree and canopy densities had no significant effect on internal cavity or external air temperatures at cavity-sites, and live conifer and canopy densities did not have a significant effect on nightly or sunset temperature increments. However, live conifer densities significantly affected external air temperatures at cavity-sites and marginally affected internal cavity temperatures (P=0.052). Air temperatures at cavity-sites may be warmer where there are higher densities of live conifer trees as they do not drop their leaves in winter and, therefore, they may protect cavity-sites from convective heat loss. Such an effect may also be supported by results that showed densities of all trees combined (coniferous and deciduous) to have no effect on cavity-site temperatures.

The influence of temperature on winter cavity selection

The average nightly temperature increments were not significantly higher for cavities used by three-toed woodpeckers and all species combined than for unused cavities. This suggests that there are other considerations in winter roost-site selection by birds, such as protection from predators (Campbell and Lack 1985; Mazgajski 2002). When the nightly average temperature increments and average increments at sunset were combined with other cavity-site characteristics in logistic regression analyses, there was no significant relationship between temperature and cavity-use by all species combined. However, temperature increment at sunset was a predictor of cavity-use for three-toed woodpeckers, along with cavity height, depth, and volume. Furthermore, cavities used by three-toed woodpeckers were marginally warmer at sunset than unused cavities (*P*=0.068). This confirms predictions that, at least for three-toed woodpeckers, cavity temperatures are an important consideration in winter roost-site selection and supports other research (Velky et al. 2010) that found that birds select cavities that are warmer at sunset.

A selection preference for cavity depths between 10 and 20 cm and avoidance of shallower cavities (see Chapter 2), combined with a significant positive association between depth and nightly average temperatures may suggest that three-toed woodpeckers consider cavity depth an indicator of a cavity's overall thermal quality. Furthermore, as sunset temperatures and cavity depths were predictors of cavity-use, three-toed woodpeckers may compare cavity temperatures when selecting a roost-site, but also take cavity depth into consideration as deeper cavities are more thermally stable throughout the night. A combination of both strategies would ultimately minimize the total nightly energy expenditure for thermoregulation and, thus, the risk of winter starvation. The same logic can be applied to cavity volume as there was an avoidance of larger cavities by three-toed woodpeckers (see Chapter 2) and a significant negative association between volume and average nightly cavity temperatures. The selection of deep and narrow cavities was shown to reduce energy expenditure in Siberian tits (Andreev 1980) and smaller cavities have been shown to have the potential for increasing energy savings in roosting birds (Pinowski et al. 2006; Gruebler et al. 2014). Cavity height predicting cavity use was not likely solely due to the temperatures of cavities, as height only had a slight positive effect on average nightly cavity temperatures and three-toed woodpeckers preferred lower cavities (see Chapter 2).

Though cavity orientation was not a predictor of cavity-use, an avoidance of south-oriented cavities (see Chapter 2) may be due to south-facing cavities having marginally lower average nightly temperatures. All used cavities were north, east, and west-oriented and there was a significant preference for easterly-oriented cavities (see Chapter 2). This is likely due to convective heat loss from prevailing south-west winds making south-oriented cavities cooler and more energy-costly, and cavities with other orientations, particularly east-facing cavities, being more protected from winds. Though live conifer density had a positive effect on cavity-site temperatures, it was not a predictor of cavity use by three-toed woodpeckers or all species combined. Therefore, as live conifer cover was a predictor of cavity use when temperature increments were not included in step-wise regressions (see Chapter 2), it is likely that roost-site temperatures are a more important selection factor, at least for three-toed woodpeckers.

Conclusion

The average sunset temperature increments were marginally higher for cavities used by three-toed woodpeckers, suggesting that microclimate is somewhat a factor in winter roost-site selection. Furthermore, results showed that average sunset increments were a predictor of cavity use by three-toed woodpeckers. Notably, all cavity-using species preferred deeper, smaller-volume cavities and avoided those with south-facing entrances (see Chapter 2), and these characteristics were shown to be significantly related to cavity temperatures. Therefore, it can be inferred that birds select roost-sites with certain traits that indicate thermal quality. Furthermore, as average sunset temperature increment was a predictor of cavity use by three-toed woodpeckers, it can be suggested that they look for warmer cavities when choosing a roost-site, but also take smaller, deeper cavities with entrances on the leeward sides of trees into consideration as they are more thermally stable throughout the night. There may be a survival advantage to three-toed woodpeckers selecting cavities that are warmer at sunset and more thermally stable roost-sites, as the combination of these strategies would minimize the nightly energy expenditure for thermoregulation and, thus, the risk of over-winter mortality due to starvation.

Table 3.1. Relationships among cavity characteristics and average nightly temperature increments, and cavity characteristics and average sunset temperature increments.

Characteristics	Estimate	Standard error	T-value	*P*-value
		Nightly temperature increments		
Continuous variables				
Bark retention	-0.458	0.263	-1.742	0.088
DCH	0.060	0.016	3.801	<0.001*
Height	0.186	0.289	0.642	0.524
Entrance area	0.238	0.758	0.315	0.754
Cavity depth	1.175	0.399	2.943	0.005*
Cavity volume	-0.903	0.279	-3.230	0.002*
Live conifer density	0.602	0.449	1.341	0.186
Canopy density	-0.864	0.646	-1.337	0.188
Categorical variables				
Orientation (north)[a]	-0.067	0.214	-0.313	0.756
Orientation (south)[a]	-0.607	0.285	-2.127	0.039*
Orientation (west)[a]	-0.051	0.211	-0.241	0.810
Wood decay (>50 %)[b]	-0.030	0.190	-0.158	0.875
		Sunset temperature increments		
Continuous variables				
Bark retention	-0.330	0.320	-1.031	0.308
DCH	0.014	0.019	0.764	0.449
Height	0.424	0.347	1.219	0.229
Entrance area	0.947	0.893	1.061	0.294
Cavity depth	0.943	0.474	1.990	0.053
Cavity volume	-0.177	0.341	-0.519	0.607
Live conifer density	<0.001	<0.001	0.125	0.901
Canopy density	-1.709	0.890	-1.921	0.061
Categorical variables				
Orientation (north)[a]	-0.182	0.255	-0.716	0.478
Orientation (south)[a]	-0.167	0.378	-0.445	0.659
Orientation (west)[a]	-0.117	0.249	-0.472	0.639
Wood decay (>50 %)[b]	-0.147	0.226	-0.650	0.519

* indicates a significant relationship.

[a] Reference category = east orientation.

[b] Reference category = <50% decay.

Table 3.2. Relationships among structural forest characteristics and average nightly internal cavity temperatures, and structural forest characteristics and external air temperatures.

Characteristics	**Estimate**	**Standard error**	**T-value**	***P*-value**
		Internal Temperatures		
Live conifer density (ha^{-})	0.005	0.002	1.982	0.052
Canopy density (%)	0.096	0.100	0.966	0.338
Tree density (ha^{-})	-0.004	0.002	-1.839	0.071
		External Temperatures		
Live conifer density (ha^{-})	0.005	0.002	2.067	0.043*
Canopy density (%)	0.102	0.100	1.013	0.316
Tree density (ha^{-})	-0.004	0.002	-1.902	0.062

* indicates a significant relationship.

Table 3.3. Results from a backwards step-wise logistic regression using Akaike's Information Criterion, showing the best predictors of winter cavity-use by three-toed woodpeckers and all species combined.

All observed species				**American three-toed woodpecker**			
				Global model			
Variable	***Df***	***Deviance***	***AIC***	***Variable***	***Df***	***Deviance***	***AIC***
Canopy density	1	48.328	72.328	Canopy density	1	43.308	67.308
Nightly increment	1	48.553	72.553	Live conifer density	1	43.352	67.352
Cavity volume	1	48.64	72.64	DCH	1	43.381	67.381
Wood condition	1	48.784	72.784	Wood condition	1	43.649	67.649
Live conifer density	1	48.839	72.839	Entrance orientation	1	43.819	67.819
DCH	1	49.314	73.314	Nightly increment	1	43.885	67.885
Bark retention	1	49.323	73.323	Entrance area	1	44.062	68.062
Entrance orientation	1	49.402	73.402	Bark retention	1	44.317	68.317
Entrance area	1	49.424	73.424	Cavity volume	1	44.427	68.427
Sunset increment	1	49.711	73.711	Cavity depth	1	44.615	68.615
<none>		48.314	74.314	<none>		43.296	69.296
Cavity depth	1	50.793	74.793	Cavity height	1	45.603	69.603
Cavity height	1	55.125	79.125	Sunset increment	1	46.487	70.487
				Best model			
Variable	***Df***	***Deviance***	***AIC***	***Variable***	***Df***	***Deviance***	***AIC***
<none>		55.229	63.229	<none>		47.045	57.045
Cavity volume	1	58.164	64.164	Cavity height	1	49.436	57.436
Cavity depth	1	59.214	65.214	Cavity depth	1	49.886	57.886
Cavity height	1	63.004	69.004	Sunset increment	1	50.108	58.108
				Cavity volume	1	50.668	58.668

AIC scores determined the best model for predicting winter cavity use. The AIC scores associated with "<none>" are the result when no variables are dropped, and those associated with other variables are the resulting scores when a variable is individually dropped. The global model shows all variables included in the regression.

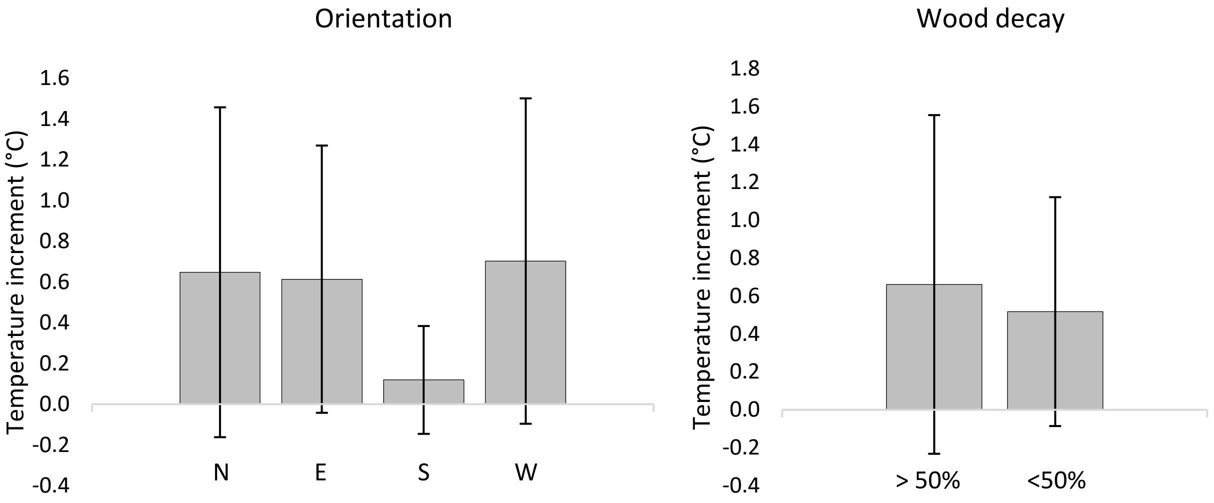


Figure 3.1. Average nightly temperature increments and standard deviations for orientation and wood decay classes. South-oriented cavities were marginally colder (*P*=0.079) than cavities with other orientations. There were no significant differences in average nightly temperature increments between wood decay classes.

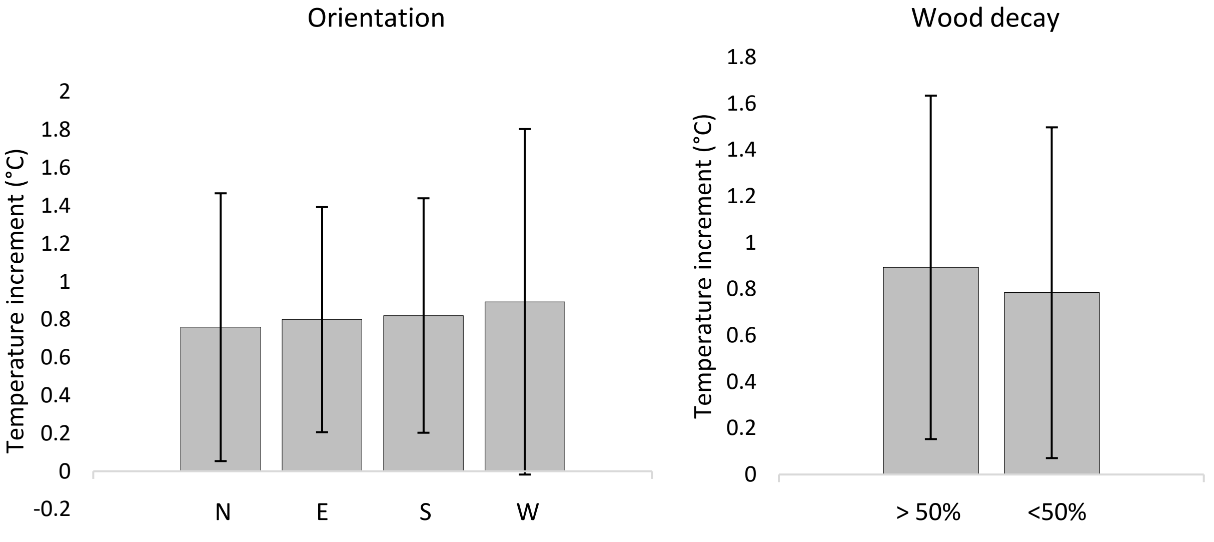
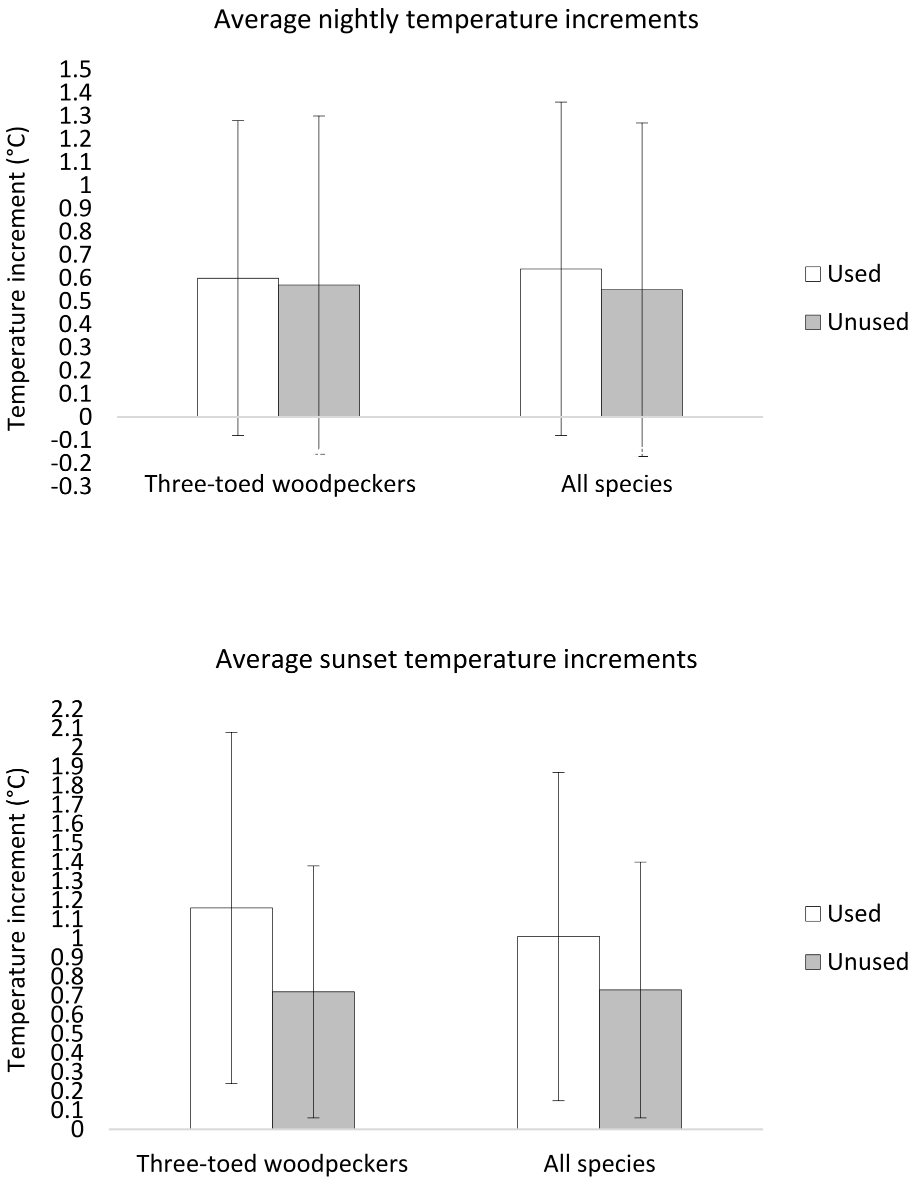


Figure 3.2. Average sunset temperature increments and standard deviations for orientation and wood decay classes. There were no significant differences in average sunset temperature increments among orientation or wood decay classes.



Average nightly temperature increments

Average sunset temperature increments

Figure 3.3. Average nightly and sunset temperature increments of cavities used by three-toed woodpeckers and all species combined. There were no significant differences between the average nightly and sunset temperature increments of used and unused cavities for all species combined. However, cavities used by three-toed woodpeckers were marginally warmer at sunset than unused cavities (*P*=0.068).

Chapter 4:
General conclusions

Thesis summary

The availability of tree cavities suitable for roosting and nesting is thought to be critical for supporting viable populations of cavity users (Newton 1994; Aitken and Martin 2012), which may be especially true of over-wintering, northern species that use cavities to withstand extreme cold weather conditions. However, few studies have quantified the availability and characteristics of cavities in boreal forests or the roost-site requirements of winter cavity using species. For many bird species, cavity-roosting reduces the energy requirements for thermoregulation, thus, reducing the risk of starvation and allowing for the reallocation of energy to other vital processes (Wolf and Walsberg 1996; Mainwaring 2011; Gruebler et al. 2014). Though the thermal qualities of available roost sites are likely to be critical for roosting birds that need to conserve energy during long, cold nights, few studies have investigated the relationship between cavity microclimate and winter roost-site selection by birds (for example, Andreev 1980; Velky et al. 2010). If conservation and forest management practices are to be well informed, more information is needed about winter cavity use and selection by North American boreal bird and mammal species and the availability of cavities suitable for withstanding northern winters. The focus and objective of my thesis research, presented in Chapters 2 and 3, was to gain a better understanding of cavity availability and the winter roost and rest-site requirements of northern birds and mammals, and to investigate the importance of cavity microclimate to winter cavity selection by northern boreal birds.

Cavity availability and winter-use

Tree densities did not differ among mixedwood, pine and spruce forests, which is contrary to the findings of cavity availability research in the boreal forests of Mongolia (Bai et al. 2003). However, this is a similar result to research in the northeastern United States (Clugston 1999) that found no significant difference in cavity and cavity-tree densities among forest type classes, defined solely by species composition. Densities of cavities likely related more to the structural complexities of the forest sites and abundance of dead-standing trees, as was observed in other circumboreal forests (Andersson et al. 2018), and Paragi (2010), which would explain the high densities of excavated cavities in beetle-affected spruce forests. Some cavity characteristics differed among spruce, mixedwood and pine forests (i.e. cavity height, entrance shape and tree appearance), and between healthy and beetle-affected forests (i.e. cavity height, entrance area and tree appearance). The differences in characteristics among forest types were likely the result of a combination of disturbance history (i.e. insect and fire) and the natural histories of the cavity-excavator species that inhabit the forests (Conner 1981; McBride 1983; Covert-Bratland 2006; Covert-Bratland 2007; Hadley and DesRochers 2008). Cavity volume, height and live conifer cover best predicted cavity-use for all bird species; however, only live conifer cover was a predictor of cavity-use for three-toed woodpeckers. Furthermore, three-toed woodpeckers preferred to roost in healthy spruce forests, and boreal chickadees and hairy woodpeckers preferred to roost in pine forests; however, all species avoided beetle-affected spruce forests suggesting that they are less important for roosting than for nesting and foraging. All cavity-site characteristics preferred and avoided by birds (see Table 2.6), and all characteristics that predicted cavity-use, were likely attributed to reasons related to predator avoidance, food availability, and microclimate (Derby and Gates 1966; Andreev 1980; Mayer et al. 1982; Cooper 1999; Wiebe 2001; Mazgajski 2002; Covert-Bratland et al. 2006; Paclik and Weidinger 2007; Coombs et al. 2010). Surprisingly, mammals were not observed resting in tree-cavities; however, red squirrels and northern flying squirrels did use cavities for caching food and appeared to prey or scavenge on cavity-roosting birds.

Though many cavity, tree and habitat characteristics were measured, some likely important factors in winter cavity selection were not measured or quantified. For example, as suggested in other research (Pinowski et al. 2006), the type and amount of cavity lining materials in a cavity are likely to be important considerations in winter roost-site selection and should be examined in future studies. Furthermore, as only a few cavity-roosting species were observed, further species-specific studies should focus on winter roost and rest site preferences by species not observed in this study, as well as the preferences of those that may roost and rest in deadfall, snow, ground burrows, and non-tree cavities to better understand the requirements of other resident birds and mammals for withstanding northern winters.

Influence of microclimate on roost-cavity selection

The importance of cavity microclimate to roost-site selection was examined by determining which cavity, tree and habitat characteristics affect cavity temperatures, and by exploring the relationships between cavity-site temperatures and cavity use. Results showed that average temperature increment at sunset was a predictor of cavity-use for three-toed woodpeckers, along with cavity height, depth, and volume; however average nightly temperature was not a predictor of cavity-use. Neither nightly or sunset temperatures were predictors of cavity-use when all species were combined, which suggests that microclimate was a less important consideration in cavity selection by boreal chickadees and hairy woodpeckers; however, sample sizes were too small to make any conclusions. Though not a predictor of cavity-use, DCH had a significant positive effect on cavity temperatures, which is consistent with other research results (Wiebe 2001; Coombs et al. 2010) and reflects how insulative quality tends to increase with tree diameter (Derby and Gates 1966). Entrance orientation had a significant negative effect on nightly cavity temperatures, with south-facing entrances having lower average nightly temperatures likely due to wind effects (Mayer et al. 1982; Cooper 1999). Cavity depth had a significant positive effect on cavity temperatures, and volume had a significant negative effect, and both variables were predictors of cavity-use. The negative relationship between cavity volume and temperature supports other research (Andreev 1980; Paclik and Weidinger 2007) that found that smaller cavities increase energy savings in roosting birds by reducing heat loss as they are warmer than larger cavities. Though live conifer density had a positive effect on cavity-site temperatures, it was not a predictor of cavity use by three-toed woodpeckers or all species combined. Therefore, it is likely that roost-site temperatures are a more important factor in cavity selection by birds. As was observed in great tits (Velky et al. 2010), three-toed woodpeckers likely compared cavity temperatures when selecting a roost-site, but selected smaller, deeper cavities with entrances on the leeward sides of trees to stay warmer throughout the night to minimize nightly energy expenditure for thermoregulation.

To fully understand the importance of microclimate to winter cavity selection and the relationships between cavity characteristics and cavity temperatures, other factors such as relative humidity and wind need to be measured and compared. Furthermore, the direct effect of temperature on thermoregulation needs to be examined to determine the importance of roost-site temperature to the energy balances of over-wintering cavity-users in cold climates. Though cavity temperature was found to be a winter roost-site selection factor for three-toed woodpeckers, it is likely that there are many other important factors, such as predator avoidance and food availability.

Conservation and management implications

Beetle-affected forests contained more potential roost-sites than did other forest types; however, relatively few were used, which suggests that these forests may be more important for nesting and foraging than for winter roosting. Though salvage-logging in beetle-affected forests may not have much of an effect on winter-roosting, more research is needed to fully understand the importance of these forests to cavity-using birds and mammals during both the winter and breeding seasons. Woodcutters and salvage loggers typically target dead, whole, beetle-killed trees with minimal decay, which are likely important as potential cavity sites for primary excavators such as woodpeckers; however, all cavities used for winter roosting were in dead, broken trees with considerable decay. That said, the retention of recently dead trees is necessary for the recruitment and persistence of wildlife trees (Tremblay et al. 2015; Hardenbol et al. 2018) and, therefore, for ensuring that there are a sufficient number of suitable cavity trees for maintaining future populations of over-wintering, cavity-using species.

Wildfire management practices, such as FireSmart, involve the thinning of conifer trees and the removal of dead-standing trees, dead fall, and low branches (Partners in Protection 2003). These practices reduce the structural complexity of forests which could negatively affect cavity-site microclimates, wildlife tree recruitment, and the populations of species such as American marten, boreal chickadees, and three-toed woodpeckers that require dense, mature conifer forests (Imbeau and Desrochers 2002; Payer and Harrison 2003; Sinclair, et al. 2003; Hadley and Desrochers 2008; Thompson et al. 2016). However, as one cavity within the fire-managed forest plot was frequently used by downy woodpeckers and brown creepers, these management practices may not have a negative effect on some over-wintering, cavity-using species.

Boreal chickadees, and hairy and three-toed woodpeckers roosted in mature and old-growth conifer forests containing a patchwork of dense canopies and open forest gaps, 50-75% live conifer cover, and an abundance of dead-broken standing trees. Furthermore, three-toed woodpeckers almost exclusively used dense spruce forests containing 12-45% beetle-killed or infested spruce trees, and 50-75% live conifer cover, likely for reasons related to food abundance and roost-site microclimate. These results support the growing body of research that has illustrated the importance of unmanaged, unlogged, and structurally complex forests to many cavity-using species (for example, Buskirk and Powell 1994; Imbeau and DesRochers 2002; Hadley and DesRochers 2008; LaMontagne et al. 2015; Thompson et al. 2016; Andersson et al. 2018). Furthermore, as dense, mature forests with an abundance of beetle-infested trees may be important for the over-winter survival of three-toed woodpeckers, and as they play an important role in cavity supply (Tremblay et al. 2015; Hardenbol et al. 2018), conserving these forests would ultimately preserve the integrity of the cavity-using boreal forest community.

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