NEST SITE SELECTION AND INFLUENCE OF WOODPECKERS ON RECOVERY IN A BURNED FOREST OF THE SIERRA NEVADA

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NEST SITE SELECTION AND INFLUENCE OF WOODPECKERS ON RECOVERY IN A BURNED FOREST OF THE SIERRA NEVADA

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Abstract

of

NEST SITE SELECTION AND INFLUENCE OF WOODPECKERS ON RECOVERY IN A BURNED FOREST OF THE SIERRA NEVADA

by

Gina Tarbill

Understanding how woodpeckers re-occupy burned areas is important as they provide a keystone function by creating habitat for other organisms. This thesis research investigated the possible influence of three species of Picoides woodpecker on re-colonization by birds and mammals in a burned forest and compared nest site selection and factors influencing nest presence of woodpeckers. Woodpecker nests were found in 2009 and 2010. Woodpecker cavities found in 2009 were monitored for use by small mammals and birds, resulting in indices of recovery that describe the quantity and quality of secondary cavity use. White-headed woodpeckers had highest indices of cavity utilization, although Black-backed and Hairy woodpeckers were important to some secondary cavity users. Factors influencing nest site selection were compared with ANOVA and Kruskal-Wallis tests, with significant differences found in mean tree height and decay, and density of small and large snags, and canopy closure. Logistic regression
was utilized to determine the factors with the greatest influence on nest presence. These were found to differ among the woodpecker species, although percent scorch of nest tree was important for all species. Densities of medium and small snags were positively associated with presence of Black-backed and Hairy woodpecker nests, respectively. Nest presence of White-headed woodpeckers was positively associated with decay and negatively associated with tree height and canopy closure. Differences in mean nest characteristics and factors influencing nest presence may explain differences in secondary cavity use, suggesting that cavity height, snag density, and decay play important roles in determining secondary cavity use in burned forests.

Woodpeckers play an important role in post-fire habitats by rapidly colonizing burned areas and creating cavities that are used by many other species that rely upon them for nesting, denning, roosting, and resting. Understanding how wildlife species respond and recover from fires is critical for conservation and management of forest ecosystems.

______________________________, Committee Chair

William Avery, Ph.D.
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INTRODUCTION

Keystone species are organisms that exert a disproportional effect on the structure or function of their community by virtue of life history traits or interactions with other species (Paine, 1969). Keystone species may drive ecosystem processes by influencing productivity, nutrient cycling, species richness, or the abundance of one or more dominant species or functional groups of species (Power et al., 1996). Keystone species are particularly important in terms of conservation and management because the loss of these species from a community can have catastrophic effects on those organisms that rely upon them to drive ecosystem processes (Estes and Palmisano, 1974). Focusing conservation efforts on keystone species preserves their influence on ecosystem function and may also have direct and indirect benefits at the community level (Simberloff, 1998; Power et al., 1996).

Keystone species impact the community by modifying ecosystem structure (Mills et al., 1993) and maintain or create habitat by modulating resource availability for other species through physical changes in biotic or abiotic materials (Lawton and Jones, 1995). Woodpeckers have been identified as keystone species in forest habitats, largely due to modification and creation of habitat with their unique foraging and nesting activities (Lawton and Jones, 1995; Simberloff, 1998; Martin and Eadie, 1999; Bonar, 2000; reviewed in Aubrey and Raley, 2002; Bednarz et al., 2004). By scaling bark and pecking and drilling into dead and decaying trees, woodpeckers create foraging areas for
other species (Conner, 1981; Bull et al., 1986), accelerate decomposition and nutrient
cycling (Farris et al., 2002, 2004; Jackson and Jackson, 2004), and mediate insect
populations (Otvos, 1970, 1979). Additionally, as primary cavity excavators,
woodpeckers create cavities for nesting and roosting. These cavities are later used by
secondary cavity users, species dependent on cavities but unable to excavate them.
Cavities excavated by woodpeckers provide nesting, roosting, denning, and resting sites
for secondary cavity users (Raphael and White, 1984; Bull et al., 1997). In the Sierra
Nevada alone, there are over thirty secondary cavity users from several functional groups
including seed-dispersing small mammals, insectivorous birds, small raptors, and small
carnivores (Raphael and White, 1978, 1984; Verner and Boss, 1980). Natural (non-
excavated) cavities are limited in most habitats, indicating that secondary cavity users are
dependent on primary cavity excavators for cavity creation (Aitken and Martin, 2007).
Competition for cavities has been shown to limit population growth of secondary cavity
users (Holt and Martin, 1997). This creates a guild structure in the community with
strong dependence of secondary cavity users on primary cavity excavators (Martin and
Eadie, 1999).

Determining the specific relationships between secondary cavity users and
primary cavity excavators is necessary to understand community structure and
composition. Nest webs have been used to study the direct and indirect effects of primary
cavity excavators on secondary cavity users and the community at large (Martin and
Eadie, 1999; Aitken et al., 2002; Martin et al., 2004; Blanc and Walters, 2007, 2008ab;
Gentry and Vierling, 2008). Nest webs are analogous to food webs, with trees or snags
as the fundamental “producers,” primary cavity excavators as the “manufacturers,” and secondary cavity users as the “consumers” of cavities (Martin and Eadie, 1999; Fig. 1). At the base of the web is the cavity substrate, generally a tree or snag. Primary cavity excavators (PCEs) utilize the cavity substrate, the raw resource, to produce cavities (Fig. 2). Secondary cavity users (SCUs) are those species that generally cannot create cavities of their own, but rely upon the cavities created by primary excavators for nesting, denning, roosting, and/or resting. Lines connect species that use resources provided by the species below and are associated with the proportion of resource used by the species. This allows identification of generalists and specialists, and the relationships between them, and the potential cascading effects of changes in habitat elements, such as changes in the number or character of snags, on secondary cavity users through decreases in one or more primary cavity excavators.

Secondary cavity users may prefer cavities excavated by a particular species of woodpecker due to similar preferences in cavity or habitat characteristics. Woodpeckers have been shown to select nest sites based on features at several spatial scales, and species differ in nest site preferences (Saab et al., 2004). Some species of woodpecker support more secondary cavity users by created more cavities or creating cavities that are preferred by secondary cavity users (Martin et al., 2004; Saab et al., 2004). Cavities that are used by multiple taxonomic groups (Aubry and Raley, 2002) or cavities that are used for reproduction may have more value in terms of supporting cavity-dependent
Figure 1. Nest web structure. Nest webs are analogous to food webs, with trees or snags as the fundamental “producers,” primary cavity excavators as the “manufacturers,” and secondary cavity users as the “consumers” of cavities.
Figure 2. Nest web illustrating relative influence of primary cavity excavators on secondary cavity users. PCE=Primary cavity Excavator, SCU=Secondary Cavity User. Primary cavity excavators (PCEs) utilize the cavity substrate, the raw resource, to produce cavities. Secondary cavity users (SCUs) are those species that generally cannot create cavities of their own, but rely upon the cavities created by primary excavators for nesting, denning, roosting, and/or resting. Lines connect species that use resources provided by the species below and are associated with the proportion of resource used by the species.
communities (Brawn and Balda, 1988; Steele, 1993).

Although previous studies have focused on nest site selection and secondary cavity use (Martin and Eadie, 1999; Aitken et al., 2002; Martin et al., 2004; Walters and Kneitel, 2004; Blanc and Walters, 2007, 2008a; Gentry and Vierling, 2008), data are lacking on the impact of fire to these systems (but see Saab et al., 2004; Gentry and Vierling, 2008). Fire is a natural and regular disturbance in mixed conifer forests and may create snags, change forest structure and composition, and alter arthropod populations (Kotliar, 2002). Trees weakened or killed by fire are typically invaded by beetles, which rely upon dead, dying, and stressed trees for reproductive and foraging sites (Bradley and Tueller, 2001). Beetles feed on the woody tissues and inner bark of trees and are generally found in low levels in healthy forests, but experience population explosions after fires. Intensity of bark beetle invasion in burned forests depends upon scorch and diameter at breast height of individual trees, and also density of stands (Ferrell, 1996; Bradley and Tueller, 2000). Because fires often result in a mosaic of killed and weakened trees, bark beetles may successfully invade, utilizing less burned trees for reproduction and more burned trees for foraging (Ferrell, 1996). The most common beetles of the Sierra Nevada are Western pine beetles (*Dendroctonus brevicomis*), mountain pine beetles (*D. ponderosae*), Jeffrey pine beetles (*D. jeffreyi*), red turpentine beetles (*D. valens*), pine engraver beetles (*Ips* species), and fir engraver beetles (*Scolytus ventralis*) (Ferrell, 1996; Parker et al., 2006). Most beetles are positively associated with highly scorched small diameter trees with thin bark in dense stands (Parker et al., 2006). Beetles are an important source of prey for many insectivorous birds re-colonizing burned areas,
and beetle outbreaks have resulted in significant increases in bird populations, especially woodpeckers (Martin et al., 2006; Dixon and Saab, 2000).

Woodpeckers are generally early colonizers of burned areas, exploiting the abundance of beetles and nest resources (Hutto, 1995). Their unique foraging and nesting strategy may allow them to utilize habitat unsuitable to many other bird and mammal and their keystone functions facilitate the re-colonization and occupation of other species. Different species of woodpeckers appear to be better adapted to different levels of burn severity and preferentially nest in these areas (Saab et al., 2004; Hutto, 2006; Haney et al., 2008; Nappi and Drapeau, 2009; Pope et al. 2009). Factors that may influence nest site selection include habitat characteristics such as snag size, burn severity, snag density, and post-fire management practices (Saab et al., 2004). Management often includes salvage logging, a form of logging that removes trees and other biomass from disturbed areas (Lindenmayer and Noss, 2006). Salvage logging is practiced to minimize economic loss, reduce fuel loads, and protect property and human life. Cavity-dependent communities may be negatively affected by salvage logging due to loss of snags that provide foraging areas and cavity substrates for nesting, denning, roosting, and resting (Saab et al., 1998, 2002, 2007, 2009; Hanson and North, 2008). Nesting densities and foraging activities of woodpeckers tend to be higher in burned areas that have not been logged than those that have been logged (Saab et al., 2007; Hanson and North, 2008). Reduction in numbers of primary cavity excavators may limit the number of cavities available for secondary cavity users, limiting re-colonization and persistence in burned forests. Determining factors that positively or negatively influence woodpecker nest
presence in burned forest will allow for community-wide predictions on recovery of secondary cavity users.

As keystone species, woodpeckers play an active role as facilitators of re-colonization after fire, and the magnitude of their contribution to post-fire community recovery varies among species as a function of the strength of their association with secondary cavity users. In order to investigate these relationships, I studied secondary cavity use and nest site selection of three species of Picoides woodpeckers in a recently burned and salvage logged forest.

Understanding habitat selection of primary cavity excavators and their interspecific interactions within post-burn communities may provide valuable insights into how to manage pre-burn and post-burn forests to maximize short and long-term ecological benefits and the conservation of forest ecosystems. The objectives of this study are the following:

1. Determine what habitat characteristics have the greatest influence on nest site selection by each of three primary cavity excavators.
2. Determine the relative influence of the three primary cavity excavators on bird and small mammal community recovery.
In this study, I predict the following relationships:

1. Secondary cavity users will exhibit preference towards cavities excavated by particular woodpecker species.
2. Species diversity of secondary cavity users will differ among the three species of woodpecker.
3. Habitat characteristics of nest tree, nest site, and territory will differ among the three species of woodpecker.
4. Snag density will affect site occupancy for each species of woodpecker.
METHODS

Focal species

Three members of the *Picoides* genus were selected as focal species for this study: Black-backed woodpeckers (*P. arcticus*, BBWO), Hairy woodpeckers (*P. villosus*, HAWO), and White-headed woodpeckers (*P. albolarvartus*, WHWO). These species are characterized by strong excavation abilities and are unlikely to re-use nest cavities (Garrett et al., 1996; Dixon and Saab, 2000; Saab et al., 2004). Members of this genus differ in observed nest site preferences with regards to nest tree and habitat characteristics, although data were lacking in the Sierra Nevada (but see Melne and Hejl, 1989). Black-backed woodpeckers are fire specialists and tend to nest in areas of high burn severity (Dixon and Saab, 2000). Burned areas may act as source habitat for Black-backed woodpeckers (Nappi and Drapeau, 2009) and they may be rare in unburned habitats (Dixon and Saab, 2000). Hairy woodpeckers tend to nest in moderate to severe burns, but are also common in unburned areas perhaps due to preferences for nesting in live trees with advanced heartwood rot (Jackson et al., 2002). White-headed woodpeckers are one of the least studied woodpeckers of this region and use of burned areas for nesting is largely unknown. White-headed woodpeckers tend to occupy habitat with several species of *Pinus* and a high proportion of their diet is composed of pine seeds (Lingon, 1972). Preliminary avian survey data in the study area indicates that these three
species are fairly common during the breeding season (P. Manley, unpublished data, 2009).

Study area and site selection

The Angora Fire burned approximately 1,255 hectares in South Lake Tahoe, California in June and July 2007 (Fig. 3). As a mixed conifer forest, pre-fire dominant tree species included *Pinus jeffreyii*, *P. contorta*, *P. lambertiana*, *Abies concolor*, *A. magnifica*, *Populus tremuloides*, and *Calecedrus decurrens* and dominant shrub genera included *Artemesia*, *Artostaphylos*, and *Ceanothus*. The fire occurred in an area with a high level of private and public land intermixed and adjacent to large expanses of undeveloped public land. The severity of the burns varied within the area, resulting in a mosaic of post-fire conditions (Fig. 3). Portions of the burn area were salvage logged immediately following the burn in 2007.

Sites were selected that represented a range of burn intensity and post-fire treatments. The burn intensity map (Fig. 3) representing percent tree mortality (30m resolution) based on satellite imagery and created for multi-agency use by the United States Forest Service (USFS) was used to classify sites into four burn intensity intervals (0, 1-20%, 20-70%, >70%). Salvage logging treatments were determined by using maps created by the USFS and field validation and sites were classified into two salvage classes: no treatment or logged. Sites were randomly selected from each of the 12 combinations of conditions in roughly equivalent proportions. The USFS established a systematic grid of points spaced 400 meters apart across the fire area to monitor post-fire
Figure 3. Footprint of Angora fire with burn severity and sampling points.
vegetation response. Grid points occurring in each burn-salvage category were selected first to ensure all combinations of treatment conditions were represented. A total of 57 sample points were selected for the 2009 field season. In 2010, 37 sites were re-sampled and 27 new sites were sampled, for a total of 84 points sampled over the two-year period.

Nest searching

Nest searches for Black-backed, White-headed, and Hairy woodpeckers were conducted between May and July in 2009 and 2010. Sites were nest searched on a rotating basis, with each site visited a minimum of three times, with at least a week between each visit. Trained observers conducted all nest searches. Observers were made aware of breeding bird behaviors and used cues from adults and nestlings, systematic search, and luck to locate nests (Martin and Geupel, 1993; Appendix A). Nests were found during construction, egg laying, incubation, or nestling stages.

The search area associated with each sample point had two distance zones: 60 meters and 100 meters. Observers first searched within 60 meters of each sample site (approximately 1 hectare area) for a minimum of 15 minutes for active cavity nests (Martin and Geupel, 1993) and foraging cavity nesters (Covert-Bratland et al., 2006). The time allotted corresponded to an effective use of time to locate focal species. Once a focal species was located, no maximum time was set for following it to determine if it was nesting. If an individual was located while searching the 60-meter area, they were followed outside this search area to locate their nests. Once the 60-meter radius area was
thoroughly canvassed, observers moved out into the area between 60 and 100 m from the site (approximately 2 hectare area), and spent approximately 1 additional hour searching this area for focal species (i.e., a less intensive search per unit area). Nests that were encountered in the course of moving to and from sites in the study area were considered in the “matrix.” The distance and azimuth to the nearest sample point was estimated for all nests. When an active nest was confirmed, the bird species, location of the nest and stage of nest development was recorded, along with the Universal Transverse Mercator coordinates (North American Datum 83) of the nest site.

Secondary Cavity Use

Field Methods

Nest cavities of focal species found in 2009 were monitored to determine preferential use by secondary cavity users and relative influence of each species of woodpecker. Remote-triggered digital cameras (Leaf River Outdoor Products, Taylorsville, MS) were set twice per season to determine use during breeding (April-August) and non-breeding seasons (November-February). Cameras monitored cavities for 7-day sessions. The use of cameras allowed for detection of elusive, diurnal, and nocturnal organisms. Cameras were set on a tree facing the cavity at the appropriate height and angle to maximize detections. Cameras were tested to ensure functionality and loaded with fresh batteries and empty camera cards. After seven days of monitoring, cameras were collected and photos from memory cards were downloaded. All organisms
detected were identified to species whenever possible and assigned to either “breeding” or “non-breeding” categories.

**Analysis**

Mean species richness and occupancy frequency were compared between the three species using Analysis of Variance (ANOVA, SAS 9.2). Species richness was calculated as the number of different species detected over the entire study period at each cavity, then averaged over all cavities excavated by each species of woodpecker. Nest use data were used to create nest webs for each woodpecker species following Martin and Eadie (1999). Nest webs reflect the relative dependence of secondary cavity user on individual species of woodpecker by showing the proportion of cavities used by secondary cavity users. Proportional use was calculated as the number of cavities used by a species of secondary cavity user for each species of woodpecker divided by the number of cavities used by this species of secondary cavity user for all woodpeckers.

Secondary cavity users were divided into groups of “open” and “closed” canopy species, based on known habitat preferences (Verner and Boss, 1980). Fisher’s Exact Test was used to analyze preferences of each group for cavities excavated by the different species of woodpecker. Preferences of individual species were not analyzed because sample sizes were very small.

The relative contribution of each species of woodpecker to bird and small mammal re-colonization was represented by the Utilization Index (UI) based on the
richness and diversity of secondary cavity users associated with cavities of each species of woodpecker (Eq. 1),

Equation 1. Utilization Index

\[ UI = (2S_b + S_{nb} + T - 1) \]

Where \( S_b \) = the number of breeding species detected, \( S_{nb} \) = the number of non-breeding species, and \( T \) = the number of taxonomic classes detected.

This index was averaged over all nests for each species of woodpecker and multiplied by the proportion of nests with detections to obtain the Cavity Utilization Index (CUI, Eq. 2).

Equation 2. Cavity Utilization Index

\[ CUI = UI \ast n_d / n \]

Where \( n_d \) = number of nests with detections and \( n \) = total number of nests monitored.

Breeding species are weighted by a factor of two to highlight the importance of providing reproductive habitat (Brawn and Balda, 1988; Steele, 1993). Taxonomic diversity (T) is included to highlight the importance of providing habitat to multiple classes, which in this study included birds (Aves) and mammals (Mammalia).
Nest site Selection

Field Methods

Habitat associated with nests was characterized at three scales: nest tree, nest site, and territory. Nest tree and site habitat protocols described below largely followed the BBIRD protocol (Martin et al., 1997). The following nest tree characteristics were recorded for each nest: nest height; substrate species, height, diameter at breast height (DBH), vigor (live or dead), decay, and percent scorch (blackened). Decay classes were assigned based on the 5-class method which characterizes decay based on amount of bark left on bole, whether the top, bole, and branches are intact, and degree of heartwood and sapwood rot (Cline, 1980; Appendix B).

Nest site characteristics were described in the vicinity of the tree within an area of 0.04 ha (radius: 11.3 m; adaptation of Martin et al., 1997). The plot boundaries were created using four line transects laid out in each cardinal direction, delineating one quarter of the circular plot. In each 0.4-ha plot, the species, DBH, and decay class (Appendix B) were recorded for each tree and snag with DBH greater than 12.5-cm. Tree and snag counts were divided into DBH classes based on salvage logging prescriptions and converted to densities (stems/ha). Large trees were defined as those with DBH greater than 27.1cm, small trees were those with DBH between 12.5 and 27cm. Definitions of snag sizes are as follows: small snags have DBH 12.5 and 27cm, medium snags have DBH between 27.1 and 60cm, and large snags have DBH over 60cm. Coarse woody debris with minimum diameter of 8cm at smaller end were identified to
species if possible, and measured for diameter and length. Percent cover of coarse woody debris was calculated utilizing methods described in Wadell (2002). Canopy closure was estimated with a densiometer within 2-m of the nest tree in the four cardinal directions and averaged to obtain overall canopy closure at the nest.

Nest territory scale was estimated with a 150-m radius area around each nest. This radius defines a 7.04-ha area, which corresponds to the smaller territory sizes of the three species (7 ha for Hairy woodpeckers [Jackson et al., 2002], 8 ha for White-headed woodpeckers [Garrett et al., 1996] and 13 ha for Black-backed woodpeckers [Dixon and Saab, 2000]). Habitat at the territory scale was characterized by the following variables derived from Geographic Information Systems (GIS) data: percent vegetation cover by category, burn severity, percent cover of impervious surfaces. Vegetation data were obtained from the Tahoe GIS Data Clearinghouse and were created through analysis of IKONOS satellite imagery at a 30m pixel scale. I classified vegetation into categories of conifer, shrub, and wetland. Impervious surface data were obtained from the California Tahoe Conservancy and consisted of spatial data of paved and dirt roads and trails. Burn severity data were obtained from the US Forest Service and were created with pre-burn and post-burn satellite imagery that corresponds to percent loss of basal area of trees at a 30m pixel scale. Burn severity percentages were obtained for analysis at all three spatial scales. GIS-based habitat values were derived with ArcGIS 9.3 (ESRI, Redlands, CA).

Data were also collect at all spatial scales for 38 “non-nest” sites for comparison with nest sites. Non-nest sites were defined as sites that were nest searched, but had no
active nests within 100m. Non-nest sites were spread throughout the study area and spaced at least 100m apart to best represent available habitat without pseudoreplication.

Analysis

Nest data from 2010 were analyzed for nest site selection in order maximize sample size and independence. Comparisons of nest site selection between the three species of woodpecker were analyzed using one-way ANOVA to determine if they differed in mean nest tree, site, and territory characteristics. At the nest tree scale, means of nest tree DBH, height, decay, and scorch were compared. At the nest site scale, means of canopy closure, density of small, medium, and large DBH snags, density of live trees, and percent cover of coarse woody debris were compared. At the nest territory scale, means of percent cover of coniferous forest, shrub, wetland, and impervious surfaces were compared. Mean burn severity at each spatial scale was also compared. Data transformations were utilized to meet assumptions of normal distributions and homoscedasticity. Proportional data were transformed with arcsine square root transformations and other data were transformed with either natural log or square root transformations. Bonferroni post hoc tests were utilized to determine significant differences between individual species for any significant result of the ANOVA. Means of decay class, burn severity at all scales, and all territory variables were compared with Kruskal-Wallis test due to non-normal distribution. Mann-Whitney U post hoc test with Bonferroni correction was utilized to determine differences for significant results between individual species of woodpecker.
Models representing the most influential environmental factors were obtained for each spatial scale and each woodpecker species using stepwise multiple logistic regression analysis. Logistic regression compared nest sites of each species with “non-nest” sites to determine how characteristics at active nests differed from available habitat. At the nest tree scale DBH, tree height, percent scorch, and burn severity were entered into the model. At the scale of nest site, the following variable were entered into the model: density of small and large trees, density of small, medium, and large snags, percent cover of coarse woody debris, canopy closure, and burn severity. At the territory scale, percent cover of coniferous forest, shrub, wetland, and impervious surfaces, and burn severity were entered into the model. Environmental variables were added at a significance level of 0.05 and subtracted at a significance level of 0.1 to obtain the model with the highest $R^2$ value. Individual regression coefficients were tested with Wald’s chi-squared to determine the influence of individual predictors included in best models. Models were evaluated with Likelihood ratio tests, which test the null hypothesis that the intercept-only model is the same as the model that included covariates. Model fit was evaluated with Pearson goodness-of-fit tests, which tests the null hypothesis that the data fits the model. Thresholds for significant parameters were determined by plotted predicted probability of nest presence and determining the value for habitat characteristics when the probability is 0.75. This threshold was selected to maximize sensitivity and specificity of habitat models. While thresholds of 0.5 are often used (Luck, 2002; Woolf et al., 2002), this measure has been criticized as giving nonsense results for unbalanced samples (Liu et al., 2005). Using 0.75 as a threshold follows
methods used to determining appropriate habitat necessary to prevent extinction (Fahrig, 2001) and is less sensitive to unbalanced samples.
RESULTS

Nest Searching

A total of 169 nests were found for focal species in 2009 and 2010 combined. In 2009, 15 Black-backed woodpecker nests, 37 Hairy woodpecker nests, and 20 White-headed woodpecker nests were found. In 2010, 24 Black-backed woodpecker nests, 41 Hairy woodpecker nests, and 26 White-headed woodpecker nests were found.

Secondary Cavity Use

All detections of secondary cavity use occurred between March and August, 2010. Eighty-one percent of cavities monitored had some secondary cavity use detected. A total of 53 detections were observed at all nests, of which 70% were birds and 30% were small mammals. Nine species of secondary cavity users were detected (Table 1). Western bluebirds (*Sialia mexicana*) and chipmunks (*Tamias species*) were detected at the most nests overall (Table 1).

Mean species richness of secondary cavity users detected at cavities excavated by Black-backed woodpeckers was 1.143 (n=7, s.d. =0.69). Cavities excavated by Hairy woodpeckers had mean species richness of 1.20 (n=10, s.d.=0.632). Mean species richness of secondary cavity users for cavities excavated by White-headed woodpeckers
<table>
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<td>Northern flying squirrel</td>
<td><em>Glaucousmys sabrinus</em></td>
<td>GLSA</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>House wren</td>
<td><em>Troglodytes aedon</em></td>
<td>HOWR</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mountain bluebird</td>
<td><em>Sialia currooides</em></td>
<td>MOBL</td>
<td>2</td>
<td>0</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Mountain chickadee</td>
<td><em>Poecile gambeli</em></td>
<td>MOCH</td>
<td>4</td>
<td>0.25</td>
<td>0.25</td>
<td>0.5</td>
</tr>
<tr>
<td>Northern flicker</td>
<td><em>Colaptes auratus</em></td>
<td>NOFL</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Douglas squirrel</td>
<td><em>Tamiosciurus douglasii</em></td>
<td>TADO</td>
<td>5</td>
<td>0</td>
<td>0.6</td>
<td>0.4</td>
</tr>
<tr>
<td>Chipmunk</td>
<td><em>Tamias species</em></td>
<td>TAMIAS</td>
<td>6</td>
<td>0.33</td>
<td>0</td>
<td>0.67</td>
</tr>
<tr>
<td>White-breasted nuthatch</td>
<td><em>Sitta carolinesis</em></td>
<td>WBNU</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Western bluebird</td>
<td><em>Sialia mexicana</em></td>
<td>WEBL</td>
<td>6</td>
<td>0.17</td>
<td>0.33</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Table 1. Proportional use of cavities by secondary cavity users. Secondary cavity users detected at cavities are described by common and scientific names and codes in the left side of the table. The column with number of detections indicates the total number of detections for each secondary cavity user. The right side of the table describes the proportion of use of secondary cavity users for cavities excavated by each species of woodpecker. The proportion of use is equal to the number of detections of a species of secondary cavity user at cavities excavated by each species of woodpecker divided by the total number of detections.
was 1.82 (n=11, s.d.=1.32). The one-way ANOVA did not find any significant differences in mean species richness (F=1.54, df=2.25, P=0.234) between the three species of woodpecker.

All three woodpeckers created cavities that were used by both birds and small mammals (Table 1, Figure 4). Cavities created by both White-headed woodpeckers and Black-backed woodpeckers were utilized by six species (Table 1, Figure 4). Hairy woodpecker nests had the lowest secondary cavity user diversity, with only 4 species utilizing these cavities (Table 1, Figure 4). Nest webs indicate that species preferred cavities excavated by a particular species of woodpecker, excluding Mountain bluebirds, which equally utilized White-headed and Hairy woodpecker nests (Table 1, Figure 4). Northern flying squirrels, House wrens, and Northern flickers exclusively utilized cavities excavated by Black-backed woodpeckers, while White-breasted nuthatches were only detected in cavities excavated by White-headed woodpeckers (Table 1, Figure 4). Chipmunks preferred White-headed woodpecker cavities (67%). Douglas squirrels preferred cavities excavated by Hairy woodpeckers (60%). Both Mountain chickadees and Western bluebirds preferred White-headed woodpecker cavities (50%), although they used cavities excavated by all three species. Overall sample sizes for all detections were very small.

Although sample sizes were too small to directly compare differences in species composition, Fisher’s Exact Test did reveal significant difference in use of cavities
Figure 4. Nest web for Angora fire. The bottom of the nest web is the species of trees utilized as cavity substrate, the middle is the focal species of woodpeckers, and the top is the secondary cavity users. Lines connect species that use resources provided by the species below and are associated with the proportion of resource used by the species. BBWO=Black-backed woodpecker, WHWO=White-headed woodpecker, HAWO=Hairy woodpecker, GLSA=Northern flying squirrel, HOWR=house wren, NOFL=Northern flicker, TAMIAS=Chipmunk species, MOCH=Mountain chickadee, WEBL=Western bluebird, WBNU=White-breasted nuthatch, MOBL=Mountain bluebird, TADO=Douglas squirrel.
excavated by a particular species of woodpecker and groups of secondary cavity users. Species associated with open canopy included House wrens, Western and Mountain bluebirds, White-breasted nuthatches, and Tamias species. Species associated with closed canopy included Northern flying squirrels, Douglas squirrels, Northern Flickers, and Mountain chickadees. Secondary cavity users associated with open canopy cover preferred cavities excavated by White-headed woodpeckers (Fisher’s Exact Test, P=0.019). Ninety percent of White-headed woodpecker nests had detections of species associated with open canopy cover. Sixty-two percent of Black-backed woodpeckers had detections of species associated with open canopy. Only 31% of Hairy woodpecker nests had detections of species associated with open canopy. No significant preferences were found for species associated with closed canopy (Fisher’s Exact Test, P=0.797), with detections of these species at 43% of Black-backed woodpecker nests, 40% of White-headed woodpecker nests, and 31% of Hairy woodpecker nests.

Cavities of Black-backed woodpeckers had five nesting bird, one additional bird, and two small mammal detections, resulting in a Cavity Utilization Index of 1.64, with 88% of cavities used. Hairy woodpeckers created cavities that had detections of six nesting birds, two other birds, and three small mammals, for Cavity Utilization Index of 0.959. For Hairy woodpeckers, 69% of cavities were used. White-headed woodpeckers had seven detections of nesting birds, four detections of other birds, and six detections of small mammals, resulting in a Cavity Utilization Index of 2.12, with 83% of cavities used.
Nest site selection

Nest trees of Black-backed woodpeckers had mean DBH of 35.3cm (s.d.=9.44), mean height of 17.47m (s.d.=8.07), mean decay of 1.7 (s.d.=1.17), and mean percent scorch of 88.3% (s.d.=20.4). The mean burn severity at the nest was 90.2% (s.d.=16.1). Nest sites for Black-backed woodpeckers had mean canopy closure of 25.1% (s.d.=12.3). The mean total density of trees was 9.75 stems/ha (s.d.=26.7), mean density of small trees was 1.04 stems/ha (s.d.=5.10), and mean density of large trees was 11.46 stems/ha (s.d.=27.56). Mean density of small snags was 62.5 stems/ha (s.d.=54.2). Mean density of medium snags was 186.46 stems/ha (s.d.=101.1). Mean density of large snags was 23.96 stems/ha (s.d.=25.0). Mean percent cover of coarse woody debris at the nest site was 3% (s.d.=3.6). Mean burn severity in the nest site was 90.5% (s.d.=15.5). Within the nest territory, mean percent cover for coniferous forest was 94.6% (s.d.=10.9). Mean percent cover of shrub was 5.0% (s.d.=10.9). No wetland habitat was detected within the nest territory. Mean percent cover of impervious surface was 5.4% (s.d.=6.7). Mean burn severity within the nest territory was 86.6% (s.d.=18.1).

Nest trees of Hairy woodpeckers had mean DBH of 40.25cm (s.d.=8.82), mean height of 17.7m (s.d.=8.13), mean decay of 1.7 (s.d.=1.66), and mean percent scorch of 89% (s.d.=16.1, range=35 to 100%). The mean burn severity at the nest was 89% (s.d.=18.5). Mean slope at the nest was 21.7% (s.d.=13.7) and mean elevation was 2,016m (s.d.=73.5). Nest sites for Hairy woodpeckers had mean canopy closure of 21.5%
The mean total density of trees was 9.76 stems/ha \( (s.d. = 26.7) \), the mean density of small trees was 1.83 stems/ha \( (s.d. = 6.59) \), and the mean density of large trees was 7.93 stems/ha \( (s.d. = 25.3) \). Mean density of small snags was 95.7 stems/ha \( (s.d. = 89.77) \). Mean density of medium snags was 160.97 stems/ha \( (s.d. = 88.22) \). Mean density of large snags was 24 stems/ha \( (s.d. = 40.85) \). Mean percent cover of coarse woody debris at the nest site was 4\% \( (s.d. = 2.7) \). Mean burn severity in the nest site was 90.7\% \( (s.d. = 21.2) \). Within the nest territory, mean percent cover for coniferous forest was 94.6\% \( (s.d. = 10.9) \) with mean percent cover of high elevation coniferous forest was 39.4\% \( (s.d. = 41.7) \) and mean percent cover of low coniferous forest was 55.3\% \( (s.d. = 38.8) \). Mean percent cover of shrub was 2.3\% \( (s.d. = 6.5) \) and mean percent cover of wetland was 1.7\% \( (s.d. = 6.7) \). Mean percent cover of impervious surface was 4.6\% \( (s.d. = 6.01) \). Mean burn severity at the territory scale for Hairy woodpeckers was 85.9\% \( (s.d. = 20.5) \).

Nest trees of White-headed woodpeckers had mean DBH of 39.2 cm \( (s.d. = 10.6) \), mean height of 7.8 m \( (s.d. = 5.9) \), mean decay of 3.1 \( (s.d. = 1.3) \), and mean percent scorch of 97.3\% \( (s.d. = 10.4) \). Mean burn severity at the nest was 90.5\% \( (s.d. = 14.9) \). Mean slope was 21.7\% \( (s.d. = 13.7) \) and mean elevation was 2018 m \( (s.d. = 69.8) \). Nest sites of White-headed woodpeckers had mean canopy closure of 17.2\% \( (s.d. = 10.1) \). Mean total tree density was 19.23 stems/ha \( (s.d. = 34.9) \), with mean density of small trees of 0.96 stems/ha \( (s.d. = 4.9) \) and mean density of large trees of stems/ha of 18.27 stems/ha \( (s.d. = 32.83) \). Mean density of small snags was 44.2 stems/ha \( (s.d. = 35.6) \) and mean density of medium snags was 76.9 stems/ha \( (s.d. = 73.1) \). Mean density of large snags was 26.9 stems/ha \( (s.d. = 32.3) \). Mean percent cover of coarse woody debris was 2.4\% \( (s.d. = 2.4) \). Mean burn
severity within the nest site was 90.5% (s.d.=14.4). Nest territories of White-headed woodpeckers had mean percent cover of coniferous forest of 88.1% (s.d.=22.2), with mean percent cover of high elevation conifer of 42.4% (s.d.=37.1) and mean percent cover of 50.2% (s.d.=35.4). Mean percent cover of shrub of 6% (s.d.=13.0), mean percent cover of wetland of 0.64% (s.d.=3.3), and mean percent cover of impervious surfaces of 8.4% (se=8.8). Mean burn severity within nest territory was 82.5% (s.d.=17.4).

Significant differences were found in mean nest site characteristics between species of woodpecker. Mean height of nest trees and mean height of cavities (Table 2) varied significantly between species. Nest trees for White-headed woodpeckers were significantly shorter than both Black-backed and Hairy woodpeckers. Mean cavity height was significantly higher for Hairy woodpeckers than both Black-backed and White-headed woodpeckers. Mean nest tree decay class also differed between the species (Table 2), with significantly higher decay classes observed in nest trees of White-headed woodpeckers nests than both Black-backed and Hairy woodpecker nests. Mean percent scorch of the nest trees, slope, and elevation were not significantly different between the three species (Table 2).

Significant differences were observed for mean densities of small snags, with Hairy woodpeckers utilizing more dense stands than White-headed woodpeckers (Table 2). Mean densities of medium sized snags also differed among woodpeckers.
### Results of ANOVA comparing nest site selection

df = 2, 85

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Black-backed woodpecker (n = 24)</th>
<th>Hairy woodpecker (n = 41)</th>
<th>White-headed woodpecker (n = 26)</th>
<th>Test</th>
<th>P</th>
<th>Post-hoc test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cavity height (m)</td>
<td>4.6 (3.05)</td>
<td>7.46 (4.54)</td>
<td>4.30 (2.39)</td>
<td>8.09</td>
<td>0.0006*</td>
<td>HAWO &gt; BBWO, HAWO &gt; WHWO</td>
</tr>
<tr>
<td>Diameter at breast height (cm)</td>
<td>35.3 (9.44)</td>
<td>39.66 (9.29)</td>
<td>39.8 (11.3)</td>
<td>2.1</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>Height (m)</td>
<td>17.5 (8.07)</td>
<td>17.2 (8.2)</td>
<td>7.6 (5.7)</td>
<td>21.84</td>
<td>&lt;0.0001*</td>
<td>BBWO &gt; WHWO, HAWO &gt; WHWO</td>
</tr>
<tr>
<td>Decay</td>
<td>1.7 (1.67)</td>
<td>1.7 (0.96)</td>
<td>3.2 (1.3)</td>
<td>22.12</td>
<td>&lt;0.0001*</td>
<td>WHWO &gt; BBWO, WHWO &gt; HAWO</td>
</tr>
<tr>
<td>Scorch (%)</td>
<td>88.3 (20.4)</td>
<td>84.9 (26.2)</td>
<td>86.9 (31.3)</td>
<td>0.14</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td>Slope (%)</td>
<td>19.7 (12.5)</td>
<td>25.6 (14.8)</td>
<td>21.7 (13.7)</td>
<td>1.52</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2.009 (52.2)</td>
<td>2017 (73.5)</td>
<td>2018 (69.8)</td>
<td>0.14</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>Burn severity (%)</td>
<td>90.1 (16.1)</td>
<td>86.7 (28.1)</td>
<td>78.6 (33.8)</td>
<td>3.46</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td>Nest site (.04 ha)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>25.1 (12.3)</td>
<td>23.2 (14.5)</td>
<td>17.9 (10.1)</td>
<td>3.25</td>
<td>0.04</td>
<td>BBWO &gt; WHWO</td>
</tr>
<tr>
<td>Density of tree (stems/ha)</td>
<td>1.04 (5.1)</td>
<td>5.23 (17.7)</td>
<td>5.8 (17)</td>
<td>1.33</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>Density small snags (stems/ha)</td>
<td>62.5 (54.17)</td>
<td>91.3 (42.5)</td>
<td>36.6 (7.03)</td>
<td>0.029*</td>
<td>HAWO &gt; WHWO</td>
<td></td>
</tr>
<tr>
<td>Density medium snags (stems/ha)</td>
<td>186.5 (101.1)</td>
<td>153.5 (70)</td>
<td>71.1 (21.22)</td>
<td>&lt;0.0001*</td>
<td>BBWO &gt; WHWO, HAWO &gt; WHWO</td>
<td></td>
</tr>
<tr>
<td>Density large snags (stems/ha)</td>
<td>24 (25)</td>
<td>39 (43.7)</td>
<td>31.5 (2.98)</td>
<td>0.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coarse woody debris (%)</td>
<td>3 (3.6)</td>
<td>3.6 (2.7)</td>
<td>2.3 (2.4)</td>
<td>1.91</td>
<td>0.16</td>
<td></td>
</tr>
<tr>
<td>Burn severity (%)</td>
<td>90.5 (15.5)</td>
<td>86.5 (28.3)</td>
<td>78.6 (33.6)</td>
<td>4.95</td>
<td>0.08</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Comparison of nest characteristics. * indicates significant P-value at alpha = 0.05. BBWO = Black-backed woodpecker, HAWO = Hairy woodpecker, WHWO = White-headed woodpecker. s.d. = standard deviation, df = degrees of freedom, Test = Test statistic.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Black-backed woodpecker (n=25)</th>
<th>Hairy woodpecker (n=41)</th>
<th>White-headed woodpecker (n=26)</th>
<th>Results of ANOVA comparing nest site selection (df=2, 85)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest territory (7.06 ha)</td>
<td>Average: 94.6 s.d.: 10.9</td>
<td>Average: 94.3 s.d.: 11.3</td>
<td>Average: 88.1 s.d.: 22.2</td>
<td>Test: 5.87 P: 0.07 P: Post-hoc test</td>
</tr>
<tr>
<td>Coniferous forest (%)</td>
<td>94.6: 10.9</td>
<td>94.3: 11.3</td>
<td>88.1: 22.2</td>
<td></td>
</tr>
<tr>
<td>Shrub (%)</td>
<td>5: 11</td>
<td>3.3: 9.1</td>
<td>7.2: 15.8</td>
<td>3.68: 0.16</td>
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<tr>
<td>Wetland (%)</td>
<td>0: 0</td>
<td>1.8: 6.6</td>
<td>3.8: 12.7</td>
<td>4.02: 0.13</td>
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<tr>
<td>Impervious surface (%)</td>
<td>5.4: 6.7</td>
<td>5.4: 7.4</td>
<td>8.9: 9.6</td>
<td>3.19: 0.20</td>
</tr>
<tr>
<td>Burn severity (%)</td>
<td>86.5: 18.1</td>
<td>81.9: 27.1</td>
<td>72.7: 30.7</td>
<td>1.88: 0.39</td>
</tr>
</tbody>
</table>

Table 2 continued.
with Black-backed and Hairy woodpeckers both utilizing more dense stands than White-headed woodpeckers (Table 2). Mean canopy closure at the nest differed between the species, with higher mean canopy closure at Black-backed woodpecker nests than White-headed woodpecker nests (Table 2). Mean density of large snags and mean total tree density did not differ significantly between the species of woodpecker (Table 2). Non-significant trend were observed for differences in mean burn severity (Table 2), with Black-backed nests in highest burn severity, Hairy woodpeckers in intermediate burn severity, and White-headed woodpecker nests in lowest burn severity sites. There was no significant difference in mean percent cover of coarse woody debris at the nest site for the three species (Table 2).

There were no significant differences between the species in any parameter analyzed at the nest territory scale, however, there were non-significant trends toward differences in mean coniferous forest (Table 2) with Black-backed and Hairy woodpeckers selecting higher percent cover of coniferous forest than White-headed woodpeckers.

Factors influencing nest presence varied among the species of woodpecker. For Black-backed woodpeckers, the strongest model predicting nest presence at the scale of the nest tree only included percent scorch (Table 3), with threshold value of 90%. According to this model, the probability of nest presence for Black-backed woodpeckers was positively related to percent scorch of the nest tree (Fig. 5a). At the scale of nest site,
the best model included density of medium snags (Table 3), with threshold value of 250 stems/ha. Probability of nest presence increased with increasing density of medium snags (Fig. 5b). No parameter met the minimum standards to enter the model at the territory scale (Table 3). All models improved on the null, intercept-only model, based on the Likelihood ratio test. Pearson goodness-of-fit statistic indicated that the models adequately fit the data.

The best model predicting nest presence of Hairy woodpeckers at the scale of the nest tree included percent scorch (Table 3) of the nest tree, with threshold value of 80%. Probability of nest presence increased with increasing percent scorch of nest tree (Fig. 6a). At the site scale, the best model included density of small snags and density of large trees (Table 3). Threshold values were 85 stems/ha for density of small snags and 0 stems/ha for large trees. Probability of nest presence was positively associated with increasing small snag density (Fig. 6b) but negatively associated with increasing large tree density (Fig. 6c). At the territory scale, the best model included only percent cover of coniferous forest (Table 3). Probability of nest presence increased as percent cover of coniferous forest increased (Fig. 6d). Threshold value for percent cover of coniferous forest was 100%. All models improved on the null, intercept-only model, based on Likelihood ratio test. Pearson goodness-of-fit statistic indicated that the models adequately fit the data.
<table>
<thead>
<tr>
<th>Black-backed</th>
<th>Maximum Likelihood Estimates</th>
<th>Likelihood ratio test</th>
<th>Pearson goodness-of-fit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>Estimate</td>
<td>SE</td>
<td>Wald $\chi^2$</td>
</tr>
<tr>
<td>Nest tree ($R^2=0.411$)</td>
<td>22.376</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Intercept</td>
<td>-3.191</td>
<td>0.951</td>
<td>11.267</td>
</tr>
<tr>
<td>Scorch</td>
<td>0.0393</td>
<td>0.0112</td>
<td>12.348</td>
</tr>
<tr>
<td>Nest site ($R^2=0.17$)</td>
<td>8.387</td>
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<td>0.0038</td>
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<tr>
<td>Intercept</td>
<td>-0.716</td>
<td>0.300</td>
<td>5.698</td>
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<tr>
<td>Density medium snags</td>
<td>0.748</td>
<td>0.280</td>
<td>7.146</td>
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<tr>
<td>Nest Territory</td>
<td>Intercept</td>
<td>-0.460</td>
<td>0.2607</td>
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</table>

<table>
<thead>
<tr>
<th>Hairy</th>
<th>Maximum Likelihood Estimates</th>
<th>Likelihood ratio test</th>
<th>Pearson goodness-of-fit</th>
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</thead>
<tbody>
<tr>
<td>Model</td>
<td>Estimate</td>
<td>SE</td>
<td>Wald $\chi^2$</td>
</tr>
<tr>
<td>Nest tree ($R^2=0.458$)</td>
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<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.555</td>
<td>0.361</td>
<td>2.362</td>
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<tr>
<td>Scorch</td>
<td>1.916</td>
<td>0.446</td>
<td>18.419</td>
</tr>
<tr>
<td>Nest site ($R^2=0.333$)</td>
<td>22.721</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.755</td>
<td>0.448</td>
<td>2.848</td>
</tr>
<tr>
<td>Density large trees</td>
<td>-1.518</td>
<td>0.726</td>
<td>4.376</td>
</tr>
<tr>
<td>Density small snags</td>
<td>0.719</td>
<td>0.287</td>
<td>6.264</td>
</tr>
</tbody>
</table>

Table 3. Models of nest site selection created with stepwise multiple logistic regression. SE=Standard error, df=degrees of freedom. Maximum likelihood estimates evaluate the influence of individual variables. Likelihood ratio tests the null hypothesis that intercept-only model is same as that with covariates and goodness-of-fit tests the null hypothesis that the data fit the model.
<table>
<thead>
<tr>
<th>Hairy</th>
<th>Maximum Likelihood Estimates</th>
<th>Likelihood ratio test</th>
<th>Pearson goodness-of-fit</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
<td>Wald χ²</td>
</tr>
<tr>
<td>Nest Territory (R²=0.080)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.04</td>
<td>0.235</td>
<td>0.029</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>0.611</td>
<td>0.306</td>
<td>3.982</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>White-headed</th>
<th>Maximum Likelihood Estimates</th>
<th>Likelihood ratio test</th>
<th>Pearson goodness-of-fit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>Estimate</td>
<td>SE</td>
<td>Wald χ²</td>
</tr>
<tr>
<td>Nest tree (R²=0.903)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-6.349</td>
<td>2.925</td>
<td>4.712</td>
</tr>
<tr>
<td>Scorch</td>
<td>9.000</td>
<td>4.261</td>
<td>4.469</td>
</tr>
<tr>
<td>Decay</td>
<td>3.688</td>
<td>1.995</td>
<td>3.417</td>
</tr>
<tr>
<td>Tree height</td>
<td>-3.827</td>
<td>1.921</td>
<td>3.970</td>
</tr>
<tr>
<td>Nest site (R²=0.109)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.788</td>
<td>0.345</td>
<td>5.21</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>-0.867</td>
<td>0.408</td>
<td>4.51</td>
</tr>
<tr>
<td>Nest Territory</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.38</td>
<td>0.255</td>
<td>2.22</td>
</tr>
</tbody>
</table>

Table 3 continued.
Figure 5a. Probability of presence of Black-backed woodpecker nests with percent scorch of nest trees. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, scorch of nest tree is 90%.
Figure 5b. Probability of presence of Black-backed woodpecker nests with density of medium snags. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, density of medium snags is 250 stems/ha.
Figure 6a. Probability of presence of Hairy woodpecker nests with percent scorch of nest trees. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, scorch of the nest tree is 80%.
Figure 6b. Probability of presence of Hairy woodpecker nests with density of large trees. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, density of large trees is 0 stems/ha.
Figure 6c. Probability of presence of Hairy woodpecker nests with density of small snags. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, density of small snags is 85 stems/ha.
Figure 6d. Probability of presence of Hairy woodpecker nests with percent cover of coniferous forest. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, percent cover of coniferous forest is 100%.
For White-headed woodpeckers, the best model predicting nest presence at the scale of the nest tree included percent scorch, decay, and tree height (Table 3). Probability of nest presence was positively associated with percent scorch (Fig. 7a) and decay (Fig. 7b), but was negatively associated with height (Fig. 7c). Threshold for high quality habitat for percent scorch was 90%. High quality habitat threshold for decay was 3.25 and threshold for height was 0m. At the site scale, the best model included canopy closure (Table 3). Probability of nest presence decreased with canopy closure in the nest site (Fig. 7d), with a threshold of 0% closure. No parameter met the minimum standards to enter the model at the territory scale (Table 3). All models improved on the null, intercept-only model, based on Likelihood ratio test. Pearson goodness-of-fit statistic indicated that the models adequately fit the data.

Woodpeckers differed in factors that strongly influenced nest presence. All species were positively influenced by scorch of the nest tree, with similar threshold values for each. With 75% probability of presence, nest trees were 90% scorched for Black-backed woodpeckers and White-headed woodpeckers and 80% scorched for Hairy woodpeckers. White-headed woodpeckers relied upon short, well-decayed snags for nesting. Black-backed woodpeckers were positively influenced by increasing density of
Figure 7a. Probability of presence of White-headed woodpecker nests with percent scorch of nest trees. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, scorch of the nest tree is 90%.
Figure 7b. Probability of presence of White-headed woodpecker nests with decay of nest trees. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, decay of the nest tree is 3.25.
Figure 7c. Probability of presence of White-headed woodpecker nests with height of nest trees. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, tree height is 0m.
Figure 7d. Probability of presence of White-headed woodpecker nests with canopy closure. Shaded area represents 95% confidence interval. Arrows represent threshold of predicted probability of occurrence of a nest of 0.75 and represent high quality habitat. At this threshold, canopy closure is 0%.
medium snags while Hairy woodpeckers were positively influenced by density of small snags and negatively influenced by large trees. While White-headed woodpeckers were not influenced significantly by snag or tree density, they were negatively associated with canopy closure, indicating they prefer more open areas for nesting. At the territory level, only Hairy woodpeckers had a significant relationship with any parameter, percent cover of coniferous forest.
DISCUSSION

Woodpeckers play a large role in facilitating the re-colonization of secondary cavity users after a fire. All three species of woodpecker supported the cavity-dependent community in the burned area, with White-headed and Black-backed woodpeckers exerting the strongest influence based on Cavity Utilization Indices and nest webs. While cavities of Hairy woodpeckers supported fewer species and were used in lower proportion, they were preferred by one species of secondary cavity user. This suggests that while White-headed and Black-backed woodpeckers are the most important excavators influencing re-colonization, all three species of woodpecker may be required to provide preferred habitat to all secondary cavity users.

Woodpeckers differed in influence on recovery of secondary cavity users, due in part to differences in habitat selection. White-headed woodpeckers had the highest Cavity Utilization Index and their cavities were preferred by secondary cavity users associated with open habitat. White-headed woodpeckers differ from Black-backed and Hairy woodpeckers in several ways. These differences may stem from morphological and behavioral adaptations of White-headed woodpeckers related to their diet based heavily upon pine nuts (Ligon, 1973). There may be a trade-off in excavation ability and seed foraging ability, and in fact, White-headed woodpeckers are rarely observed drilling deeply while foraging (Ligon, 1973). Weak excavators may depend upon more decayed snags because they are softer and easier to excavate and these snags are likely to be
shorter as their tops break off due to advanced decay. White-headed woodpeckers build their cavities in significantly more decayed and shorter snags than both Black-backed or Hairy woodpeckers, and these cavities were preferred by secondary cavity users. Additionally, White-headed woodpeckers had the lowest snag densities surrounding the cavity of the three primary excavators and were negatively associated with canopy closure. Cavities created by White-headed woodpeckers may be preferred by secondary cavity users based on these selection criteria. White-headed woodpecker cavities may provide foraging areas for secondary cavity users, including wood-probing insectivores that prefer decayed wood, aerial insectivores that prefer low density of trees and snags, and species associated with dense understory and low canopy closure.

Black-backed and Hairy woodpeckers were also important in supporting the cavity-dependent community. Black-backed woodpeckers had a greater influence on recovery of secondary cavity users than Hairy woodpeckers, although nest site selection between the two species of woodpecker was quite similar. These two species are likely to compete for appropriate snags and stands in burned areas. Black-backed woodpeckers, as fire specialists, peak in number within three to five years post-fire, and then decline rapidly, due to snag attrition, reductions in beetle populations, and re-colonization by nest predators (Saab et al., 2007). Although Black-backed and Hairy woodpeckers shared many similarities in nest habitat, Hairy woodpeckers had a much lower Cavity Utilization Index, which may be due to higher cavity heights associated with Hairy woodpecker nests. As Black-backed woodpeckers and their influence on recovery of secondary cavity
users decline in time since fire, the influence of Hairy woodpeckers may increase. Cavities excavated by Hairy woodpeckers may become particularly important to breeding birds as nest predators re-colonize burned areas and higher cavities provide refuge from predation risk (Nilsson, 1984).

Based on differences in Cavity Utilization Indices and nest site selection, the most important factors influencing secondary cavity use are cavity height and decay class of nest trees, and density of snags surrounding nest trees. White-headed and Black-backed woodpeckers had much higher Cavity Utilization Indices than Hairy woodpeckers, and both excavated cavities significantly lower than Hairy woodpeckers. Past research suggests that lower cavity heights may be associated with increased predation (Nilsson, 1984) although in burned forests this pattern has not always been observed (Saab and Vierling, 2001). In fact, secondary cavity users prefer lower cavity heights in burned forests, as shown by Gentry and Vierling (2001) and this study. Selection of low cavities by secondary cavity users indicates that risk of nest predation is low in recently burned forests. Preferences for low cavities may decrease as time since fire and predation risk increase. Decay class of nest trees and density of snags in the surrounding area were also important in determining which cavities were utilized by secondary cavity users. Cavities excavated by White-headed woodpeckers were in more decayed trees and in areas with lower canopy cover and less dense stands of snags than other woodpecker nests. These cavities had the highest Cavity Utilization Index, indicating that they provided the greatest influence on recovery of secondary cavity users. This is likely due to
specializations and preferences of secondary cavity users that commonly re-colonize burned forests: aerial insectivores, bark-foragers, and species associated with open canopy forest with dense understory.

Eighty-one percent of all cavities monitored had detections of secondary cavity use. This indicates that there is strong competition among secondary cavity users for cavities within the burned area. Cavities may be rare immediately after a burn, as existing snags are lost (Saab et al., 2004, 2007; Bagne et al., 2008). Cavities may continue to be limited as burned snags have lower persistence than unburned snags (Bagne et al., 2008), and this may be exacerbated by woodpecker activity that reduces structural integrity (Farris et al., 2002, 2004; Jackson and Jackson, 2004). Limited numbers of available cavities may result in increased competition among cavity users. Anecdotally, I observed two attempts of “cavity usurping”: once when a pair of Western bluebirds harassed a White-headed woodpecker that was excavating a new cavity and again when a pair of Tree swallows (*Tachycineta bicolor*) attempted to drive a pair of Pygmy nuthatches (*Sitta pygmaea*) out of their nest cavity. Cavities appear to be limited within the burned area and species are competing to use them. Because population growth of secondary cavity users may depend upon an adequate number of cavities available (Holt and Martin, 1997), successful re-colonization of secondary cavity users in burned forests will depend on continued presence of woodpeckers to replenish the supply of cavities.

While woodpeckers differed in nest site selection and influence on recovery, all played an important role in supporting other species through habitat creation for nesting,
resting, denning, and roosting. This role may be affected by post-fire management activity. All three species of woodpecker nested exclusively in snags in this study and both Black-backed and Hairy woodpeckers were significantly and positively correlated with density of snags. Post-fire management activities that reduce suitable habitat for woodpecker nests, such as salvage logging, will impact the overall community (Hutto, 2004; Aitken and Martin, 2008). Because the three species of woodpecker have different preferences for densities and character of snags within the nest site, and because snags serve dual use as foraging and nesting sites for many species re-colonizing burned forests, heterogeneous habitat will be the most valuable for the overall community. Salvage logging prescriptions that leave patches of snags of different sizes and decay classes in different densities will support all three species of woodpecker, providing habitat for cavity-dependent communities (Saab and Dudley, 1998; Saab et al., 2007). Currently, salvage logging prescriptions generally call for the removal of most or all small snags, leaving approximately 5-10 large snags per hectare for wildlife use. Salvage logging prescriptions that remove small snags may greatly reduce habitat for both Hairy and Black-backed woodpeckers because they prefer areas with high densities of small to medium sized snags. White-headed woodpeckers are also likely to be impacted as they utilize moderate to large, well-decayed snags for nest trees, which are often logged for safety reasons. Reduction in woodpecker nest sites will likely result in losses in the overall cavity-dependent community (Aitken and Martin, 2008). Cavity-dependent communities include seed dispersing birds and mammals, insectivores, and predators, which play important roles in the overall ecosystem (Raphael and White, 1978, 1984;
Verner and Boss, 1980). In order to preserve cavity-dependent communities, suitable cavities, and therefore, habitat for woodpeckers, must be conserved. Salvage logging prescriptions that leave mixed stands of size, species, and density of snags will provide habitat for woodpeckers and the community as a whole.

This study was limited by the number of cavities that were monitored for secondary cavity use. Many snags fell during the study period, reducing sample sizes. Increasing the number of nests discovered and monitored for each species of woodpecker will allow for comparison of preference of individual species of secondary cavity users and identification of keystone excavators. Keystone species may also be identified by blocking access to cavities and measuring response of secondary cavity user richness and abundance. Additionally, because the most-used cavities were lowest, a study evaluating nest predation and nest success of secondary cavity users may reveal source or sink habitat.

Woodpeckers play an important role in post-fire habitats by rapidly colonizing these areas and creating cavities that are used by many other species that rely upon them for nesting, denning, roosting, and resting (Aitken and Martin, 2002; Blanc and Walters, 2007). Woodpeckers select habitat based on excavation ability and foraging preferences, resulting in differences in selection between species. These differences result in differential use by secondary cavity users, with some species of woodpecker influencing recovery more strongly than others. Because woodpeckers may act as keystone species (Lawton and Jones, 1995; Simberloff, 1998; Martin and Eadie, 1999; Bonar, 2000;
reviewed in Aubrey and Raley, 2002; Bednarz et al., 2004), factors that influence nest site selection for woodpeckers may influence the structure and composition of cavity-dependent communities. Understanding the relationships between woodpeckers, cavity-dependent communities, and habitat is crucial for forest management and conservation.
APPENDICES
Appendix A. Bird behavior indicative of nesting. (Martin and Geupel, 1993)

<table>
<thead>
<tr>
<th>Bird behavior observed</th>
<th>Observer Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bird seen with nest material (grass, spider web, hair, lichens)</td>
<td>Follow bird carefully from a distance while it is gathering and carrying nest material.</td>
</tr>
<tr>
<td>Copulation</td>
<td>Search immediate area where copulation was observed. Copulation often occurs in the same tree above a nest</td>
</tr>
<tr>
<td>Female staying in area without actively foraging</td>
<td>Watch the female to see if she looks repeatedly at a certain area. Often females repeatedly look at their nest when an observer/predator is detected.</td>
</tr>
<tr>
<td>Female foraging quickly, or making rapid hops, short flights, or rapid wing flicks</td>
<td>Keep an eye on the female, she may be returning to her nest soon</td>
</tr>
<tr>
<td>Female call notes</td>
<td>Be aware of short “chips”, “chucks” or other call notes.</td>
</tr>
<tr>
<td>Male is quiet</td>
<td>May indicate presence of foraging female or nest nearby</td>
</tr>
<tr>
<td>Male carrying food</td>
<td>Some males carry food to incubating females</td>
</tr>
<tr>
<td>Female disappears into tree or shrub</td>
<td>Lightly tap potential nest shrubs with a stick, listen or watch for female to flush.</td>
</tr>
<tr>
<td>Male or female carrying food</td>
<td>Follow bird from a distance to the nest.</td>
</tr>
<tr>
<td>Male or female carrying/dropping fecal sacs</td>
<td>Watch for bird to return to the nest site</td>
</tr>
<tr>
<td>Bird drops mouthful of food</td>
<td>You are much too close</td>
</tr>
<tr>
<td>Bird flushes from tree or shrub upon approach</td>
<td>Search immediate area and adjacent area. Birds often sneak quietly to adjacent tree/shrub before making a quick exit.</td>
</tr>
<tr>
<td>Bird is feigning injury</td>
<td>Nest is very close by. Do not follow bird, it will try to lead you away from the nest</td>
</tr>
<tr>
<td>Bird is agitated, scolding</td>
<td>You are close to the nest. Search immediate area.</td>
</tr>
<tr>
<td>Noisy babies</td>
<td>Especially good for detecting activity in cavities</td>
</tr>
</tbody>
</table>
Appendix B: Decay classes for snags

<table>
<thead>
<tr>
<th>Code</th>
<th>Bark</th>
<th>Heartwood Decay</th>
<th>Sapwood Decay</th>
<th>Limbs</th>
<th>Top Breakage</th>
<th>Bole Form</th>
<th>Time Since Death</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Tight, intact</td>
<td>Minor</td>
<td>None to incipient</td>
<td>Mostly Present</td>
<td>May be present</td>
<td>Intact</td>
<td>1-5 years</td>
</tr>
<tr>
<td>2</td>
<td>50% loose or missing</td>
<td>None to advanced</td>
<td>None to incipient</td>
<td>Small limbs missing</td>
<td>May be present</td>
<td>Intact</td>
<td>&gt;5 years</td>
</tr>
<tr>
<td>3</td>
<td>75% missing</td>
<td>Incipient to advanced</td>
<td>None to 25%</td>
<td>Few remain</td>
<td>Approx. 1/3</td>
<td>Mostly intact</td>
<td>&gt;5 years</td>
</tr>
<tr>
<td>4</td>
<td>75% missing</td>
<td>Incipient to advanced</td>
<td>25%+</td>
<td>Few remain</td>
<td>Approx. 1/3 to ½</td>
<td>Losing form, soft</td>
<td>&gt;5 years</td>
</tr>
<tr>
<td>5</td>
<td>75%+ missing</td>
<td>Advanced to crumbly</td>
<td>50%+ advanced</td>
<td>Absent</td>
<td>Approx. ½+</td>
<td>Form mostly lost</td>
<td>&gt;5 years</td>
</tr>
</tbody>
</table>


