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Drill, baby, drill: the influence of woodpeckers on post-fire vertebrate communities through cavity excavation

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Abstract

Several studies have addressed the importance of woodpeckers as ecological engineers in forests due to their excavation of cavities. Although research in green, unburned forests has identified the influence of different excavators on secondary use by cavity-dependent species, little is known about the relative importance of cavities created by woodpeckers in recently burned forests. By excavating cavities, woodpeckers create habitat for secondary cavity users that can facilitate post-fire regeneration through seed dispersal, seed germination and regulation of insect populations that affect vegetative growth. In this study, we monitored 77 cavities created by three species of *Picoides* woodpeckers for use by secondary cavity species in a fire that burned in the Sierra Nevada, California. At each cavity we measured nest tree and site-specific parameters to determine if these characteristics could explain differential use by secondary cavity users. We found substantial overlap in cavity characteristics between woodpecker species, with the white-headed woodpecker differing most notably in their placement of cavities in larger diameter, shorter and more decayed trees in less dense stands than either hairy or black-backed woodpeckers. These differences in cavity placement may have resulted in the high diversity and large number of detections of secondary cavity species in white-headed woodpecker cavities. Black-backed and hairy woodpeckers were similar in the number of detections of secondary cavity use, although black-backed woodpecker cavities were used by more species than hairy woodpecker cavities. Secondary cavity use was high (86%) suggesting these woodpeckers, and the white-headed woodpecker in particular, can have an accelerating affect effect on ecological succession by providing valuable habitat features for seed dispersing birds and mammals, insectivorous birds, and small predators, thereby impacting ecological processes and functions.

Introduction

Ecological succession describes changes in plant and wildlife community composition over time and is often illustrated by changes in habitat following disturbance (Clements, 1904; Connell & Slatyer, 1977). The path of ecological succession is unpredictable and may depend on the facilitative effects of ecosystem engineers. Ecosystem engineers have the ability to influence succession by altering or creating habitat (Lawton & Jones, 1995) and may facilitate colonization or re-colonization by other species after disturbance (Andersen & MacMahon, 1985; Nummi & Holopainen, 2014). Many species of woodpeckers may act as ecosystem engineers that affect successional dynamics following fire, the dominant source of disturbance in mixed conifer forests of western North America (Skinner & Chang, 1996). They may colonize burned areas immediately after fire by exploiting the abundance of food (bark and wood-boring beetles) and nest resources (snags), utilizing habitat unsuitable to many other bird and mammal species (Kotliar *et al*., 2002). As ecosystem engineers, woodpeckers excavate cavities that provide nesting, roosting, denning and resting sites for secondary cavity users (SCUs), species dependent on cavities, but unable to excavate them (Raphael & White, 1984). In many coniferous habitats cavities that are not created by woodpeckers are rare (Aitken & Martin, 2007) and competition for cavities has been shown to limit population growth of SCUs (Holt & Martin, 1997), creating a strong dependence of SCUs on woodpeckers (Martin & Eadie, 1999). In the Sierra Nevada alone, there are over 50 SCUs from several functional groups including seed and spore dispersers, insectivores and small carnivores (Raphael & White, 1978, 1984).

In green, unburned forests, Northern flickers *Colaptes auratus* are considered keystone excavators because their cavities are abundant and used by many species of SCUs (Martin & Eadie, 1999; Martin, Aitken & Wiebe, 2004; Robles & Martin, 2013, 2014); however, this species is relatively rare in burned forests in the first years after fire. This suggests that immediately after fire, woodpeckers that are early colonizers of burned habitat will provide the majority of cavities that support SCUs. Whereas abundance patterns and reproductive success of woodpeckers colonizing recent burns is well-documented (Saab, Dudley & Thompson, 2004; Nappi & Drapeau, 2009), little attention has been given to their contribution as ecosystem engineers for SCUs in burned forests, although they may be especially important after fire has consumed previously existing snags with cavities (Horton & Mannan, 1988; Bagne, Purcell & Rotenberry, 2008).

In coniferous forests of the western US, three members of the *Picoides* genus can be commonly found in burned habitat: the black-backed woodpecker *Picoides arcticus*, hairy woodpecker *Pic. villosus* and white-headed woodpecker *Pic. albolarvatus*. These three species rarely re-use cavities and are characterized by strong excavation abilities (Garrett, Raphael & Dixon, 1996; Dixon & Saab, 2000; Jackson, Ouellet & Jackson, 2002). Because these species are similar in size, their cavities have roughly the same dimensions, with nearly identical minimum diameter at entrance, depth and internal cavity diameter (Raphael & White, 1984). Although it is likely that these species differ in aspects of nest characteristics, there is a limited understanding of how they differ and the influence those differences may have on the structure and composition of SCUs utilizing post-fire habitat.

The objective of this study was to investigate cavity use by SCUs in recently burned coniferous forest. In the second and third year following fire we located cavities, recorded the excavating species and collected data on nest tree and site characteristics. Each cavity was monitored for subsequent use by SCUs in the following breeding season. We compared cavity characteristics between these species to determine if any observed differences were associated with different SCUs. In this way, we were able to estimate the influence or importance of each of these woodpecker species in providing habitat to SCUs.

Methods

Study area

We conducted our study on the south-west shore of Lake Tahoe (38.91°N, 120.04°W), *c.* 140 km east of Sacramento, California, where the human-caused Angora fire burned *c.* 1245 ha of coniferous forest in June and July 2007. The fire occurred in an area with a high degree of intermixed private and public land and adjacent to large expanses of undeveloped public land. Some public lands around the fire had been treated in the past to reduce fuels. Burn severity varied within the area, resulting in a mosaic of post-fire conditions. Pre-fire vegetation was predominately Jeffrey pine *Pinus jeffreyi* and white fir *Abies concolor* forest with red fir *A. magnifica* found at the highest elevations and incense cedar *Calocedrus decurrens*, sugar pine *Pin. lambertiana* and lodgepole pine *Pin. contorta* found at the lower elevations. For a more complete site description and characterization of the fire, see Safford, Schmidt & Carlson (2009).

Woodpecker nest searching

The US Forest Service established a systematic grid of points spaced 400-m apart across the fire area. From this grid, we selected a sample of survey points that were roughly balanced across burn severity classes. In order to increase our sample size and help balance the design, we selected a limited number of points on other public lands that had also burned in the fire. A total of 98 unique points were sampled over the 2-year period, with 41 of these sites sampled in both years. We categorized each point into one of four burn severity classes based on satellite-derived per cent tree mortality (0, 1–20, 20–70, >70%). The total area surveyed was *c.* 308 ha with 72% of the surveyed area within the fire perimeter and 18% in unburned forest surrounding the fire area.

Cavity searches were conducted between May and July in 2009 and 2010, 2 and 3 years after the fire burned. At each survey point, observers first thoroughly canvassed a 60-m radius (*c.* 1 ha) area for active cavity nests (Martin & Geupel, 1993) and cavity nesters (minimum of 15 min). Then observers moved out into the area between 60 and 100 m from the survey point (*c.* 2-ha area), and spent a minimum of 1 h searching this larger area. If a cavity or bird was observed, no maximum time was set to determine if the cavity was active or to locate the bird's nest. Nests that were encountered while moving to and from sites were also included in our sample. Survey points were searched a minimum of three times per season, with at least 1 week between visits.

Woodpecker nest tree and nest site characteristics

When an active nest was confirmed, the bird species, stage of nest development and location of the nest were recorded. After the nesting attempt ended we recorded tree species, diameter at breast height (DBH) and tree height, cavity height, per cent scorch of the bole and decay class (Cline, Berg & Wight, 1980). To quantify vegetation structure at the nest site, we established an 11.3-m radius plot (0.04-ha) surrounding the cavity tree (James & Shugart, 1970; Martin *et al.*, 1997). Although this area does not represent the home range for the woodpecker species, it does represent the scale of habitat that may influence use by SCUs. At each nest site, we collected data on the density of snags and live trees and the per cent cover of coarse woody debris (CWD), shrubs and herbs. Stems of trees and snags were categorized as medium (28–61 cm DBH) or large (>61 cm DBH) and densities were calculated for each size class as the number of stems per hectare. Smaller diameter trees and snags were rare within the fire and were not included in this measure. Because burn severity varied within each 0.04 ha plot, we weighted each burn severity value by the per cent area it represented. To determine if human infrastructures influenced use of nest sites, we used an impervious surfaces (houses, roads, buildings) data layer (Manley *et al.*, 2009) to calculate a per cent cover of urban constructs around each nest.

We used discriminant function analysis to identify the nest characteristics that best differentiated the species at both the nest tree and nest site scale. At the scale of the nest tree we included cavity height, tree height and DBH, decay class, and per cent of the bole that was scorched. At the nest site scale we analyzed medium- and large-snag densities, total tree density, per cent cover of CWD, per cent cover of shrubs, per cent cover of herbs, per cent cover of impervious surfaces and burn severity. Explanatory variables were standardized and transformed prior to analysis.

Secondary cavity use

Because our interests were in understanding how different species of woodpeckers may influence vertebrate assemblages following fire, we monitored woodpecker cavities for one breeding season following excavation to quantify use by SCUs. Remote-triggered digital cameras (Leaf River Outdoor Products, Taylorsville, MS, USA) were placed at cavities to monitor use for two, 7-day sessions in the breeding season of 2010 and 2011, allowing for detection of elusive, diurnal and nocturnal wildlife. All individuals detected in photographs were identified to species when possible. In addition, we used a Treetop Peeper (Sandpiper Technologies, Manteca, CA, USA) to observe the interior of cavities twice during each season to check for active nests or dens, nesting material and other evidence of use. Data on SCUs were used to create nest webs to compare the influence of each woodpecker species on the SCU community (Martin & Eadie, 1999).

To quantify and compare the biodiversity supported by each woodpecker species, we calculated an effective species number (ESN) based on the number of species of SCUs and the number of individual sightings of each species found in cavities excavated by each woodpecker (Jost, 2006). The ESN is derived from the Shannon Diversity Index (H); however, the ESN is measured in units of number of species and is linearly scaled such that communities with ESNs that differ by a factor of two represent an actual difference in diversity such that one community is twice as diverse as the other.

$$ENS = \exp\left(H = -1 \times \sum_{i=1}^{S} p_i \ln p_i\right)$$

where S is the total number of species and p is the proportion of species i relative to the total number of species (p_i).

The ENS represents the number of species in a community given that each species is equally abundant.

Results

Woodpecker nest tree and nest site characteristics

A total of 257 cavities were found during the two surveyed breeding seasons (110 in 2009, 147 in 2010). The majority of cavities found were attributed to the three target woodpecker species including 39 black-backed woodpecker nests (15 in 2009 and 24 in 2010), 80 hairy woodpecker nests (37 in 2009 and 43 in 2010) and 48 white-headed woodpecker nests (18 in 2009 and 30 in 2010). Nests were found in roughly equal proportions for each species in each stage; therefore, we assume that our sample is not biased toward successful nests or biased by species-specific detection probabilities related to parental behavior. Nests of the black-backed woodpecker occurred within the fire and were almost exclusively located in *Pinus* species. In contrast, white-headed woodpeckers (five nests) and hairy woodpeckers (two nests) built nests in unburned areas and utilized the different tree species in similar proportions. Mean values for nest tree and site characteristics for each species of woodpecker in the burned area are shown in Table 1, nests located in unburned areas were omitted from analysis. Other cavities excavated within the burned survey area included 10 Northern flicker, three pileated woodpecker *Dryocopus pileatus*, two Williamson's sapsucker *Sphyrapicus thyroideus*, two red-breasted nuthatch *Sitta canadensis* and 16 pygmy nuthatch *Si. pygmaea* nests, plus one cavity that was created by a broken branch and rot. We also located 41 woodpecker-excavated nests that were already occupied by SCUs. To ensure a robust sample size, we focused our monitoring efforts on cavities created by the *Picoides* species.

The variance in individual nest tree and site characteristics across the focal species overlapped substantially (Table 1). The results of the discriminant function analysis indicate that the mean values of the tree characteristics were more effective at differentiating nests of woodpecker species than the mean site characteristics (Table 2). At the tree scale we found that both canonical axes were significant (Table 2a), with the first axis explaining 75% of variation among species. The first axis represented a gradient of short, large diameter, decayed snags to tall, smaller diameter, hard snags. This first axis primarily separated the mean value of white-headed woodpecker nests from the mean values of hairy and black-backed woodpecker nests. On average, white-headed woodpeckers tended to utilize larger, shorter and more decayed snags than the other two species (Fig. 1). The second axis primarily represented cavity height (Table 2a), with increasing values along the axis. This axis primarily separated the black-backed woodpecker from the hairy and white-headed woodpeckers (Fig. 1). Black-backed woodpeckers excavated cavities lower on the bole than hairy woodpeckers and in higher trees than white-headed woodpeckers. However, despite the separation in canonical variate means, the probability of correctly assigning a cavity to a focal species based on nest tree characteristics was relatively low, with only the most extreme values having predictive power (Fig. 1).

Table 1 Summary of means and standard deviations of nest characteristics for three woodpecker species

	Black-backed woodpecker	Hairy woodpecker	White-headed woodpecker
Nest tree			
Pinus species (%)	82	55	45
Cavity height (m)	4.72 ± 3.01	7.23 ± 4.10	4.03 ± 2.35
DBH (cm)	34.48 ± 8.64	38.73 ± 8.69	50.62 ± 48.11
Tree height (m)	16.49 ± 6.24	16.58 ± 7.52	9.20 ± 7.41
Decay (1–5)	1.56 ± 1.02	1.49 ± 0.85	2.85 ± 1.33
Scorch on tree (%)	93 ± 15	93 ± 13	99 ± 4
Nest site			
Herb cover (%)	14 ± 13	13 ± 16	17 ± 20
Shrub cover (%)	25 ± 18	30 ± 26	26 ± 23
CWD cover (%)	2 ± 3	3 ± 2	2 ± 2
Trees (stems per hectare)	5.02 ± 16.7	3.34 ± 14.2	10.04 ± 24.84
Small snags (stems per hectare)	178.69 ± 95.08	139.96 ± 90.98	94.69 ± 75.66
Large snags (stems per hectare)	19.37 ± 20.61	23.64 ± 33.39	16.50 ± 24.55
Burn severity (%)	93 ± 9	93 ± 10	91 ± 10
Impervious cover (%)	7 ± 7	5 ± 7	9 ± 8

CWD, coarse woody debris; DBH, diameter at breast height.

Table 2 Tests of dimensionality and standardized discriminant coefficients for discriminant function analysis of nest characteristics of black-backed woodpecker, hairy woodpecker and white-headed woodpecker at two scales: (a) nest tree and (b) nest site

	Canonical dimensions	
(a) Nest tree		
Predictors	1	2
Tree height	0.495	−0.710
DBH	−0.339	0.144
Decay	−0.603	0.002
Cavity height	0.297	1.180
Scorch	−0.145	0.191
Canonical correlation	0.57	0.38
	$F_{10,302} = 9.64$	$F_{4,152} = 6.30$
	$P < 0.001$	$P < 0.001$
(b) Nest site		
Predictors	1	2
Herb cover	0.141	−0.001
Shrub cover	−0.057	−0.194
Coarse woody debris	−0.079	−0.386
Total tree density	0.099	0.258
Small snag density	0.978	0.413
Large snag density	0.031	−0.442
Burn severity	0.120	0.274
Impervious cover	−0.346	0.752
Canonical correlation	0.358	0.658
	$F_{16,296} = 1.89$	$F_{7,149} = 1.25$
	$P = 0.021$	$P = 0.279$

Standardized coefficients indicate the relationship of each variable to one standard deviation of change in the dimension.
DBH, diameter at breast height.

At the site scale, only the first canonical axis was statistically significant ($P = 0.02$; Table 2b; Fig. 2) and eigenvalues indicate that it explained 71% of the variation that existed among the species. The single most influential variable in classifying nests by species was density of medium-diameter snags, which increased along the axis. White-headed woodpecker nests were characterized by the lowest density of medium snags surrounding the nest, black-backed woodpeckers had the highest medium snag density and hairy woodpeckers nested in sites with intermediate densities of medium snags. Again, we found that the substantial degree of overlap in the use of site characteristics between species made it difficult to distinguish nests of one species from another.

Secondary cavity use

Despite the abundance of cavities found in the burned forest, a large proportion of nests were lost during the first winter following excavation as a result of snags falling or breaking at or below the cavity. Of the 158 nests monitored for secondary cavity use, 81 fell prior to the subsequent breeding season. Black-backed and hairy woodpecker nests had the greatest attrition, with losses of 54 and 65%, respectively. In contrast, only 24% of white-headed woodpecker nests fell 1 year after excavation. The remaining 77 woodpecker cavities were available for secondary cavity use observations the following breeding season: 18 black-backed (2010 = 8, 2011 = 10), 27 hairy (2010 = 13, 2011 = 14) and 32 white-headed (2010 = 11, 2011 = 21).

A total of 111 detections of secondary cavity use were observed across the 77 nests monitored with a high percentage (86%) of cavities receiving visits by one or more SCUs. The white-headed woodpecker had the highest proportion of their cavities visited (94%), followed by the black-backed woodpecker (89%) and the hairy woodpecker (73%). Cavities of all three species of woodpeckers were utilized by both birds and small mammals. Ten species of SCUs were detected: seven bird species, two small mammal species, plus chipmunks (representing multiple *Tamias* species; Fig. 3). White-headed woodpecker cavities had both the largest number of individual

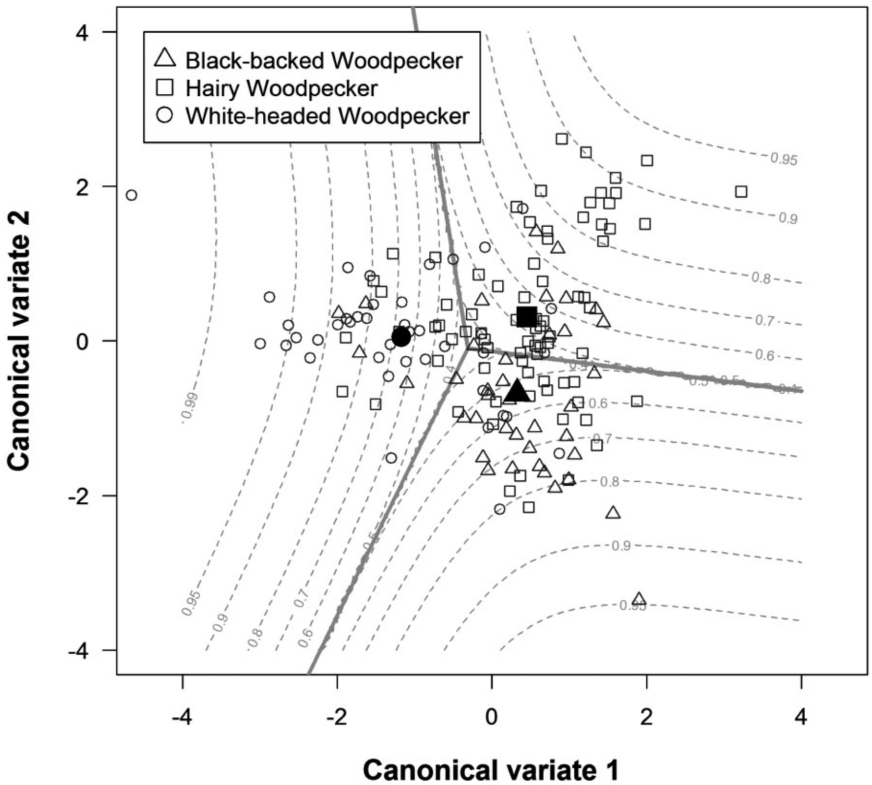

Figure 1 Canonical dimension scores of the three species of woodpecker at the tree scale. Small symbols are the individual sample points and the larger symbols (shown in the legend) represent the location of the canonical variate means. The gray lines show the separation of the predictions from the linear discriminant function. The associated prediction is the same as that of the species where the location of the canonical variate mean resides. The contour lines represent the posterior probability of assignment for each of the three species.

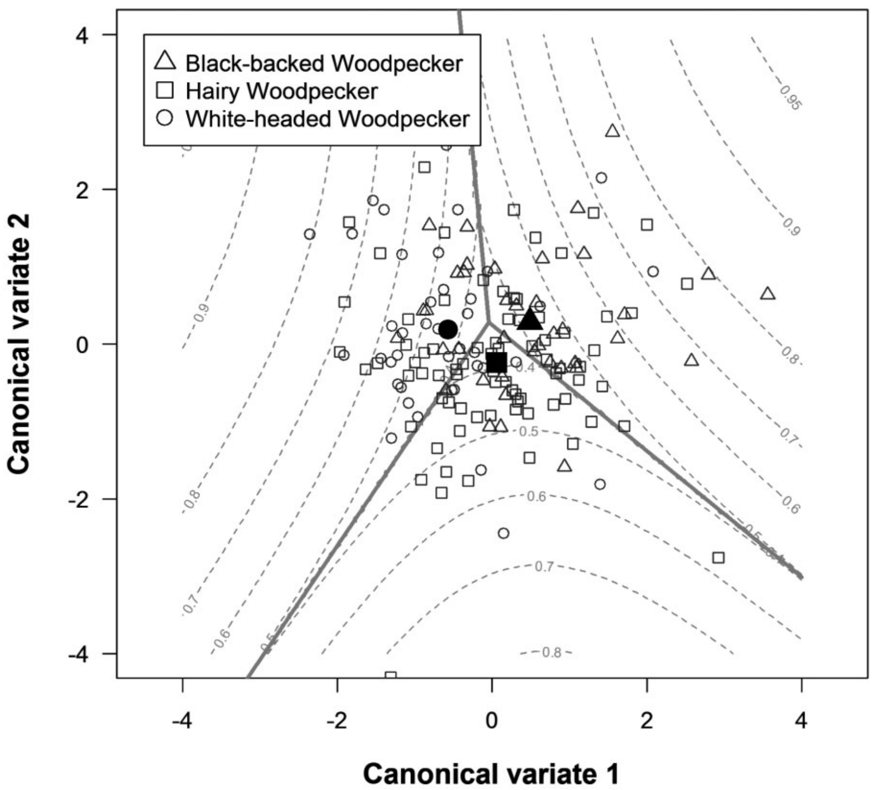

Figure 2 Canonical dimension scores of the three species of woodpecker at the site scale. Small symbols are the individual sample points and the larger symbols (shown in the legend) represent the location of the canonical variate means. The gray lines show the separation of the predictions from the linear discriminant function. The associated prediction is the same as that of the species where the location of the canonical variate mean resides. The contour lines represent the posterior probability of assignment for each of the three species.

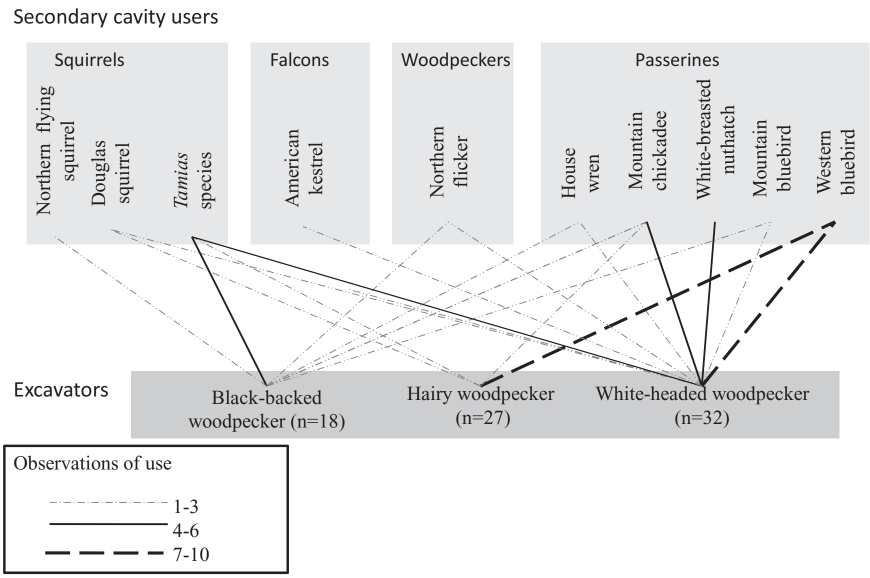

Figure 3 Nest web of cavity-dependent community after the Angora Fire. Lines indicate the number of observations of species using a particular resource. 'Use' occurred when an organism was observed in the cavity or observed entering the cavity.

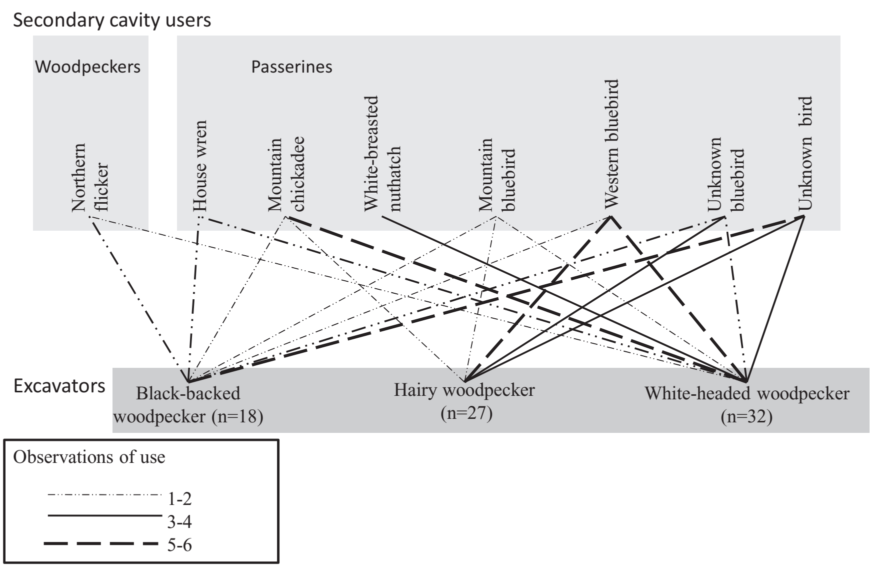

Figure 4 Nest web of breeding cavity nesting birds in the Angora Fire. Lines indicate the number of observations of species using a particular resource. 'Use' occurred when a bird was observed building a nest, incubating eggs or feeding nestlings or mate.

sightings and highest diversity of SCUs detected. White-headed woodpecker cavities were used by every species of SCU, with the exclusion of the Northern flying squirrel. Black-backed and hairy woodpeckers were similar in the number of detections in their cavities, although cavities excavated by the black-backed woodpecker were used by more species. Subsequently, the diversity index for white-headed woodpeckers had the highest value (ESN = 8 species), followed by the black-backed woodpecker (ESN = 6 species) and the hairy woodpecker (ESN = 4 species). This indicates that white-headed woodpeckers supported two more species than the black-backed woodpecker and a community that was twice as diverse as that supported by the hairy woodpecker. Of the 111 detections of SCUs, 52 were classified as breeding attempts by cavity nesting birds. We observed denning material in seven cavities used by small mammals, but could not confirm that these cavities were used specifically for breeding. White-headed woodpecker cavities were used by every breeding bird in the study and had the most total detections, followed by black-backed and hairy woodpeckers, respectively (Fig. 4).

Discussion

Many species of woodpeckers play an important role in forests by creating cavities that are used by other species that rely on them for aspects of their life history (Martin & Eadie, 1999). This ecosystem engineering by woodpeckers may be paramount post-fire when some species of woodpeckers can rapidly colonize burned forests that are less accessible to other animals (Kotliar *et al*., 2002). We found a high density of cavities in the first few years following fire indicating that several woodpecker species, and in particular the white-headed, hairy and black-backed woodpeckers, capitalized on this newly created habitat. Nearly all cavities that were monitored had detections of use, indicating that by excavating cavities, woodpeckers allowed SCUs to take advantage of the ephemeral resources provided by the fire. By facilitating movement into the burned area, woodpeckers may accelerate forest succession by providing habitat for seed and spore dispersing small mammals, insectivorous birds and small predators, thereby impacting ecological processes and functions (Otvos, 1979; Maser & Maser, 1988; Carey & Harrington, 2001). Although this study does not address whether these species would enter the burned area in the absence of cavities, engineering by woodpeckers undoubtedly facilitates the colonization or re-colonization of burned areas by SCUs.

Although all three species of woodpecker play a role in facilitating the presence of SCUs and could potentially impact forest succession, the objective of this study was to investigate whether different species of woodpeckers support unique communities of SCUs in burned forests. We found the amount of overlap in SCUs commensurate with the amount of overlap in the characteristics at the nest and site scales of these excavating species. However, there appeared to be some differences in the communities that the excavators supported. In particular, white-headed woodpecker cavities were utilized the most, supported the highest diversity of SCUs and were used in the highest proportion by nesting birds.

White-headed woodpeckers may provide cavities that are preferred by SCUs due to their nest tree or site characteristics. White-headed woodpecker cavities differed most notably from the other two woodpeckers in their placement in larger DBH, shorter and more decayed snags in less dense stands. In our study, white-headed woodpecker cavities, although they occurred in more decayed snags, were more likely to remain standing after excavation (at least 1 year more) because the cavities were low on the bole of large diameter snags. Cavities placed lower on the bole may be more persistent because the snag is unlikely to break at or below this height. In comparison, hairy woodpecker cavities, located highest on the bole in smaller diameter snags, fell the most frequently. Due to their relative persistence, white-headed woodpecker cavities were the most abundant in the fire area and may have been used more regularly by SCUs based on the formation of a search image.

Although not as readily used as white-headed woodpecker nests, black-backed woodpecker cavities supported a higher diversity than hairy woodpecker cavities. Black-backed woodpecker cavities were similar to white-headed woodpecker cavities in their low placement on the bole of the tree. Cavity height may affect the likelihood of predation and may therefore influence whether cavities are occupied by SCUs. Although in green forests, lower cavities are reportedly depredated more than higher cavities (Li & Martin, 1991; Fisher & Wiebe, 2006), this relationship has not been described in burned forests. Overall, predation in burned forests tends to be lower than in green forests (Saab & Vierling, 2001) and burned forests may be dominated by visual predators such as corvids (Jones *et al*., 2002) that may depredate higher nests that are visible to these aerial predators.

In green forests, Northern flickers are the most influential woodpecker, providing abundant cavities and supporting a diverse community of SCUs (Martin & Eadie, 1999; Martin *et al*., 2004; Robles & Martin, 2013, 2014). However, in the first two years of nest searching following the fire, we only located 10 Northern flicker nests within the burned area. This is likely to change over time as snags fall, shrubs and herbs dominate the live cover and arthropods and ants re-populate the area, providing forage for flickers. Northern flickers create larger holes and may provide habitat for larger SCUs, increasing the overall diversity in the burned area. However, Northern flickers often enlarge cavities created by other species rather than creating their own nest hole. Although the direct role of the *Picoides* woodpeckers may diminish as time since fire increases, their cavities may indirectly support the movement of Northern flickers and larger SCUs into the burned area.

Despite the common classification of black-backed woodpeckers as fire specialists and white-headed woodpeckers as green forest specialists, burn severity was not a factor that differentiated nest sites of the three species of woodpeckers. This discordance may be partially explained by the smaller habitat scale considered in this study, however, when investigating larger scale habitat features (7.04-ha scale) at our survey points we found a lack of variability in burn severity (Tarbill, 2010), suggesting that for a fire of this size with densely packed resources, smaller scales may be more important. The relatively small size and the elongated shape of the fire also resulted in highly burned areas near green edge habitat. We observed that the burned forests, even in the first few years after fire, supported a wide array of species not commonly considered burn specialists including chipmunks, Northern flying squirrels and mountain chickadees. Forest edge habitat has been associated with increases in avian species richness and abundance (Sisk & Battin, 2002). However, cavities in burned areas may be ecological sinks (Pulliam & Danielson, 1991) or traps (Dwernychuk & Boag, 1972) for SCUs. If cavities in the surrounding green forest are rare, SCUs may be forced to use cavities in burned areas or forego reproduction.

Although new snags are created by fire and new cavities are created by these early colonizing species of woodpeckers, cavities may continue to be limited due to the ephemeral nature of burned snags. Most fire-killed trees die within 2 years of fire, although delayed mortality occurs at least 10 years post-fire (Angers *et al*., 2011). Snags with cavities are structurally compromised and may be more susceptible to decay (Farris & Zack, 2005), leading to increased fall rates. We observed a loss of 51% of snags with excavated cavities in the second year following the fire, supporting the notion that cavities could be limited even in areas with high-snag densities. Communities of SCUs in burned forests will depend on continued presence of woodpeckers to replenish the supply of cavities. As time since fire increases, the rate of snag fall will quickly outpace the rate of tree death and the forest will slowly regenerate, producing areas rich in shrubs and small trees (Bock, Raphael & Bock, 1978). Snags will again become rare and the engineering of woodpeckers will continue to be important to SCUs.

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