Forest Ecology and Management 257 (2009) 151–159

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Nest-site selection by cavity-nesting birds in relation to postfire salvage logging

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ARTICLE INFO

Article history:
Received 16 May 2008
Received in revised form 20 August 2008
Accepted 21 August 2008

Keywords:
Colaptes auratus
Melanerpes lewis
Picoides spp.
Salvage logging
Sialia spp.
Wildfire
Woodpeckers

ABSTRACT

Large wildfire events in coniferous forests of the western United States are often followed by postfire timber harvest. The long-term impacts of postfire timber harvest on fire-associated cavity-nesting bird species are not well documented. We studied nest-site selection by cavity-nesting birds over a 10-year period (1994–2003), representing 1–11 years after fire, on two burns created by mixed severity wildfires in western Idaho, USA. One burn was partially salvaged logged (the Foothills burn), the other was primarily unlogged (the Star Gulch burn). We monitored 1367 nests of six species (Lewis's Woodpecker *Melanerpes lewis*, Hairy Woodpecker *Picoides villosus*, Black-backed Woodpecker *P. arcticus*, Northern Flicker *Colaptes auratus*, Western Bluebird *Sialia mexicana*, and Mountain Bluebird *S. currucoides*). Habitat data at nest and non-nest random locations were characterized at fine (field collected) and coarse (remotely sensed) spatial scales. Nest-site selection for most species was consistently associated with higher snag densities and larger snag diameters, whereas wildfire location (Foothills versus Star Gulch) was secondarily important. All woodpecker species used nest sites with larger diameter snags that were surrounded by higher densities of snags than at non-nest locations. Nests of Hairy Woodpecker and Mountain Bluebird were primarily associated with the unlogged wildfire, whereas nests of Lewis's Woodpecker and Western Bluebird were associated with the partially logged burn in the early years after fire. Nests of wood-probing species (Hairy and Black-backed Woodpeckers) were also located in larger forest patch areas than patches measured at non-nest locations. Our results confirm previous findings that maintaining clumps of large snags in postfire landscapes is necessary for maintaining breeding habitat of cavity-nesting birds. Additionally, appropriately managed salvage logging can create habitat for some species of cavity-nesting birds that prefer more open environments. Our findings can be used by land mangers to develop design criteria for postfire salvage logging that will reserve breeding habitat for cavity-nesting birds.

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1. Introduction

Despite considerable expenditures and infrastructure dedicated to fire suppression during the past century, the annual area burned by wildfire in North America has increased over the last decade (Stephens and Ruth, 2005). As a result, opportunities for postfire timber harvest (i.e. salvage logging) have increased in coniferous forests of the western United States (McIver and Starr, 2001; Nappi et al., 2003; Beschta et al., 2004; Lindenmayer and Noss, 2006). Postfire salvage logging alters the forest landscape by reducing snag densities, preferentially removing large trees, and opening the forest canopy. Forests recently (<5 years) burned by stand replacement wildfires provide habitat for a diverse community of breeding cavity-nesting birds (Bock and Lynch, 1970; Raphael and White, 1984; Hutto, 1995; Saab et al., 2005), and habitat alterations caused by timber harvest may significantly impact populations of these species (Haggard and Gaines, 2001; Hutto and Gallo, 2006; Saab et al., 2007).

Species such as cavity-nesting birds that rely on dead and downed trees for breeding, roosting, and foraging habitat (Murphy and Lehnhausen, 1998; Morissette et al., 2002; Hutto and Gallo, 2006; Koivula and Schmiegelow, 2007; Saab et al., 2007) are directly affected by the removal of large snags after fire. Reduced snag densities and smaller diameter snags in salvage logged areas result in snags that fall sooner after fire than snags in unlogged areas (Russell et al., 2006). Fallen snags are no longer available as nesting habitat for cavity-nesting birds. Timber harvest can influence nest-site selection and increase territory sizes of breeding birds by removal of foraging and nesting snags and creation of forest gaps (Schwab et al., 2006). A more open canopy

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0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2008.08.028

can benefit some species by providing more room for aerial insectivores to maneuver (Bock, 1970; Saab et al., 2004; Hannon and Drapeau, 2005).

Nest-site selection of fire-associated species is potentially influenced by many factors other than snag removal, including severity and extent of the wildfire as well as pre-fire conditions (Russell et al., 2007; Vierling et al., 2008). Trees killed or damaged by wildfire provide habitat for bark (Scolytidae) and wood-boring beetles (Cerambycidae and Buprestidae) (Werner, 2002), primary food sources for Black-backed and Hairy Woodpeckers. Nutrient releases after fire enhance plant growth and vigor (Agee, 1993), subsequently providing substrate for colonizing insects and bird species that forage on flying insects (Bock, 1970; Saab et al., 2004; Hannon and Drapeau, 2005). Fire severity can impact the time scale on which shrubs regrow, the number of beetles colonizing the wildfire (McHugh et al., 2003), and nest predator recolonization rates (Roppe and Hein, 1978; Fisher et al., 2005). Additionally, pre-fire forest conditions such as pre-fire crown closure and forest patch area can influence nest-site selection of fire-associated cavity-nesting bird species (Saab et al., 2002; Russell et al., 2007). Pre-fire crown closure may provide an index of postfire snag densities and burn severity, whereas forest patch size could influence the availability of continuous foraging habitat in postfire landscapes.

As time since fire increases, vegetation conditions change and the suitability of the habitat for particular species may change as well. As shrubs regrow and snags fall, woodpeckers that forage on bark beetles and wood borers, such as Hairy and Black-backed Woodpeckers, will be replaced in the community by aerial insectivores and secondary cavity-nesting birds (Bock et al., 1978; Apfelbaum and Haney, 1981; Hobson and Schieck, 1999; Hannon and Drapeau, 2005; Saab et al., 2007). Retaining postfire habitats in the short-term provides suitable nesting conditions for early successional species and in the longer-term provides habitat for species colonizing older burned forests, both of which are essential for preserving the diversity and functionality of burned forest ecosystems.

Our study evaluates nest-site selection of cavity-nesting birds for multiple years after wildfire and salvage logging in relation to habitat variables measured on several spatial scales. We predicted that wood-probing species (those that obtain their insect prey from bark and wood) would favor unlogged areas with high snag densities that provide greater foraging opportunities; whereas, aerial/ground insectivore species would favor partially logged areas with openings that allow for shrub development, associated arthropods, and aerial maneuvers to capture flying insects. We also predicted that high pre-fire crown closure, and more severely burned areas would be associated with wood-probers, and act as an index to postfire snag characteristics and beetle populations.

The scale at which habitat influences nest-site selection and bird distributions may vary, depending on the local suite of predators, distribution of food or competitors, and other factors (Martin and Roper, 1988; Martin, 1992; Saab, 1999; Warren et al., 2005). In burned ponderosa pine forests of western North America, unburned forest patches may represent source habitat for nest predators such as red squirrels that are relatively scarce in postfire habitat (Rusch and Reeder, 1978; Fisher et al., 2005). Therefore, we included variables on multiple spatial scales to evaluate the potential impacts of predation risk as well as forage availability on nest-site selection.

We predicted that wood-probing species would be highly associated with habitat characterized at larger (coarser) spatial scales because their foraging movements and territory sizes are generally larger (Moore, 1995; Dixon and Saab, 2000; Covert-Bratland et al., 2006) than aerial/ground insectivores (Power and Lombardo, 1996; Tobalske, 1997; Guinan et al., 2000); likewise, we predicted that aerial/ground insectivores would be more associated with habitat characterized at smaller (finer) spatial scales. Additionally, we predicted that areas surrounding nest locations at larger (coarse) spatial scales would contain small amounts of unburned forest (a potential predator source) and higher pre-fire canopy closure (more foraging habitat for wood probers). At the finer spatial scale, we also expected higher snag densities at nest locations than at non-nest locations. Higher snag densities presumably provide greater foraging opportunities for species consuming bark and wood-boring beetles, and potentially reduce predation risk for all cavity nesters because higher snag densities may require predators to search more area to locate nest trees (cf. Li and Martin, 1991).

We predicted that temporal effects would also influence nest-site selection, primarily for aerial/ground insectivores and Northern Flickers whose nesting densities continued to increase beyond 5 years postfire (Saab et al., 2007). Previous research documented that smaller diameter snags in lower density stands on salvage logged areas fell faster than snags in unlogged areas (Russell et al., 2006). Therefore, we expected aerial/ground insectivore species that initially select more open partially logged areas (i.e. salvage logged) for nesting to shift from salvage logged areas to unlogged areas as snags become less available in logged areas.

Lastly, the suitability of ponderosa pine snags as nest cavities may increase with time since fire. The relatively thick sapwood of ponderosa pine compared with other coniferous trees is preferred for nest excavation by woodpeckers (Bull et al., 1997). The thicker sapwood of fire-killed ponderosa pine decays more slowly, not until 3–4 years after fire, than the thinner sapwood of fire-killed Douglas-fir snags, which decays soon after fire (Kimmey, 1955; Bull et al., 1997). Therefore, we expected that ponderosa pine snags would increase in suitability as they decay and are more easily excavated beyond 4 years after fire.

2. Materials and methods

2.1. Study site

We conducted nest surveys on two wildfire locations in western Idaho (43°35′N, 115°42′W) over a 10-year period, during May–June in 1994–1999 and in 2002–2003, representing 1–11 years after fire. Elevation ranged from 1120 to 2300 m and the perimeters of the burns were separated by 10 km on average. The Foothills burn was created in 1992 by a mixed-severity fire and about 40% of snags over 23 cm diameter at breast height (dbh) were harvested after the fire (Saab et al., 2007). The 1994 Star Gulch fire was also of mixed severity. Two survey units (each 400 ha) in the Star Gulch burn were excluded from logging for our research purposes, while remaining areas of the wildfire were a mix of partially logged and unlogged management units. Pre-fire vegetation in both wildfire locations was similar and dominated by ponderosa pine *Pinus ponderosa* and Douglas-fir *Pseudotsuga menziesii*, with lesser amounts of quaking aspen *Populus tremuloides*, subalpine fir (*Abies lasiocarpa*), and buckbrush (*Ceanothus* spp.; Saab et al., 2004).

Prelogging snag densities, pre-fire crown closure, and burn severity of the two study locations were similar, suggesting that any differences detected between the two burns would likely be the result of salvage logging and not other factors (Saab et al., 2007). Prelogging densities of large snags ($\geq$23 cm dbh) averaged 73.4 ± 9.3 (SE) snags per ha in the salvage-logged Foothills burn. After salvage logging, large snag densities were reduced by nearly 40% to 45.0 ± 5.1 snags per ha. In the unlogged study areas of the Star Gulch burn, large snag densities (67.8 ± 11.5 snags per ha) 1 year after the fire were similar to those reported for the Foothills burn before logging (t_{58} = 0.4, P = 0.71).

We characterized cavity-nesting bird species as either wood probers or aerial/ground insectivores based on their foraging behavior. Wood probers in our study areas were Black-backed and Hairy Woodpeckers (Villard and Beninger, 1993; Dixon and Saab, 2000; Jackson et al., 2002). We also classified Northern Flicker *Colaptes auratus* as a wood prober, although this species feeds often on the ground and on a variety of foods and substrates other than wood (Moore, 1995). We characterized Lewis's Woodpecker (Tobalske, 1997), Western Bluebird *Sialia mexicana* (Guinan et al., 2000), and Mountain Bluebird *Sialia currucoides* (Power and Lombardo, 1996) as aerial/ground insectivores.

2.2. Selection of focal trees

We surveyed for occupied nest cavities during May–June using the same belt transects (0.2 km × 1.0 km, and covering the entire survey area; see Dudley and Saab, 2003) in an area that averaged 849 ha each year in the partially logged Foothills burn from 1994 to 2003, excluding 2000–2001. We surveyed an average of 832 ha each year in the unlogged area of the Star Gulch burn from 1995 to 2003, excluding 2000–2001. Additionally, we used a random number generator to create randomly selected coordinates for a total of 29 non-nest locations in the Star Gulch burn and 30 non-nest locations total in the Foothills burn to compare characteristics of nest locations to randomly selected unused (non-nest) locations. Random plots were remeasured each year and each plot represented a repeated measure in our analysis.

2.3. Nest plot and fine scale data

We collected fine scale or field data annually within an 11.3-m radius plot (0.04 ha) centered on each tree containing a nest and non-nest, random location. Measurements of snags within a plot included diameter, total number, and tree species (Table 1). At non-nest locations, a snag (in rare cases a live tree) was randomly selected from among all the snags in a plot to represent snag characteristics not selected for nesting. These individual nest and random snags are referred to collectively as focal trees. More than 90% of focal trees were dead (i.e. snags) and conifer species (ponderosa pine or Douglas-fir); therefore, for our modeling purposes, we included only two categories, ponderosa pine and Douglas-fir/Other. Douglas-fir comprised 82% of the snags in the Douglas-fir/other category. We recorded the number of snags >1.37 m in height, for snags ≥23 cm, and the number of shrub stems taller than 50 cm with a diameter ≤12 cm within 5 m of focal trees. Shrub stem densities were estimated with smaller plot sizes (5 m) than snags because they were abundant; larger plots (11.3 m) were necessary to estimate snag numbers because they were less common on the landscape (Bate et al., 1999). Snags of ≥23 cm diameters were of interest to us because these trees are preferred by cavity-nesting birds and represent marketable timber (Saab et al., 2002).

2.4. Coarse scale data

We derived vegetation classification and burn severity for coarse scale data from two 30 m × 30 m (pixel) resolution Landsat Thematic Mapper (TM) images, representing pre- and postfire conditions. The pre-fire image was taken in September 1991, and the postfire image in September 1995. Aerial photographs (1:16,000) from July 1988 and August 1996 were used to assist in the classification process (Johnson et al., 2000; Saab et al., 2002).

Four pre-fire vegetation types mapped from the September 1991 image were used in our calculations of patch area: (1) ponderosa pine; (2) mixed conifer, predominantly Douglas-fir with some subalpine-fir and ponderosa pine; (3) other, consisting of mesic areas composed of riparian habitat and mountain shrub communities; and (4) xeric areas, composed of dry shrub communities. Pre-fire crown closure was mapped from the same imagery. An assessment found that overall accuracy for the pre-fire forest crown closure map was 78%, and for vegetation type was 79% (Johnson et al., 2000). Pre-fire crown closure categories included: (1) low (<40%), (2) moderate (≥40–70%), and (3) high (>70%). The Foothills site consisted of 56% low, 32% moderate, and 12% high pre-fire crown closure, whereas the Star Gulch site was composed of 46% low, 41% moderate, and 13% high pre-fire crown closure. Composition of pre-fire crown closures at the two locations was not statistically different ($\chi^2_2 = 4.3$, P = 0.11) (Saab et al., 2007).

Burn severity was quantified by calculating the change in normalized burn ratio (ΔNBR) between pre- and postfire conditions (Key and Benson, 2006). To calculate landscape level metrics, ΔNBR was classified as unburned or burned (Table 1; Key and

Table 1
Candidate models of nest-site selection for three wood-probing species (Hairy and Black-backed Woodpecker and Northern Flicker) and three aerial/ground insectivores (Lewis's Woodpecker, and Mountain and Western Bluebird) in burned ponderosa pine forests of Idaho

Model type	Covariates
A priori	
Wood probers	
Nest plot	Nest snag dbh, tree species, snag densities, pre-fire pixel vegetation type
Fine-scale	Nest snag dbh, snag densities
Coarse-scale	% unburned (1-km radius), patch area, pre-fire pixel crown closure
Multi-spatial scale	Nest snag dbh, snag densities, patch area, % pre-fire crown closure (1-km radius)
Aerial/ground insectivores	
Nest plot	Nest snag dbh, tree species, snag densities, pre-fire pixel vegetation type
Fine-scale	Nest snag dbh, snag densities, shrub densities
Coarse-scale	% unburned (1-km radius), patch area, pre-fire pixel crown closure.
Multi-spatial scale	Shrub densities, patch area, % pre-fire crown closure (1-km radius)
Exploratory	
All species	
Temporal effects of salvage logging	Fire location, postfire period, interaction term
Temporal changes in nesting tree suitability	Postfire period, tree species, interaction term

All *a priori* models were run with and without fire location for a total of eight candidate models for each species. Habitat features varied by spatial scale: shrub stem densities were measured within a 5-m radius plot; snag densities were measured within an 11.3-m radius plot for snags ≥23 cm diameter at breast height (dbh); and pixel-level measurements were derived remotely from 30 m × 30 m pixel size (see Section 2 for details).

Benson, 2006) (unburned [−500 to 99], low severity burn [100 to 269], moderate to high severity burn [270 to 1300]). The Foothills fire was comprised of 17% unburned, 51% low, and 32% moderate–high burn severity; the Star Gulch fire consisted of 14% unburned, 47% low, and 39% moderate–high burn severity (Saab et al., 2007). Composition of burn severities at the two burned locations was not statistically different ($\chi^2_2 = 1.9$, $P = 0.38$). However, pixel-level ΔNBR was confounded with fire location. Pixel-level ΔNBR was higher in the Foothills fire than in the Star Gulch fire (Appendix 1), therefore we dropped this variable from our analysis.

We calculated forest patch area by summing the total contiguous area of pixels with the same vegetation type that contained the focal tree (Patch area; Table 1). We used neighborhood statistics in the Spatial Analyst extension of ArcMap software (Environmental Systems Research Institute, Version 8.3, 1999–2002) to calculate the percentage of pixels within a 1-km radius of the focal tree categorized as each of three pre-fire crown closures and three burn severity categories. We chose the 1-km radius because this area (314 ha) incorporates the home range sizes and foraging movements of the species studied (Moore, 1995; Tobalske, 1997; Dixon and Saab, 2000; Covert-Bratland et al., 2006). We classified each nest as being located within the Foothills or Star Gulch burn.

2.5. Statistical analysis

We used a generalized linear repeated measures model with a binomial distribution of the response variable and a logit link (PROC GENMOD, SAS Version 9.1, 2002–2003) to identify habitat descriptors that best distinguished between nest and non-nest locations for excavators, i.e. Lewis's Woodpecker, Hairy Woodpecker, Black-backed Woodpecker, and Northern Flicker. Parameter estimates and 95% confidence intervals were derived from the repeated measures analysis. Confidence intervals that did not overlap with 0 were considered statistically significant. Random plots were remeasured each year and therefore each plot represented a repeated measure. Some species of cavity-nesting birds will reuse a nest cavity from 1 year to the next (Martin and Eadie, 1999; Saab et al., 2004) therefore, for nest locations, the nest tree was considered the repeated measure (Table 2). A nest tree was considered available and not used for 1 year prior to the first nesting attempt and 1 year after the last nesting attempt. For non-excavators, i.e. Mountain and Western Bluebirds, a nest tree was defined as available when a cavity was excavated by a woodpecker until 1 year after the last nesting attempt.

For each bird species, we generated an *a priori* list of candidate models (Table 1), which reflected habitat characteristics that we predicted were most likely to influence species-specific nest-site selection. We framed our *a priori* models in terms of characteristics of the nest plot and nesting tree, fine-scale variables within the nest plot, coarse-scale variables surrounding the nest plot, and multiple spatial scales about the nest plot that included both fine- and coarse-scale covariates (Table 1). Each model was run with and without fire location for a total of eight models for each species. Models were evaluated using Akaike's Information Criteria adjusted for small sample sizes (AIC_c; Hurvich and Tsai, 1989). To determine the strength of support for each model, we calculated ΔAIC_c (the difference in AIC_c between each candidate model and the model with the lowest AIC_c), and AIC_c weights (Anderson et al., 2001). In general, ΔAIC_c between 0 and 2 indicates substantial support for a model being the best approximating model given the data (Burnham and Anderson, 2002). We calculated profile likelihood confidence limits for parameter estimates of best models. We also included exploratory models with a temporal component [postfire period (early 1–4 years), late (>5 years)], where we added the time covariates to the variables included in the best *a priori* model as selected by AIC_c. The time component corresponds to temporal changes in populations of the cavity-nesting bird community (Saab et al., 2007), and to changes in falling rates of snags (Russell et al., 2006).

3. Results

3.1. Numbers of nests found

We used data from 1367 nest attempts to model nest-site selection by six species of cavity-nesting birds in burned forests over a 10-year period, 1994–2003. Lewis's Woodpecker was the most abundant species, comprising 34% of all nesting attempts, whereas Black-backed Woodpecker was rare, constituting only 3% of nesting attempts (Appendixes 2 and 3). Forty-eight percent of nests were located in the Foothills burn, whereas 52% were in the Star Gulch burn. Of the 1367 nesting attempts, 766 were monitored during the early postfire period (1–4 years after fire) and 601 nests were monitored during the late postfire period (5–11 years after fire). Fifty-nine non-nest

Table 2
Numbers of unique nest cavities used, cavities used multiple times by the same species, and total number of nests found in burned dry coniferous forests of Idaho

Species	No. unique nest cavities	No. cavities used multiple times by same species	No. total nests
Lewis's Woodpecker	353	108	461
Hairy Woodpecker	209	3	212
Black-backed Woodpecker	46	0	46
Northern Flicker	201	9	210
Western Bluebird	156	51	207
Mountain Bluebird	191	40	231

	Non-excavators	
	No. of used cavities	
Original excavator of cavities	Western Bluebird	Mountain Bluebird
Lewis's Woodpecker	0	2
Hairy Woodpecker	42	46
Black-backed Woodpecker	9	6
Natural	2	25
Northern Flicker	7	12
White-headed Woodpecker	3	3
Unknown	144	137

The original excavator is identified for nest cavities used by non-excavator species.

random locations were measured annually during the same years (Appendix 1).

Lewis's Woodpeckers had the highest rates of cavity reuse. Roughly 30% of monitored Lewis's Woodpecker nests were in cavities that had been previously used by this species (Table 2). Twenty-four percent of Western Bluebird nests, and 17% of Mountain Bluebird nests were found in cavities where nests of the same species had been found previously. Of the 157 bluebird nests where the original excavator was known, 56% were excavated by Hairy Woodpeckers. Northern Flickers and Lewis's Woodpeckers were more abundant and created larger cavity entrances than Hairy Woodpeckers; however, documented use of their cavities by non-excavators was lower (Table 2; Saab et al., 2004).

3.2. A priori models

The model representing multiple spatial scales was the best model for all three wood-probing species (Table 3), providing evidence for our prediction that this group would be strongly influenced by coarse-scale habitat characteristics. Hairy, Black-backed, and Northern Flickers were positively associated with increasing patch area and increasing tree dbh (Fig. 1, Table 4 for parameter estimates). Hairy and Black-backed Woodpeckers were positively associated with snag densities (Fig. 2) and increasing area of moderate (≥40–70%) or high (>70%) pre-fire crown closure in a 1-km area surrounding the nest. An important effect of fire location (logged or unlogged) was identified for Hairy Woodpeckers only. As previously documented, this species nested in higher densities in the unlogged fire (see Saab et al., 2007).

Nest plot characteristics comprised the best *a priori* models of nest-site selection for all three aerial/ground insectivore species (Table 3), supporting our prediction that this group would be most influenced by finer-scale habitat characteristics. Lewis's Woodpeckers were positively associated with larger diameter and higher densities of snags, and in patches characterized by ponderosa pine vegetation type. In contrast, evidence existed for a negative association with snag diameter for Western Bluebird (Table 4). This species used nest cavities in the smaller range of snag diameters that were previously excavated by woodpeckers (Fig. 1). Only Mountain Bluebirds appeared to prefer nesting in Douglas-fir snags over ponderosa pine. Mountain Bluebirds favored unlogged areas, whereas Lewis's Woodpecker and Western Bluebird were associated with the partially logged Foothills Fire (Table 4).

All six species used nest sites with snag densities and diameters that were higher than the average snag densities and diameters measured in the logged Foothills burn (Figs. 1 and 2). For nesting, both bluebird species used snags with smaller diameters than the average available snags with a woodpecker cavity (Fig. 1). Mountain Bluebirds used available cavities surrounded by higher than average snag densities for nesting (Fig. 2). This pattern of use reflects the bluebirds' propensity for using snags that were excavated by Hairy Woodpeckers, who use relatively small diameter snags among woodpeckers in our study areas (Fig. 1).

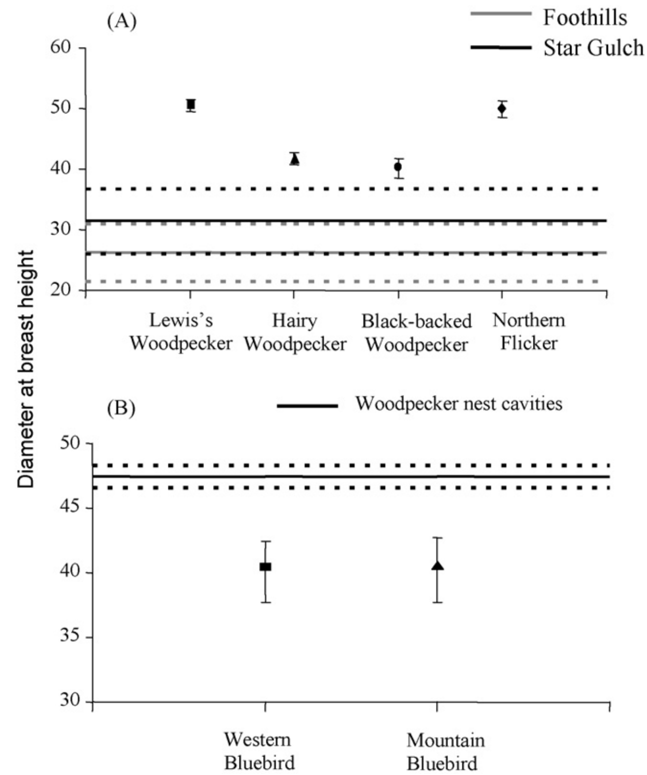

Fig. 1. Mean and standard errors for diameter at breast height of (A) nest snags (points with error bars) selected by four excavating woodpecker species, and non-nest random snags (solid line = mean, and dashed line = standard error) at two wildfire locations (Foothills Burn – partially logged; Stargulch Burn – unlogged); and (B) for nest snags of two non-excavating, bluebird species (points with error bars) and for woodpeckers as a group (solid line = mean, and dashed line = standard error) in western Idaho from 1994 to 2003.

Table 3
Model selection results for *a priori* models of nest occurrence for six cavity-nesting bird species in burned dry coniferous forests of Idaho

Model				
Wood probers	AIC_c	k	ΔAIC_c	AIC_c wt
Hairy Woodpecker (n = 209)				
Multi-scale model with fire location	1067.81	7	0.00	0.48
Multi-scale model	1068.98	6	1.17	0.27
Null	1094.47	1	26.657	0.00
Black-backed Woodpecker (n = 46)				
Multi-scale model	267.60	7	0.00	0.74
Null	296.51	1	29.77	0.00
Northern Flicker (n = 201)				
Multi-scale model	1075.54	6	0.00	0.36
Multi-scale model with fire location	1075.91	7	0.37	0.30
Fine scale model	1077.23	3	1.69	0.15
Null	1106.75	1	31.21	0.00
Aerial-ground insectivores				
Lewis's Woodpecker (n = 353)				
Nest plot model with fire location	1964.81	6	0.00	0.67
Null	2003.56	1	38.75	0.00
Western Bluebird (n = 156)				
Nest plot model	1325.59	4	0.00	0.60
Nest plot model with fire location	1326.98	6	1.39	0.30
Null	1358.05	1	32.46	0.00
Mountain Bluebird (n = 191)				
Nest plot model with fire location	1218.23	6	0.00	1.00
Null	1404.14	1	185.91	0.00

Models are ranked from most ($\Delta AIC_c = 0$) to least plausible; k is the number of parameters. Models within 2 ΔAIC_c units of the most plausible model and the null model (model of constant occupancy rate) are listed for each species. Covariates for each model are listed in Table 1. n = number of unique nest cavities; dbh = diameter at breast height.

3.3. Exploratory models

We found no evidence of a time effect on nest-site selection by wood-probing species. Exploratory modeling for aerial/ground insectivores revealed a significant interaction between postfire period and fire location for Western Bluebirds and Lewis's Woodpeckers (Table 5). Both species favored the logged area

Table 4
Parameter estimates and confidence intervals (CI) from best models of nest-site selection for three wood-probing species and three aerial/ground insectivore species in burned dry coniferous forests of Idaho

	Wood probers					
	Hairy Woodpecker		Black-backed Woodpecker		Northern Flicker	
	Estimate	CI	Estimate	CI	Estimate	CI
Intercept	−2.666	(−3.101, −2.230)	−6.867	(−8.973, −5.101)	−2.924	(−3.585, −2.292)
Fire location (FH)	−**0.424**	(−**0.802**, −**0.045**)				
Patch area	0.001	(0.000, 0.002)	0.059	(0.000, 0.005)	0.001	(0.000, 0.002)
CC (1-km radius)						
% (>40–70%)	0.003	(−0.012, 0.018)	**0.008**	(**0.020**, **0.101**)	0.006	(−0.10, 0.023)
% (>70%)	**0.022**	(**0.004**, **0.041**)	0.002	(−0.048, 0.063)	0.009	(−0.015, 0.033)
Nest snag dbh	**0.014**	(**0.008**, **0.020**)	**0.029**	(**0.010**, **0.049**)	**0.019**	(**0.012**, **0.026**)
Snag density	**0.030**	(**0.008**, **0.052**)	**0.055**	(**0.025**, **0.086**)	0.019	(−0.002, 0.038)

	Aerial-ground insectivores					
	Lewis's Woodpecker		Western Bluebird		Mountain Bluebird	
	Estimate	CI	Estimate	CI	Estimate	CI
Intercept	−2.343	(−2.743, −1.955)	−1.371	(−1.859, −0.753)	−1.030	(−1.557, −0.502)
Fire location (FH)	**0.452**	(**0.172**, **0.736**)			−**1.465**	(−**1.867**, −**1.092**)
Nest snag dbh	**0.015**	(**0.003**, **0.027**)	−**0.030**	(−**0.42**, −**0.019**)	−0.007	(−0.017, 0.002)
Tree species (P. pine)	0.090	(−0.181, 0.364)	0.326	(−0.019, 0.675)	−**1.400**	(−**1.801**, −**1.017**)
Snag density	**0.013**	(**0.008**, **0.018**)	0.012	(−0.010, 0.032)	0.018	(−0.003, 0.039)
Pre-fire pixel vegetation type (P. pine)	**0.333**	(**0.050**, **0.615**)	0.260	(−0.061, 0.578)	−0.343	(−0.736, 0.036)

Parameter estimates in bold are considered statistically significant (i.e. confidence intervals do not overlap with 0). FH = Foothills fire location; CC = crown closure; P. pine = ponderosa pine; dbh = diameter at breast height.

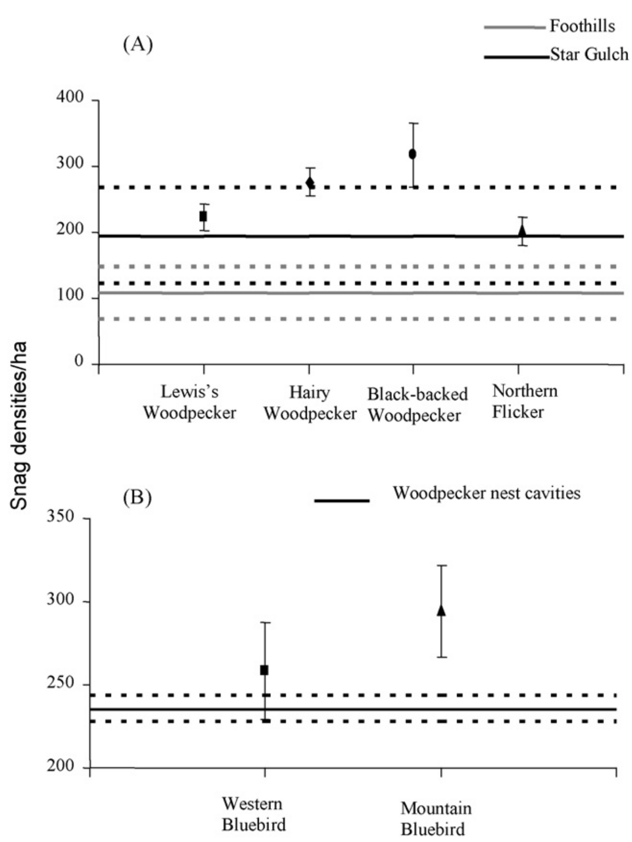

Fig. 2. Mean and standard errors of snag densities (for snags ≥23 cm diameter at breast height) (A) surrounding nest snags (points with error bars) selected by four excavating woodpecker species, and non-nest random snags (solid line = mean, and dashed line = standard error) at two wildfire locations (Foothills Burn – partially logged; Stargulch Burn – unlogged); and (B) surrounding nest snags of two non-excavating, bluebird species (points with error bars) and surrounding woodpecker nest sites as a group (solid line = mean, and dashed line = standard error) in western Idaho from 1994 to 2003.

(Foothills Fire) for nesting and their nesting numbers increased during the late postfire period. However, the strong selection for nesting in the logged area declined in the late postfire period (i.e. the interaction term was negative) (Table 6). Additionally, models of Mountain Bluebird nest-site use were improved by the addition of temporal factors relating to the selection of tree species (Tables 5 and 6). Mountain Bluebirds use of Douglas-fir snags increased in the late postfire period.

4. Discussion

Nest-site selection of cavity-nesting birds in postfire landscapes largely reflects snag distributions and individual snag characteristics. The preference of nest sites with high densities of snags and large diameter trees has been documented in several studies of cavity-nesting birds in both unburned and burned forests (Mannan et al., 1980; Raphael and White, 1984; Li and Martin, 1991; Bull et al., 1997; Vierling et al., 2008). Even within logged areas, these species used nest sites that were surrounded by areas which contained more snags than were available on average. High snag densities likely provide greater foraging opportunities for wood-probing species and potentially reduce risks of nest predation for all cavity-nesting species. Wood-probers such as Black-backed and Hairy Woodpeckers, may rely on large-scale unlogged areas such as the Star Gulch study area as primary nesting and foraging habitat within postfire landscapes (Haggard and Gaines, 2001; Saab et al., 2007). We did not detect a significant effect of fire location on Black-backed Woodpecker but we found few individuals nesting in the partially logged Foothills burn, and this species rarely inhabits logged areas (Hutto, 1995; Dixon and Saab, 2000; Haggard and Gaines, 2001; Koivula and Schmiegelow, 2007; Saab et al., 2007).

We predicted that all three aerial/ground insectivore species would favor the more open overstory, partially logged Foothills burn because of expected increases in shrub development, associated arthropods, and openings for aerial maneuvers to capture flying insects. The partial-salvage logging in the Foothills

Table 5
Best exploratory models of nest-site selection for three aerial/ground insectivore species in burned forests of Idaho

Model	AIC_c	k	AIC_c wt
Lewis' Woodpeckers (n = 353)			
Fire location, nest snag dbh, tree species, snag density, postfire period, pre-fire pixel vegetation type, postfire period × fire location	1946.71	8	1.00
Western Bluebird (n = 156)			
Fire location, nest snag dbh, tree species, snag density, postfire period, pre-fire pixel vegetation type, postfire period × fire location	1290.69	8	1.00
Mountain Bluebird (n = 191)			
Fire location, nest snag dbh, tree species, snag density, postfire period, pre-fire pixel vegetation type, postfire period × tree species	1215.96	8	0.75

dbh = diameter at breast height.

Table 6
Parameter estimates from best exploratory models of nest-site selection by three aerial/ground insectivores in burned dry coniferous forests of Idaho

	aerial/ground insectivores (exploratory models)					
	Lewis's Woodpecker		Western Bluebird		Mountain Bluebird	
	Estimate	CI	Estimate	CI	Estimate	CI
Intercept	−2.609	(−2.936, −2.282)	−1.577	(−2.333, −0.821)	−1.119	(−1.796, −0.442)
Fire location (FH)	**1.103**	(**0.815**, **1.391**)	**1.062**	(**0.609**, **1.515**)	−**1.554**	(−**2.085**, −**1.024**)
Pixel Vegetation type (P. pine)	**0.327**	(**0.124**, **0.529**)	0.217	(−0.166, 0.660)	−0.336	(−0.777, 0.105)
Nest snag dbh	**0.013**	(**0.009**, **0.0164**)	−**0.030**	(−**0.045**, −**0.015**)	−0.007	(−0.018, 0.0005)
Snag density	**0.014**	(**0.002**, **0.025**)	0.011	(−0.014, 0.037)	0.018	(−0.009, 0.045)
Tree species (P. pine)	0.056	(−0.131, 0.244)	0.186	(−0.201, 0.572)	−**0.997**	(−**1.520**, −**0.473**)
Postfire period (Late)	**0.515**	(**0.286**, **0.744**)	**0.6849**	(**0.200**, **1.170**)	0.304	(−0.188, 0.796)
Postfire period × fire location	−**1.074**	(−**1.374**, −**0.774**)	−**1.8935**	(−**2.60**, −**1.185**)		
Postfire period × tree species					−**0.936**	(−**1.700**, −**0.174**)

FH = Foothills fire; P. pine = ponderosa pine; dbh = diameter at breast height.

fire provided nesting habitat in varying degrees for all six cavity-nesting species that we observed; however, only Lewis's Woodpecker and Western Bluebird demonstrated a preference for the logged area. This preference declined over time potentially due to increased falling rates of snags in the salvage logged area (Russell et al., 2006; Saab et al., 2007). The third aerial insectivore, Mountain Bluebird, displayed a preference for the unlogged Star Gulch burn, where shrub stem densities were higher (Appendix 1). Preferences of Lewis's Woodpeckers and Western Bluebirds for forests with relatively open overstories and their presence in partially logged forests has been previously documented (Zarnowitz and Manuwal, 1985; Szaro and Balda, 1986; Tobalske, 1997; Saab and Vierling, 2001; Gentry and Vierling, 2007). In burned coniferous forests of central Washington, Mountain Bluebird numbers were greatest in stands of moderate snag densities, whereas Lewis's Woodpecker and Western Bluebird were most abundant in salvage-logged stands (Haggard and Gaines, 2001).

The non-excavators, particularly Western Bluebird, nested in the smaller diameter range of snags that were previously excavated by woodpeckers. Perhaps non-excavators prefer smaller cavities created by *Picoides* spp. for greater protection from predators. Competition for nest cavities may also influence their use of smaller diameter snags. Although Lewis's Woodpecker is the most abundant nesting species in our study areas and could provide cavities for non-excavators, their aggressive nature may prevent other species from using their cavities that are typically in larger diameter snags (Saab et al., 2004).

As we predicted, larger-scale variables, specifically patch area and pre-fire crown closure, were associated with Black-backed and Hairy Woodpecker nests, likely due to their large territories needed for foraging on bark and wood-boring beetles. Northern Flicker also preferred to nest in large patches of pre-fire conifer cover, emphasizing the importance of contiguous forest patches for this species. There was no evidence that pixel-level pre-fire crown closure was significantly related to nest sites of these species, suggesting that pre-fire crown closure may not be an appropriate surrogate for snag densities on that scale (30 m × 30 m). Contrary to our expectations and the findings of Vierling et al. (2008), we had no evidence that the amount of unburned habitat surrounding nest sites was negatively related to nest-site selection. Burn severity may have affected habitat use (Koivula and Schmiegelow, 2007; Russell et al., 2007; Vierling et al., 2008) but we were unable to model the effects of severity because it was confounded with fire location (see Appendix 1). However, we did model the effects of pre-fire crown closure, vegetation type, and on-the-ground vegetation characteristics, all of which can strongly influence burn severity (Baker and Ehle, 2001; Lentile et al., 2006). Increasing burn severity can further weaken and increase decay in trees, creating more snags for nesting and attracting greater numbers of bark and wood-boring beetles for foraging.

We demonstrated an important effect of time since fire for all three aerial/ground insectivores, suggesting that examination of fire effects for multiple years after fire may be necessary to detect meaningful biological responses (Smucker et al., 2005). Our results indicated that Lewis's Woodpecker and Western Bluebird shifted nest-site preferences from logged to unlogged areas as time since fire increased. Concurrently, we detected an increase in the preference of Douglas-fir snags by Mountain Bluebird as time since fire increased. Most cavity-nesting species, including the majority in our study area, favor large ponderosa pine trees for nesting (Bull et al., 1997). Congeneric competition for nest cavities between Western and Mountain Bluebirds may have played a role in the Mountain Bluebirds' stronger preference for Douglas-fir during the late postfire period, when Western Bluebirds became more numerous in the unlogged burn.

Importantly, the salvage logging on our study sites was not designed to create clearcuts but to retain about half the snags over 23 cm dbh, which provided suitable nesting and foraging habitat for aerial/ground insectivores during the decade following fire. Inferences about salvage logging from our study are limited because the treatments were not replicated. However, the two burns were similar in pre-fire plant species composition, pre-fire crown closure, pre-logging snag densities, and burn severity (Saab et al., 2007). This suggests that differences detected between the two burns were likely the result of salvage logging and not other factors, such as location. By combining information from this study along with information from other wildfires in dry coniferous forests, we may be able to develop predictive models of postfire habitats for cavity-nesting birds (Russell et al., 2007).

4.1. Management implications

Conditions providing nesting habitat for both wood probers and aerial/ground insectivores ranged from unlogged areas of high snag densities (mean of 275–316 snags [$\geq$23 cm dbh] per ha) for Hairy and Black-backed Woodpeckers, respectively, to partially logged areas with moderate snag densities (mean of 204–223 snags $\geq$23 cm dbh] per ha) for Northern Flicker and Lewis's Woodpecker, respectively (Appendix 2). Consequently, postfire management practices in drier mixed conifer forests that promote retention of clumps of large standing dead trees ($\geq$23 cm dbh) (particularly ponderosa pine), large contiguous patches of conifer, and areas with high pre-fire crown closure will likely be most successful at maintaining populations of cavity-nesting birds.

Wildfire events are unpredictable, and land managers are required to make postfire management decisions as quickly and efficiently as possible. Due to the importance of small-scale variables to nest-site selection by these species, establishing a predictive relationship between remotely-sensed data (pre-fire crown closure and vegetation type) and field-measured data (snag densities and diameters) would be useful (cf. Russell et al., 2007). Gradient-nearest neighbor modeling appears promising for evaluating on the ground snag characteristics without expensive field data collection (Ohmann et al., 2002). Further development of predictive modeling tools for wildlife habitat in postfire landscapes could provide valuable guidance for land managers designing salvage logging projects.

Acknowledgments

U.S. Department Agriculture, Forest Service, Rocky Mountain Research Station was the primary source of funding with additional help from other units of the Forest Service, including the Intermountain Region, Pacific Northwest Region, and Boise National Forest, principally the Mountain Home District. Other funding was provided by the National Fire Plan and the Joint Fire Science Program. L. Donohoo provided logistical support and assistance with study design. J. Evans quantified burn severity on our wildfire locations. We thank all the field assistants that endured long, hot days to collect data in the charred forests with very little shade. W. Block and R. King reviewed the manuscript and provided statistical and contextual advice that greatly improved the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.08.028.

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