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Management and Conservation Article

White-Headed Woodpecker Nesting Ecology After Wildfire

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ABSTRACT Within forests susceptible to wildfire and insect infestations, land managers need to balance dead tree removal and habitat requirements for wildlife species associated with snags. We used Mahalanobis distance methods to develop predictive models of white-headed woodpecker (*Picoides albolarvatus*) nesting habitat in postfire ponderosa pine (*Pinus ponderosa*)-dominated landscapes on the Fremont-Winema National Forests in south central Oregon, USA. The 1-km radius (314 ha) surrounding 45 nest sites was open-canopied before fire and a mosaic of burn severities after wildfire. The 1-ha surrounding nests of white-headed woodpeckers had fewer live trees per hectare and more decayed and larger diameter snags than at non-nest sites. The leading cause of nest failure seemed to be predation. Habitat and abiotic features were not associated with nest survival. High daily survival rates and little variation within habitat features among nest locations suggest white-headed woodpeckers were consistently selecting high suitability habitats. Management activities that open the forest canopy and create conditions conducive to a mosaic burn pattern will probably provide suitable white-headed woodpecker nesting habitat after wildfire. When making postfire salvage logging decisions, we suggest that retention of larger, more decayed snags will provide nesting habitat in recently burned forests.

KEY WORDS habitat suitability model, Mahalanobis distance, nest-site selection, nest survival, ponderosa pine, snags, white-headed woodpecker, wildfire.

Wildfire is the dominant natural disturbance in forested landscapes of western North America. Fire regimes, which characterize the frequency and severity of naturally occurring wildfire, vary by vegetation type, latitude, and elevation (Agee 1993, Schoennagel et al. 2004). Mixed-severity regimes that include surface and stand-replacing fires characterize higher latitude, more mesic ponderosa pine (*Pinus ponderosa*) forests (Schoennagel et al. 2004). Decades of fire suppression, logging, and grazing have increased fuel accumulation and altered fire regimes in drier forests resulting in more frequent and larger high-severity fires (Covington and Moore 1994, Fulé et al. 2002, Noss et al. 2006). Climate also has played a major role in altering the size, frequency, and severity of wildfire across forest types (Schoennagel et al. 2004).

In addition to tree mortality caused by wildfire, increases in tree mortality from bark beetle (*Dendroctonus* spp.) infestations are anticipated as a result of changing climates (Logan et al. 2003). Increased tree mortality from fire and insects will create more opportunities for salvage logging. Salvage logging removes dead, dying, damaged, or weakened trees that provide nesting and foraging habitat for woodpeckers and other cavity-nesting species (Saab et al. 2002, 2007; Hutto and Gallo 2006). Thus, land managers face challenges implementing fire management policies, while concurrently meeting the requirements of existing laws to maintain wildlife habitat for species associated with dead trees.

The white-headed woodpecker (*Picoides albolarvatus*) is listed as a sensitive or critical species by the United States Forest Service and by the states of Oregon, Idaho, and Washington, USA (Garrett et al. 1996). In addition, the white-headed woodpecker is listed as a Continental Watch-list Species in the North American Landbird Conservation Plan (Rich et al. 2004). It is considered unique from other woodpecker species in its habitat use, seeming to be associated with burned landscapes despite its reliance on mature, cone-producing pines for foraging during winter (Raphael and White 1984). Large, decayed ponderosa pine snags are frequently used as nesting sites by cavity-nesting birds after prescribed fire (Bagne et al. 2008). Habitat degradation, primarily due to conversion from pine- (*Pinus* spp.) to fir (*Abies* spp.)-dominated forests and removal of snags, has contributed to population declines of white-headed woodpeckers (Garrett et al. 1996). As such, management decisions before and after wildfire may influence nesting habitat suitability and quality for this cavity-nesting species. Despite the influence of forest management on their populations, little is known about habitat associations in postwildfire forests (but see Raphael and White 1984). Information on nest survival after wildfire, in particular, seems to be lacking from the literature.

Our goal was to evaluate white-headed woodpecker nesting ecology in postfire landscapes and to provide decision support tools to guide management of white-headed woodpecker habitat. Models based solely on

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Table 1. Characteristics of white-headed woodpecker nesting areas and postfire landscapes with eigenvector scores from partitioned Mahalanobis distance (D^2) models in postfire landscapes on the Fremont-Winema National Forests, Oregon, USA, 2003–2007.

Variable	Class	Scale	Description	Nesting habitat $\bar{x}$	Nesting habitat SD	Postfire landscapes $\bar{x}$	Postfire landscapes SD	Eigenvector values for partitioned D^2
Cover class	Prefire	Landscape[a]	% of landscape with >40% canopy cover	29.2	6.5	25.7	11.8	0.21
Quadratic mean diam	Prefire	Nest site[b]	Average of quadratic mean diam (cm) of live trees	29.2	6.5	31.8	6.1	0.02
Differential normalized burn ratio (ΔNBR)	Postfire	Landscape[a]	% of landscape with moderate to high burn severity (>270 ΔNBR)	38.0	13.8	31.0	16.5	0.73
Interspersion and juxtaposition index of ΔNBR	Postfire	Landscape[a]	Measure of patch adjacency using unburned, low, and moderate to high severity categories. No. close to zero indicate uneven patch adjacency and no. close to 100 indicate equal patch adjacency	45.4	13.3	54.6	15.6	0.65

[a] A 1-km radius around nest-site.
[b] A 1-ha plot centered on nest-site.

remotely sensed data can predict potential woodpecker habitat over larger areas (Russell et al. 2007). However, field-collected data are useful for refining potential habitat by identifying specific features important for nesting sites. Our objectives were to 1) develop landscape-scale habitat suitability models for white-headed woodpeckers that can be used to predict potential nesting habitat after wildfire, 2) identify specific features important for nest-site selection after wildfire, and 3) determine whether habitat features important for nest selection also influence nest survival.

STUDY AREA

The Toolbox and Silver fires on the Fremont-Winema National Forests in south central Oregon, USA, burned approximately 34,398 ha in 2002 between 1,500 m and 1,800 m in elevation (42°57′N, 121°0′W). Both fires were mixed-severity, stand-replacing fires typical of current-condition forests and resulted in a mosaic of burned patches across the landscape. More than 90% of the burned area was dominated by ponderosa pine (Landscape Ecology, Modeling, Mapping, and Analysis [LEMMA] 2008); other conifer species present included lodgepole pine (*Pinus contorta*) and white fir (*Abies concolor*). Land ownership within the fire boundaries included private, state, Bureau of Land Management, and United States Forest Service. Timber harvest and livestock grazing were prevalent on the forest landscape prior to the Silver and Toolbox fires. We searched for white-headed woodpeckers within 12 study units that ranged from 24 ha to 111 ha (60.2 ± 8.4; $\bar{x}$ ± SD) within the burned area of Fremont-Winema National Forests; the total area we surveyed annually was approximately 840 ha.

METHODS

Nest Surveys

Fremont-Winema National Forests selected survey units within burn areas by using remotely sensed vegetation characteristics and burn severity to include areas of high snag densities suitable for tree harvest and potentially suitable habitat for local woodpeckers based on previous research (Saab et al. 2009). We located white-headed woodpecker nests by using systematic searching and playback surveys along belt transects (0.4 × 1.0 km) distributed systematically to cover entire survey units (Dudley and Saab 2003). We surveyed all transects in all units once a year during May and early June 2003–2007, in calm, dry weather conditions. Survey effort (hr) was similar among years. Playback surveys consisted of 30 seconds of woodpecker (*Picoides* spp.) calling and drumming followed by 30 seconds of silence, repeated 3 times every 200 m along the transect line. We observed detected birds to locate cavities and considered a nest cavity occupied if it contained eggs or young.

We monitored nests by using an electronic camera mounted to a telescoping pole (TreeTop II; Sandpiper Technologies, Inc., Manteca, CA) at 3–4-day intervals. At each visit, we recorded reproductive data, including time, date, nest stage, and number of eggs or young until the nest failed or fledged ≥1 young. We determined nest fate as successful if we observed the cavity empty after the expected fledging date, there was no sign of depredation in or around the nest tree, and previous nest visits had shown the nestlings to be exhibiting prefledging signs (e.g., large size, advanced feather development, adult-like vocalizations, and head protruding from cavity entrance). We assumed cause of nest failure was predation if the nest showed signs of depredation or was empty before estimated fledging dates for that nest. We assumed cause of failure as abandoned if we found dead nestlings in the nest cavity.

Remotely Sensed Forest Characteristics

Habitat conditions before fire may influence woodpecker distributions in postfire landscapes because prefire conditions may function as an index to postfire snag densities and diameters (Saab et al. 2002, Russell et al. 2007, Vierling et al. 2008). Therefore, we used remotely sensed data from pre- and postfire coverages to assess forest variables that we assumed represented white-headed woodpecker habitat requirements at nest-sites (1 ha) and within a 1-km radius (314 ha) of nests (Table 1). We defined landscape nesting habitat as the area within a 1-km radius of a nest site because this area corresponds with the home range of many woodpecker species, including white-headed woodpeckers (Dixon 1995*a, b*; Saab et al. 2004).

To estimate prefire conditions, we acquired Gradient Nearest Neighbor (GNN) forest vegetation data for east Cascades, southern Oregon (Ohmann and Gregory 2002, LEMMA 2008). Gradient Nearest Neighbor is a predictive mapping product that provides spatially explicit species composition and forest structure data in a digital landscape map. Accuracy assessments of the GNN resulted in a 0.75 and 0.46 correlation coefficient for canopy cover and quadratic mean diameter, respectively, indicating that the GNN layer had moderate predictive ability (LEMMA 2008). We eliminated remnant forests (<10% canopy closure) and sapling–pole forests (<25-cm quadratic mean diam) from the GNN data to generate a layer of potential white-headed woodpecker habitat. We then reclassified these GNN data into open forests (10–40% canopy cover) and moderate- to high-cover forests (>40% canopy cover). We calculated the percentage of moderate- to high-cover forest within 1 km of each nest. We also used GNN data to calculate an average quadratic mean diameter of conifers near (1 ha) nest-sites.

To characterize postfire conditions, we obtained burn severity data from the United States Forest Service Remote Sensing Applications Center. We calculated burn severity as the change in the normalized burn ratio (ΔNBR) between pre- and postfire Landsat Thematic Mapper images (Cocke et al. 2005, Key and Benson 2006). We reclassified ΔNBR scores as unburned (−900 to 99), low-severity (100–269), and moderate- to high-severity (>270) burns and calculated the percentage of moderate- to high-severity burn within 1 km surrounding each nest (Key and Benson 2006, Russell et al. 2006). Using Program FRAGSTATS (McGarigal and Marks 1995), we also calculated an interspersion and juxtaposition index that describes the landscape configuration of burn severity patches by measuring the intermixing of patches based on the relative proportion of edges between patch types (i.e., unburned, low, or moderate-high severity). Interspersion and juxtaposition index values close to zero indicate unequal adjacency among patches or a landscape where size, shape, and distribution of patch types vary widely. Values closer to 100 indicate equal adjacency among patches or a landscape that contains similar sizes, shapes, and distribution of patch types. Intermediate values represent a mosaic of patches that vary somewhat in size, shape, or distribution. Resolution of all geographic data was 30 m.

Habitat Suitability Model

We used locations of 45 white-headed woodpecker nests to model characteristics of nesting habitat by using partitioned Mahalanobis distance (D^2; Browning et al. 2005, Rotenberry et al. 2006). We selected this technique because D^2 consistently performed better than other competing models for modeling presence-only data (Farber and Kadmon 2003, Tsoar et al. 2007). Conceptually, D^2 compares the similarity between each known nesting area and ideal nesting habitat conditions (Farber and Kadmon 2003). Ideal conditions are calculated as mean values for all variables selected from all occupied nest locations and assume the sample reflects optimal habitat distribution of the species in the sampled area (Rotenberry et al. 2006). Because uncertainty exists in defining optimum conditions for white-headed woodpeckers, we partitioned D^2 into separate components to identify a minimum, rather than optimum, set of habitat requirements for occupancy. We selected variables included in modeling minimum habitat requirements from features identified as important for woodpeckers in previous research (Saab et al. 2009). We restricted our observation to variable ratio to 10:1 (Rotenberry et al. 2006). We performed a principal components (PC) analysis on the 4 selected habitat variables and partitioned D^2 following Browning et al. (2005) and Rotenberry et al. (2006). We selected the partition associated with the PC axis with the smallest eigenvalue, because that value represents the combination of variables that best explains the minimum consistent relationships in white-headed woodpecker nesting distribution. We evaluated eigenvector values associated with the selected PC axis to identify habitat characteristics important for describing white-headed woodpecker habitat.

Using the partitioned model, we calculated D^2 for each pixel in the Silver and Toolbox fires to produce a habitat suitability map. From the D^2 values, we calculated a p-value, which is an index to habitat similarity and is analogous to the probability of nesting occupancy from a logistic regression but should not be interpreted for statistical inference (Rotenberry et al. 2006). We assigned each pixel in the study area a habitat similarity index score based on how similar the habitat features were to white-headed woodpecker nesting features. Scores were relative; higher numbers indicated greater similarity to white-headed woodpecker habitat. Managers may choose a threshold value to identify suitable nesting habitat for focusing management. In this context, values at or above the threshold represent potential white-headed woodpecker habitat. We identified a useful threshold for management as the maximized predictive gain obtained by selecting the similarity index that represented the greatest number of nesting sites in the smallest geographic area (Browning et al. 2005). However, we provide habitat similarity values in intervals of 0.10 so that other thresholds can be selected depending on management objectives.

To assess our model, we used a jackknife procedure for resampling that holds out one observation at a time and reruns the analysis for all observations in the data set. The removed observation is then scored by the model from which it was excluded. We assessed the mean similarity index assigned to all observations when excluded from model building to determine whether any of our data points were unduly influencing our model (Browning et al. 2005). We used Program SAS for all analyses (SAS Institute, Cary, NC) and used the code provided by Rotenberry et al. (2006) to calculate D^2 and associated similarity index values.

Nest-Site Selection

We generated random non-nest points within survey units using a Geographic Information System and random point generator. We proportionally distributed within-year ran-

Table 2. Candidate models and selection results of habitat features at the nest-site scale (1 ha) influencing nest-site selection of white-headed woodpeckers on the Fremont-Winema National Forests, Oregon, USA, 2003–2007.

Model	$-2\log(L)$	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]
Live trees/ha, decay	139.32	3	145.64	0.00	0.50
Live trees/ha, decay, nest tree dbh	137.23	4	145.71	0.07	0.48
Live trees/ha, nest tree dbh	145.95	3	152.26	6.63	0.02
Snags/ha, decay	155.41	3	161.73	16.09	0.00
Snags/ha, decay, nest tree dbh	153.83	4	162.30	16.67	0.00
Canopy cover, nest tree dbh	164.43	3	170.74	25.11	0.00
Canopy cover, nest tree dbh, snags/ha	162.85	4	171.33	25.69	0.00
Snags/ha, nest tree dbh	165.08	3	171.39	25.75	0.00
Intercept only	169.39	1	171.49	25.85	0.00
Canopy cover, snags/ha	165.87	3	172.18	26.55	0.00

[a] No. of model parameters.
[b] Akaike's Information Criterion with a second order correction for small sample sizes.
[c] AIC_c differences, or the difference in AIC_c values between model i and the model with the lowest AIC_c value.
[d] Akaike wt, or the wt of evidence in favor of model i being the best model among the models in the set.

dom points across units based on unit size and points were located >100 m apart to prevent overlapping vegetation plots. We selected the nearest available tree to the randomly generated point (snag or live tree $\geq$15 cm dbh) as the focal tree and centered in the vegetation plot. We measured habitat characteristics in the field at 45 white-headed woodpecker nests and 87 randomly selected non-nest locations. We calculated mean diameter at breast height of the nest or non-nest snag. We calculated density of snags and live trees ($\geq$23 cm dbh and >1.37 m in ht for snags and trees) per hectare after wildfire from 2 intersecting 100-m belt transects centered on the nest or non-nest snag (Appendix A). We defined snags as having no green needles. We also recorded the decay class (1–4) of nest or non-nest center trees where higher numbers equated to more decay (Bull et al. 1997). Using a 3×3-pixel (0.81-ha) moving window, we calculated the average quadratic mean diameter and prefire canopy cover from GNN data for nest and non-nest locations (Appendix A).

To identify site-based features important for nest-site selection, we used logistic regression to compare field-collected data from nest and non-nest locations (Hosmer and Lemeshow 2000). We identified a set of a priori candidate models based on species habitat requirements from the literature (Table 2). We used Akaike's Information Criterion with a second order correction for small sample sizes (AIC_c) to select the most parsimonious model and considered all models with ΔAIC_c values <2.0 as having strong support for the data (Burnham and Anderson 2002). We calculated Akaike weights (w_i) to quantify support for individual models in relation to the other models in the set. Because there was more than one model with strong support for the data, we averaged estimates across models weighted by w_i (Burnham and Anderson 2002).

We assessed receiver operating characteristic (ROC) curves to evaluate the ability of our averaged nest-site selection model to distinguish between nests and non-nest locations. Receiver operating characteristic curves evaluate the relationship between true positives (correctly classified nests) and false positives (non-nests classified as nests) at different probability of nest occupancy thresholds. The area under the ROC curve (AUC) is an index to the discriminatory power of the model (Swets 1988, Russell et al. 2007). An AUC value of 0.5 indicates no discrimination and an AUC value of 1.0 indicates perfect discrimination; in general, AUC values >0.7 reflect moderately good accuracy of the model (Swets 1988).

Nest Survival

We modeled nest survival as a function of abiotic and biotic covariates. To assess abiotic factors related to nest survival, we obtained precipitation and temperature data from the Silver Creek Snowpack Telemetry station (Natural Resources Conservation Service 2008). We recorded precipitation as the cumulative yearly precipitation on the end date for each nest visit interval. We recorded temperature as the maximum temperature for each nest visit interval. We also evaluated the influence of year and nest age on nest survival where nest age was the number of days after nest initiation. We measured biotic factors at the nest site (dbh, decay and ht of nest snag, and densities of snags and trees) and landscape scales (percentage of canopy cover $\geq$40% from GNN data and % of moderate to high burn severity from ΔNBR data).

We used generalized nonlinear mixed models to evaluate the influence of fixed and random factors on nest survival, which allowed us to calculate a daily survival rate as a function of several covariates (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004). We used PROC GENMOD in SAS (SAS Institute), following code provided in Rotella et al. (2004, appendix 3), for nest survival analysis. We evaluated 5 models of nest survival based on hypotheses about the influence of biotic and abiotic factors (Table 3). We used AIC_c to select the most parsimonious model and considered the model with ΔAIC_c values <2.0 as having the strongest support for the data (Burnham and Anderson 2002). We calculated w_i to quantify support for individual models in relation to the other models in the set.

RESULTS

Eigenvalues for the first 3 PCs accounted for approximately 88% of variation in the data set (Table 4). For D^2 modeling, we used the last axis, PC4, which represented minimum

Table 3. Candidate models and supporting hypotheses comparing random, biotic, or abiotic influences on nest survival of white-headed woodpeckers on the Fremont-Winema National Forests, Oregon, USA, 2003–2007.

Model	Variable	Alternative hypothesis
Random	Intercept only	Nest survival is random; probably due to random predation events.
Abiotic and temporal	Precipitation, temp, yr, season date, nest age	There is more variation at nest sites in abiotic factors than nest characteristics; thus, abiotic factors may have the strongest influence on nest survival.
Fine scale	Snag dbh, snag decay, tree densities, nest ht	Factors influencing nest selection will be consistent with those influencing nest survival. Physical features may provide greater protection from predators.
Coarse scale	% canopy cover class, % ΔNBR[a], IJ NBR[b]	Factors associated with nest occupancy will be consistent with those associated with nest survival. A mosaic of burn severities and open-canopied forests will provide diverse foraging options.
Combination	Precipitation, temp, nest ht, IJ NBR[b]	Higher temp, lower precipitation, higher nests, and a landscape mosaic of burn severities may increase nest survival because of good environmental conditions, protection from predators, and diverse foraging options.

[a] Differential normalized burn ratio. We reclassified ΔNBR scores as unburned (−900 to 99), low-severity (100–269), and moderate- to high-severity (>270) burns and calculated the percentage of moderate- to high-severity burn within 1 km surrounding each nest.
[b] Interspersion and juxtaposition index that describes the landscape configuration of burn severity patches by measuring the intermixing of patches based on the relative proportion of edges between patch types (i.e., unburned, low, or moderate-high severity).

habitat requirements for white-headed woodpeckers. Evaluation of the eigenvector values associated with PC4 indicated that the percent moderate to high burn severity, interspersion and juxtaposition of burn severities (patch adjacency), and percent moderate to high canopy cover before wildfire best described the similarities within 1 km of nests (Table 1). The quadratic mean diameter of prefire, live trees at the nest-site scale (1 ha) was not a good descriptor of white-headed woodpecker habitat. Specifically, white-headed woodpecker habitat was characterized by approximately 37% of the landscape as moderate to high burn severity, moderate levels of burn patch adjacency (interspersion and juxtaposition [IJ] index = 45), and approximately 30% of the landscape with ≥40% canopy cover prefire. The IJ value indicated that patches of different burn severities were typically intermixed with each other rather than occupying a few large areas.

Using our partitioned model, mean similarity index score was 0.50 ± 0.25 (SD; range <0.001–0.88) for known nest areas and 0.43 ± 0.32 (range 0.00–0.99) for postfire landscapes. Although we would expect all known nests to have high similarity scores, in fact, D^2 values are affected by the sampling variance. Thus, nest sites distant from the mean will have lower values (Rotenberry et al. 2006). Application of our model to the area of the Toolbox and Silver fires identified areas of similarity to white-headed woodpecker nest sites (Fig. 1). Based on a similarity index threshold of 0.29, which maximized the number of known nests in the smallest geographic area (Fig. 2), 82% of occupied sites had an index score of ≥0.29, whereas only 61% of the study area was in this same range. The jackknife procedure of leave one out for model assessment produced a mean habitat similarity index of 0.45 ± 0.26. Less than half of the study area (46%) had index values at or above this average. When excluded from analysis, 76% of nest sites had a similarity index greater than our probability threshold of 0.29.

Table 4. Eigenvalues and associated proportion of variance of the correlation matrix from principle components analysis of characteristics describing white-headed woodpecker nesting habitat on the Fremont-Winema National Forests, Oregon, USA, 2003–2007.

Partition	Eigenvalue	Proportion
4	0.48	0.12
3	0.76	0.19
2	1.10	0.27
1	1.65	0.42

There was strong support for 2 models and minimal support for a third model of nest selection (Table 2). The averaged model for predicting nest site selection by white-headed woodpeckers included the variables density of live trees postfire ($\beta = -0.03$, CI = −0.05 to −0.01), decay class ($\beta = 1.00$, CI = 0.28–1.73), and diameter at breast height of nest trees ($\beta = 0.02$, CI = 0.0004–0.04). Specifically, the relative probability of nest selection increased as the number of live trees decreased and the snag decay class and nest tree diameter at breast height increased. Nest sites had a higher proportion of snags with decay class 3 than did non-nest sites (Appendix B). We found no relationship of nest selection with snag density or prefire canopy closure. An AUC value of 0.77 for our model of nest selection indicated it had moderately good discriminatory power.

Only 16% of monitored nests failed to fledge young, with ≥67% assumed to have failed due to predation. Daily survival rate was high (0.993), resulting in nest success of 0.76 over a presumed 40-day nesting period. The best model among the candidate models for evaluating nest survival ($\Delta AIC_c < 2.0$) was the intercept-only model (Table 5), which indicates that none of the combinations of abiotic or habitat features we considered explained patterns in nest survival better than random.

DISCUSSION

Open-canopied ponderosa pine forests before fire and a mosaic of burn severities within 1 km of nests characterized white-headed woodpecker nest sites in postfire areas on the Fremont-Winema National Forests. Larger, more decayed snags and fewer live trees near (within 1 ha) a snag after fire were important for selection of nest sites. Even so, none of these features seemed to influence nest survival. Relatively high daily survival rates compared with other cavity-nesting birds (Saab et al. 2007) and little variation within habitat features among nest locations suggest white-headed wood-

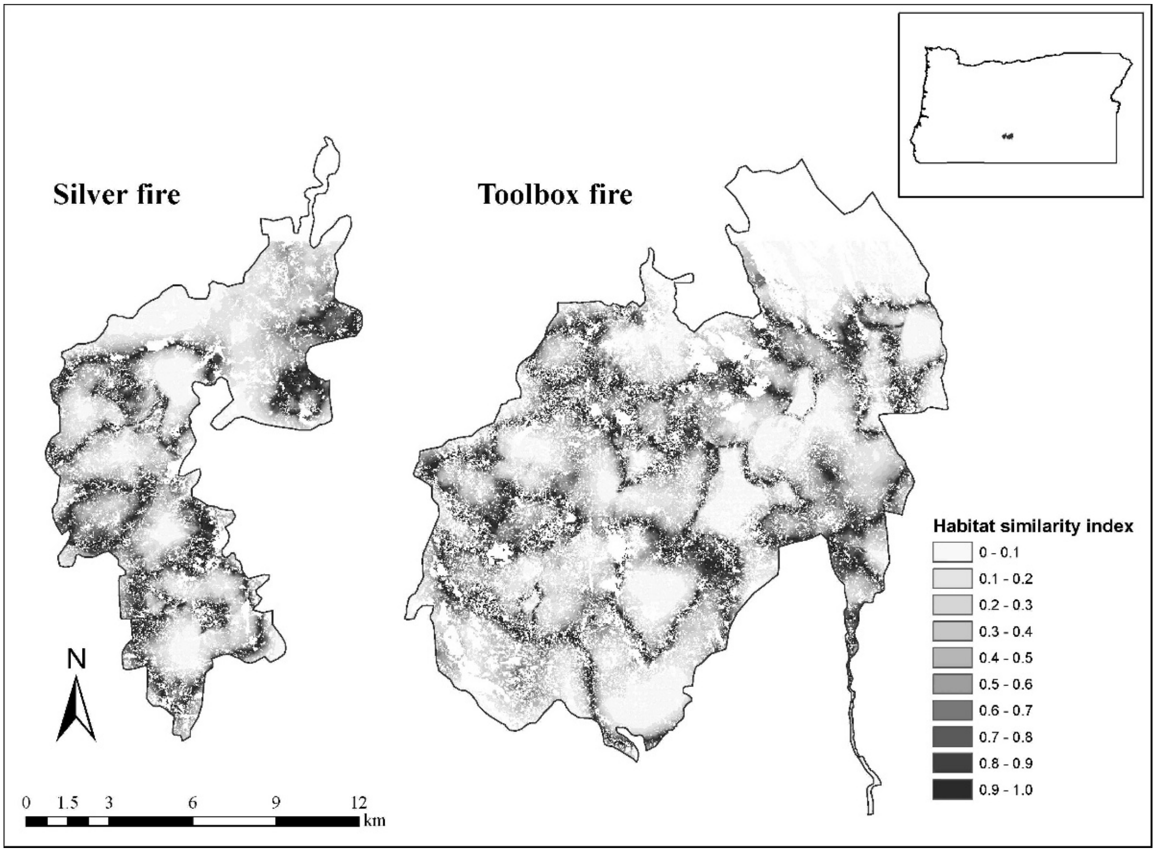

Figure 1. Partitioned habitat suitability model for white-headed woodpeckers on the Toolbox and Silver fires, Fremont-Winema National Forests, Oregon, USA, 2003–2007. The habitat similarity index represents similarity on an increasing 0–1 scale, with 1 representing environmental conditions identical to the mean conditions surrounding 45 white-headed woodpecker nests. We eliminated white areas from consideration because they did not represent potential white-headed woodpecker habitat (forest with <10% canopy closure or trees <25 cm quadratic mean diam). Curvilinear patterns in the map are an artifact of the interspersion and juxtaposition index related to areas of relative patch (burn intensity) homogeneity.

peckers were consistently selecting high suitability habitats. White-headed woodpeckers are typically found in open-canopied pine forests with mature, cone-producing trees that white-headed woodpeckers rely on during winter (Milne and Hejl 1989, Garrett et al. 1996). Our models suggest that these characteristics probably remain important for identifying white-headed woodpecker habitat after wildfire, as long as most of the landscape was not subjected to a stand replacing burn. A mosaic of burn severities across the landscape may, in fact, improve white-headed woodpecker habitat by opening forest canopies in the higher-severity burn areas, while retaining decayed snags created before wildfire and live, cone-producing trees in unburned or low-severity burn areas.

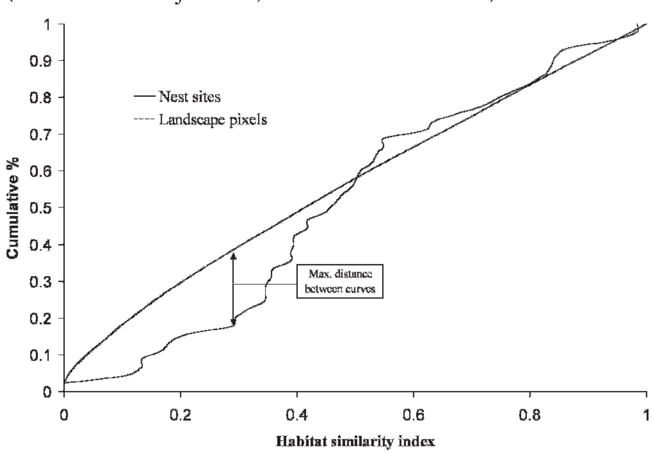

Figure 2. Habitat similarity index for white-headed woodpeckers based on 45 nest locations (within a 1-km radius of nest trees) compared with burned landscapes on the Toolbox and Silver fires on the Fremont-Winema National Forests, Oregon, USA. A similarity index of 0.29 maximizes the predictive gain (i.e., max. distance between curves) of our white-headed woodpecker habitat model in postfire landscapes and represents the greatest number of known nesting sites across the smallest portion of the landscape.

Using the Mahalanobis distance technique allowed us to identify areas that were most similar to known white-headed woodpecker nesting areas; however, it does not imply biological significance of the features considered. For example, although white-headed woodpeckers are typically found in stands with large trees, our measure of live tree diameter (QMD) was not a good descriptor for modeling white-headed woodpecker habitat (Milne and Hejl 1989, Dixon 1995*a*). There may have been considerable variation in QMD within and among nest sites resulting from the spatial distribution of large trees. In addition, we had less confidence associated with QMD values within the GNN data, suggesting that this structural forest feature may be difficult to measure remotely (LEMMA 2008).

Our D^2 model and habitat similarity index may be useful as a remote-sensing tool for targeting management or

Table 5. Model results of white-headed woodpecker nest survival from 45 nests and 313 intervals on the Fremont-Winema National Forests, Oregon, USA, 2003–2007.

Model	K^a	$-2\log(L)$	$AIC_c{}^b$	$\Delta AIC_c{}^c$	$w_i{}^d$
Intercept only (null)	1	67.38	69.38	0.00	0.76
Abiotic and temporal	5	62.94	73.00	3.61	0.12
Coarse scale	4	66.64	74.68	5.29	0.05
Combination	5	64.74	74.80	5.41	0.05
Fine scale	5	67.09	77.15	7.77	0.02

[a] No. of model parameters.
[b] Akaike's Information Criterion with a second order correction for small sample sizes.
[c] AIC_c differences, or the difference in AIC_c values between model *i* and the model with the lowest AIC_c value.
[d] Akaike wt, or the wt of evidence in favor of model *i* being the best model among the models in the set.

white-headed woodpecker surveying activities in postfire landscapes. Managers may choose to use our similarity threshold of 0.29, which maximizes potential habitat within the smallest geographic range, or adjust this threshold based on management objectives. For example, if a management goal is to identify only those areas considered highly suitable for white-headed woodpecker nest occupancy, a higher similarity index threshold of 0.5 (representing 42% of the study area) or 0.7 (21% of the study area) could be used. Model assessment indicated that none of the known nests unduly influenced the model but, depending on the threshold selected, a large portion of the study area might be classified as suitable habitat. Because our model was not validated in other postfire landscapes, we recommend field-testing the model before using it to guide management decisions.

We recommend focusing surveys for white-headed woodpeckers on areas with fewer live trees within 1 ha and larger, more decayed snags, based on the good discriminatory power of our nest-site selection model. Although the size of snags selected by white-headed woodpeckers may vary locally based on availability, in unburned areas of the Winema National Forest, mean diameter at breast height of nest trees was 80 cm, which was at the upper range of availability on our study area (Dixon 1995*b*). Thus, we recommend management for white-headed woodpeckers focus on larger snags within any given area.

Although snag density is often an important feature for cavity-nesting birds (Russell et al. 2007), our results and those of others (Saab and Dudley 1998, Bagne et al. 2008) indicate white-headed woodpeckers may rely more on decay condition than density of snags. Snags created by fire have lower retention rates than trees killed more slowly by insect or disease and fire-killed snags may not reach levels of decay favored by white-headed woodpeckers until 2–3 years postfire (Lowell and Cahill 1996, Russell et al. 2006). Concurrently, 4–6 years postfire, other benefits of fire to cavity-nesting birds, such as changes to forest structure, invertebrate availability, and predator communities, decline (Covert-Bratland et al. 2006, Saab et al. 2007). Therefore, snags existing before wildfire, if retained, or those with more advanced decay seem to be critical habitat components in postfire landscapes, especially in the first few years after fire.

Our search area was primarily in high-severity burn areas; thus, almost all nesting and random sites were in high-severity burned patches. Nests tended to have fewer live trees per hectare at the nest-site scale than random. In fact, 79% of our nesting sites had no live trees ($\geq$23 cm dbh) in the nest-site vegetation plot, which suggests white-headed woodpeckers tended to select nest snags $\geq$50 m from the unburned or low intensity burned areas that contain live trees. Forests with live trees tend to have more abundant and complex predator assemblages than do high-severity burned areas (Saab and Vierling 2001). For example, golden-mantled ground squirrels (*Spermophilus lateralis*) and yellow-pine chipmunks (*Neotamias amoenus*) are known predators on white-headed woodpecker nests (R. W. Frenzel, Deschutes National Forest, unpublished data). Golden-mantled ground squirrel densities are positively related to down wood volume, and yellow-pine chipmunk densities are positively related to shrub cover (Smith and Maguire 2004). Both wood volume and shrub cover are less in postfire habitats. Thus, nest placement in high-severity burned areas may be a viable strategy to reduce nest predation, as long as unburned or low-severity burned areas are available within the landscape for foraging.

Nest-site selection is probably adaptive such that a species will select habitat features conducive to successful nesting attempts, and we found little variation within selected habitat features at nest sites (Clark and Shutler 1999). Thus, it is not surprising that we failed to identify biotic factors influencing nest survival of white-headed woodpeckers. Predation seemed to be the leading cause of nest failure on our study area. Assuming a relationship between habitat features and predator communities, we would expect nest-site selection choices to influence nest survival. Our results, however, suggest predation was opportunistic. Our daily nest survival rate of 0.993 was high compared with other cavity-nesting birds (range 0.980–0.998; Saab et al. 2007), and our period survival rate of 0.76 was higher than nest success reported for white-headed woodpeckers in unburned forests of central Oregon (range 39.3–60.8; R. W. Frenzel, unpublished data). High survival rates regardless of physical or environmental factors suggest white-headed woodpeckers were occupying high-quality nesting sites.

MANAGEMENT IMPLICATIONS

Selective thinning and prescribed fire are often used in drier ponderosa pine forests of the southwestern United States to open forest canopies and reduce fuel loads for restoration of low-intensity fire regimes (Finney 2001, Fulé et al. 2001). Managing for mixed-severity fire regimes characteristic of more mesic, higher latitude ponderosa pine forests is more complicated and often dependent on climatic variation (Schoennagel et al. 2004). Our results indicate that prefire management activities that open forest canopies and create forest conditions conducive to a mosaic burn pattern by wildfire may encourage white-headed woodpecker nest occupation. Where white-headed woodpecker habitat is a management priority, we recommend opening of the forest canopy within stands containing medium- and larger diameter (>23 cm dbh) mature trees and snags.

To retain wildlife habitat during postfire salvage logging, forest managers historically have used guidelines based on snag distributions and densities. However, this approach has been criticized for failing to capture other wildlife habitat requirements such as snag composition (Bagne et al. 2008). Our results support consideration of snag characteristics when managing for wildlife habitat features after fire. Features of snags important to woodpeckers include larger diameters and more advanced decay. We recommend retention of snags created before wildfire, because these snags are probably of more value to white-headed woodpeckers in the early years after fire than are snags created after wildfire.

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Appendix A. Summary statistics of linear habitat features used in nest site selection analysis of white-headed woodpecker at 45 nest sites (Used) and 87 non-nest sites (Random) on the Fremont-Winema National Forests, Oregon, USA, 2003–2007. All features are at the nest-site scale (1 ha).

	Used			Random		
Variable	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Snags/ha	102.6	8.4	15–250	89.9	6.0	16–229
Nest tree dbh	40.1	2.7	18–80	34.1	2.1	15–95
Trees/ha	6.3	2.3	0–83	32.0	4.4	0–171
Prefire canopy cover (%)	39.4	1.4	22–66	42.3	1.3	1–75

Appendix B. Decay class statistics and descriptions for 45 nest trees (Used) of white-headed woodpeckers and 87 random trees (Random) on the Fremont-Winema National Forests, Oregon, USA, 2003–2007.

Decay class	Used	Random	Description
1	31	78	Snags that recently died, typically had little decay, and retained their bark, branches, and top
2	4	8	Snags with some evidence of decay and had lost some bark, branches, and often a portion of the top
3	10	0	Snags that had extensive decay, were missing the bark and most of the branches, and had a broken top
4	0	1	Burnt snag; almost entire outer shell was case-hardened by fire; looked like charcoal