The Journal of Wildlife Management 75(5):1061–1071; 2011; DOI: 10.1002/jwmg.146

Research Article

Habitat Suitability and Nest Survival of White-Headed Woodpeckers in Unburned Forests of Oregon

JEFF P. HOLLENBECK,[1,2] *USFS Rocky Mountain Research Station, 1648 S. 7th Avenue, Bozeman, MT 59717, USA*
VICTORIA A. SAAB, *USFS Rocky Mountain Research Station, 1648 S. 7th Avenue, Bozeman, MT 59717, USA*
RICHARD W. FRENZEL, *12330 SE Reedway Street, Portland, OR 97236, USA*

ABSTRACT We evaluated habitat suitability and nest survival of breeding white-headed woodpeckers (*Picoides albolarvatus*) in unburned forests of central Oregon, USA. Daily nest-survival rate was positively related to maximum daily temperature during the nest interval and to density of large-diameter trees surrounding the nest tree. We developed a niche-based habitat suitability model (partitioned Mahalanobis distance) for nesting white-headed woodpeckers using remotely sensed data. Along with low elevation, high density of large trees, and low slope, our habitat suitability model suggested that interspersion–juxtaposition of low- and high-canopy cover ponderosa pine (*Pinus ponderosa*) patches was important for nest-site suitability. Cross-validation suggested the model performed adequately for management planning at a scale >1 ha. Evaluation of mapped habitat suitability index (HSI) suggested that the maximum predictive gain (HSI = 0.36), where the number of nest locations are maximized in the smallest proportion of the modeled landscape, provided an objective initial threshold for identification of suitable habitat. However, managers can choose the threshold HSI most appropriate for their purposes (e.g., locating regions of low–moderate suitability that have potential for habitat restoration). Consequently, our habitat suitability model may be useful for managing dry coniferous forests for white-headed woodpeckers in central Oregon; however, model validation is necessary before our model could be applied to other locations. © 2011 The Wildlife Society.

KEY WORDS nest survival, niche model, partitioned Mahalanobis distance, *Picoides albolarvatus*, ponderosa pine forests, remote sensing, white-headed woodpecker.

The white-headed woodpecker (*Picoides albolarvatus*) is a regional endemic strongly associated with ponderosa pine (*Pinus ponderosa*)-dominated forests of western North America (Garrett et al. 1996). White-headed woodpeckers are dependent on the seeds of large-coned pines (e.g., ponderosa pine, sugar pine [*Pinus lambertiana*]) for a portion of their diet (Ligon 1973, Raphael and White 1984) and typically nest in mature, open forests with large-diameter trees and a sparse canopy (Garrett et al. 1996). Such forests have become increasingly scarce in western North America (Agee 1993). Loss or removal of large-diameter snags and the conversion of pine-dominated forests to other forest types absent fire disturbance have been implicated in the decline of white-headed woodpecker populations (Garrett et al. 1996). Consequently, white-headed woodpeckers are considered a species at risk by federal, state, and non-governmental organizations (e.g., Rich et al. 2004).

Effective fire suppression over the last several decades has led to vegetation changes among dry coniferous forests of the western United States (Schoennagel et al. 2004, Hessburg et al. 2005). Historically, low elevation dry coniferous forests of the Pacific Northwest experienced mixed severity fires that maintained a mosaic of open and closed forest dominated by larger diameter trees (Hessburg et al. 2005). These are the conditions that white-headed woodpeckers appear to select for nesting habitat in burned and unburned forests (Buchanan et al. 2003, Wightman et al. 2010). For example, in central Oregon and Washington, Buchanan et al. (2003) found that white-headed woodpeckers selected large-diameter snags (>50 cm dbh) for nest sites that were primarily in mature ponderosa pine forests with sparse canopy. Managed forests with smaller diameter trees (25–50 cm dbh) are also used during the nesting season (Kozma 2009, Lindstrand and Humes 2009).

Recent efforts to mitigate severe fire effects and restore ecological function in dry coniferous forests have prompted land managers to consider the implications of forest management actions on a range of resources, including wildlife (e.g., Hessburg et al. 2005). Consequently, managers need reliable

Received: 4 May 2010; Accepted: 8 November 2010;
Published: 6 June 2011

Additional Supporting Information may be found in the online version of this article.

[1] *E-mail: jhollenbeck@usgs.gov*

[2] *Present Address: USGS Forest and Rangeland Ecosystem Science Center, Oregon State University, 3200 SW Jefferson Way, Corvallis, OR 97331.*

information to effectively achieve their goals of forest restoration, while maintaining wildlife habitat and other sensitive resources. Tools for assessing wildlife habitat should be easy to use and interpret. Habitat suitability models based on remotely sensed data have good potential for ease of use and applicability to wide areas (Russell et al. 2007, Vierling et al. 2008, Bartel and Sexton 2009, Wightman et al. 2010).

Using remotely sensed data, Wightman et al. (2010) developed a habitat suitability model for nesting white-headed woodpeckers in burned ponderosa pine forests of central Oregon. That model highlighted the importance of burned and unburned patchiness for nest locations. The patchiness may have reflected a preference to place nests in burned areas with snags, nearby unburned areas with reliable sources of live, cone-bearing ponderosa pines that contain both seed and insect forage. Wightman et al. (2010) also found high nest success (probability that a nest will be successful; 76%) within burned forests. Understanding the factors influencing habitat suitability and survival of nesting white-headed woodpeckers is necessary for guiding forest management actions that ensure population persistence.

Currently, fuel reduction treatments are the primary focus of dry coniferous forest restoration. Land managers face substantial challenges implementing forest restoration activities while concurrently meeting the requirements of existing laws to maintain wildlife habitat. Therefore, tools to predict potential wildlife habitat in landscapes affected by restoration activities are needed to help managers with timely decisions regarding treatment options. Our goal was to develop a habitat suitability model for white-headed woodpeckers that can be used for predicting potential nesting habitat in unburned, dry coniferous forests. Our specific objectives were to: 1) develop a habitat suitability model that adequately identifies potential white-headed woodpecker nesting habitat, 2) evaluate applicability of the model in a management context (e.g., cross-validated nest-site suitability and proportion of landscape identified as high suitability), and 3) identify biotic and abiotic features that may affect nest survival in relation to factors that influence habitat suitability.

STUDY AREA

We developed models for 2 regions in central and south-central Oregon (Fig. 1). Region extents were defined by the boundaries of the Sisters Ranger District on the Deschutes National Forest (−121.65W, 44.40N) and the Chemult and Chiloquin Ranger Districts on the Fremont-Winema National Forest (−121.66W, 42.87N). Both regions were located on the east slopes of the Cascades Range with dominant forest types of dry ponderosa pine, lodgepole pine (*Pinus contorta*), and mixed conifer, typically including Douglas-fir (*Pseudotsuga menziesii*). Elevation ranged from 394 m to 3,150 m ($\bar{x}$ = 1,476 m). Land ownership was mostly federal (U.S. Forest Service, Bureau of Land Management) with scattered state and private in-holdings. Land use in the study area included recreation, timber production, and livestock grazing.

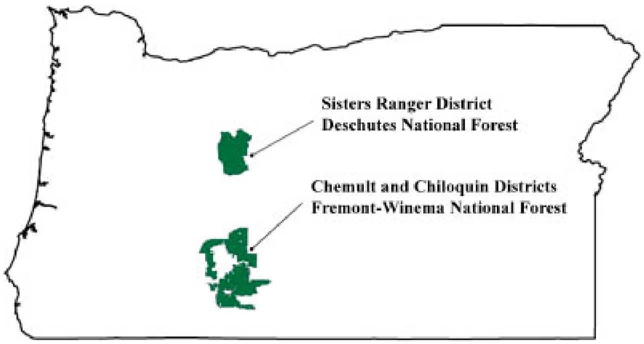

Figure 1. Study areas for white-headed woodpecker nest-site habitat suitability and nest survival in central Oregon, USA, 1997–2004.

METHODS

Field Data Collection

We randomly located 10 study sites for nest searching in ponderosa pine forests that were known nesting habitat for white-headed woodpeckers within the Deschutes and Fremont-Winema National Forests. We defined 5 study sites in each of 2 strata (>50% and <50% late-successional ponderosa pine forest). Study sites were defined by forest management units and ranged from 260 ha to 1,400 ha. We systematically searched forested areas within each study site for nest cavities using a standard protocol (cf. Martin and Geupel 1993, Dudley and Saab 2003) during May–June of 1997–2004.

We considered nests occupied if we observed eggs or young or if adult behavior indicated nesting (i.e., food delivery, frequent visits, or extended time in nest cavities; Martin and Geupel 1993). We visited each occupied nest every 1–6 days until we determined nest fate. We visually inspected ≤20% of nests each year with either a mirror or portable video device. We considered nest attempts successful if we observed ≥1 fully feathered nestling at the cavity entrance (indicating nestlings are near to fledging) previous to a nest visit where we observed a vacant nest cavity (Martin and Geupel 1993). We classified all other nests as failures. We estimated the nest fate date (successful or failed) as the midpoint between the last and previous nest visit dates.

At each nest tree and its immediate vicinity (0.4-ha circle centered on nest tree), we recorded nest tree or snag species, nest tree or snag diameter at breast height (dbh), height of nest cavity, percentage shrub cover, density of trees ≥8 cm dbh, density of snags ≥8 cm dbh, and density of trees ≥50 cm dbh (Table 1; see Supporting Material Appendix A, available online at http://onlinelibrary.wiley.com). Nest tree or snag diameter may be related to thermal effects on nest survival as well as predation effects (e.g., Wiebe 2001). Cavity height, tree and snag density, and shrub cover may be related to predation effects (Li and Martin 1991), whereas density of large trees may be related to both predation and foraging (Wightman et al. 2010).

Remotely Sensed Habitat Data

We used Gradient Nearest Neighbor (GNN) Classified Landsat (ETM+) satellite imagery (image year: 2000; Ohmann and Gregory 2002) obtained from the

Table 1. Model covariates we used for habitat suitability and survival of nesting white-headed woodpeckers in central Oregon, 1997–2004.

Variable name	Variable description	Habitat suitability	Nest survival
Year	Year of nest-site observation (1997–2004)		X
Field-collected (nest vicinity; 0.4 ha)			
dbh	Diameter at breast height (dbh) of nest snag (cm)		X
cav_hgt	Height above ground of nest cavity (m)		X
tph_trees	Tree density surrounding nest tree (trees per hectare dbh $\geq$15 cm)		X
tph_snags	Snag density surrounding nest tree (snags per hectare dbh stems $\geq$15 cm)		X
tph_large_fc	Large tree density surrounding nest tree (trees per hectare dbh $\geq$50 cm)		X
shrubcov	% cover of shrubs surrounding nest tree		X
Remotely sensed			
SNOTEL-derived[a]			
tavg	Average max. daily temp (°C) for the nest observation interval		X
precip	Cumulative annual precipitation on day nest fate determined (cm)		X
NED-derived[b]			
elev	Elevation of nest site (m)	X	
slope	Slope at nest site (% slope)	X	
cosasp	Cosine of aspect (azimuth) at nest site (range: -1 to 1)	X	X
GNN-derived[c]			
qmd	Quadratic mean diameter of trees (dbh $>$15 cm) in 1-ha surrounding nest site	X	X
LocCC	Forest canopy cover in 1-ha surrounding nest site	X	X
LandCC	Forest canopy cover in 314-ha surrounding nest site	X	
tph_large	Density of large trees (all species; $\geq$50 cm) in 1-ha surrounding nest site	X	X
IJI	Interspersion–juxtaposition index of LowCC PIPO[d] and HighCC PIPO patches in 314-ha surrounding nest site	X	X

[a] SNOTEL = Snowpack Telemetry; United States Department of Agriculture Natural Resources Conservation Service.
[b] NED = National Elevation Dataset; United States Geological Survey.
[c] GNN = Gradient Nearest Neighbor Classified Landsat Imagery.
[d] PIPO = Ponderosa pine.

Landscape Ecology Mapping, Modeling, and Analysis group (LEMMA 2009) and the National Elevation Dataset (NED; US Geological Survey 2009, Gesch et al. 2002) to derive habitat variables at 2 scales: 1 ha and 314 ha (Table 1). We derived elevation, slope, and aspect from the NED. We cosine-transformed aspect, which may be related to thermal effect on nest survival (e.g., Saab et al. 2004) and nest-site location (Buchanan et al. 2003), to represent south–north orientation at nest sites ($N = 1$, $S = -1$). We used ArcGIS 9.3 (Environmental Research Systems Institute 2004) to extract and co-register data in a common resolution (30 m) and projection.

We smoothed variables derived at the 1-ha scale (i.e., neighborhood averages) to minimize classification and registration errors associated with the intrinsic resolution (30 m) of the GNN data (Lillesand and Kiefer 2000). Thus, we derived 1-ha variables as the mean associated with a 3 × 3-pixel moving window applied to each GNN-classified data layer representing a habitat variable of interest, which resulted in data layers where pixel values represented the average of approximately 1 ha (0.8 ha). We extracted variables at the 314-ha scale, which corresponds with the home range size of several woodpecker species (Garrett et al. 1996, Saab et al. 2004, Dudley and Saab 2007), from GNN-classified data in the same manner as 1-ha variables using a circular moving window with a 1-km radius. We overlaid nest-site coordinates on each of the derived data layers to extract values associated with nest sites.

At the 1-ha scale, we derived slope, cosine of aspect, percent forest canopy cover, quadratic mean diameter (QMD) of all trees $\geq$15 cm dbh, and density (trees/ha) of large-diameter trees (all species $\geq$50 cm dbh) from GNN-classified layers. At the 314-ha scale we derived percent forest canopy cover and the interspersion–juxtaposition index (IJI) for the following types of habitat patches: 1) pure or mixed ponderosa pine with $<$40% canopy cover, 2) pure or mixed ponderosa pine with $\geq$40% canopy cover, and 3) all other forest types. We defined habitat patches as contiguous pixels of the same vegetation type and canopy cover class and subsequently imposed a minimum mapping unit of 1 ha by proportionally filling patches $<$1 ha with surrounding patches.

The IJI is a relative index that represents patch interspersion and adjacency as a percentage of the maximum possible given the total number of patch types (Fig. 2; McGarigal and Marks 1985). The IJI is independent of the size or number of patches and has good universality across landscapes (Cushman et al. 2008). The IJI of low- and high-canopy ponderosa pine patches may be related to both predation effects and foraging opportunity (e.g., Wightman et al. 2010).

We used data from climate monitoring stations in each study region (Taylor Butte and Three Creeks Snowpack Telemetry Stations; USDA Natural Resources Conservation Service 2009) to derive 2 weather variables: 1) cumulative annual precipitation on the date that each nest fate was determined, and 2) average maximum daily temperature during each nest interval (interval between nest initiation or first observation date and the date nest fate was determined; Table 1). Temperature and precipitation have been reported to influence nest survival for several bird species (Conway and Martin 2000, Newlon and Saab 2011, Saab et al. 2011).

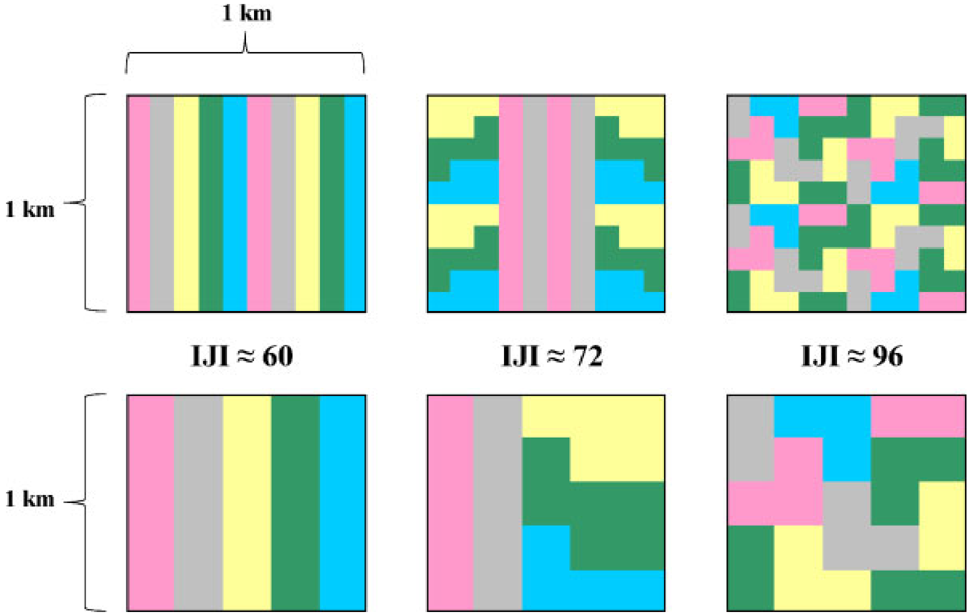

Figure 2. Examples of interspersion–juxtaposition index (IJI) values for hypothetical 1-km^2 landscapes composed of 5 patch types. Higher values of IJI indicate greater dispersion and juxtaposition of patches throughout the landscape.

Habitat Suitability Models

We used a partitioned Mahalanobis distance (D^2k) model (Rotenberry et al. 2006) to estimate and map nest-site habitat suitability. Mahalanobis distances (D^2) are the squared, standardized distances of multivariate observations (e.g., habitat variables at a nest location) from the multivariate mean of all observations (i.e., niche) and can be rescaled to produce a habitat similarity index (HSI), analogous to a habitat suitability index, that ranges from 0 to 1 (Clark et al. 1993, Rotenberry et al. 2006). Because Mahalanobis distance models use presence-only data and are easily adapted to produce maps of suitable habitat (Podruzny et al. 2002, Rotenberry et al. 2006, Barrows et al. 2008, Preston et al. 2008), they are an attractive approach for identifying suitable habitat to guide resource management.

Partitioned Mahalanobis distance models subset niche variation (using partitions; *k*) to better represent limitation of an organism's distribution (see Duncan and Dunn 2001, Rotenberry et al. 2006). We used an approach for determining the number of partitions (*k*), outlined by Preston et al. (2008), that examines the median HSI resulting from each possible *k*-partitions model and selecting the best performing model.

We considered 3 categories of candidate models for habitat suitability: 1) abiotic-only (slope, elevation, cosine of aspect), 2) biotic-only (canopy cover, IJI, large tree density, QMD), and 3) combinations of abiotic and biotic covariates (see Table 2). We constrained all combination models to include slope and IJI; slope has been implicated as an abiotic influence on white-headed woodpecker nest-site selection in Washington (Buchanan et al. 2003) and IJI was an important landscape feature for nest sites in burned forests of central Oregon (Wightman et al. 2010).

We assessed each covariate combination for performance at each *k*-partitions and retained the best performing model as

Table 2. Candidate models and selected partitions we considered for habitat suitability of nesting white-headed woodpeckers in unburned forests of central Oregon, 1997–2004.

Variable	Abiotic	Biotic	Combination									
slope	X		X	X	X	X	X	X	X	X	X	X
cosasp	X			X			X	X				X
elev	X		X		X	X		X		X	X	
LocCC		X	X		X		X	X				
LandCC		X	X		X	X			X	X		X
IJI		X	X	X	X	X	X	X	X	X	X	X
qmd		X	X	X	X		X	X	X	X	X	
tph_large		X	X	X			X	X		X	X	
Full model partitions	3	5	7	5	6	4	6	7	4	6	5	4
Selected partition (*k*)	1	5	4	5	3	4	6	3	2	3	2	4
Median HSI[a]	0.55	0.60	0.63	0.58	0.63	0.64	0.59	0.57	0.62	0.67	0.62	0.58
C-V median HSI[b]	0.55	0.59	0.62	0.57	0.62	0.55	0.58	0.56	0.61	0.66	0.62	0.52

See Table 1 for acronym definitions. Shaded column indicates selected model.

[a] All nest sites.

[b] Cross-validated habitat suitability index (HSI): iterative subsets of $n - 1$ nest sites.

indicated by the predicted median HSI value for nest locations (Preston et al. 2008). We then used a leave-one-out cross-validation (Browning et al. 2005) to confirm model performance by comparing the median cross-validated and predicted HSIs (Table 2). We expected cross-validated median HSI values for models with considerable outlier influence to differ from the predicted median HSI (all nest locations). Finally, we used the selected D^2k model to create habitat suitability maps for our study areas and assessed the predictive ability of these maps by determining and interpreting maximum predictive gain (Browning et al. 2005).

Nest Survival Analysis

We used logistic-exposure regression to estimate daily nest-survival rate (DSR; probability that a nest will survive one day; Dinsmore et al. 2002, Shaffer 2004). We developed 19 a priori candidate models for DSR in 5 categories: 1) null (constant survival), 2) abiotic (weather and year), 3) field-plot covariates, 4) remotely sensed covariates (1-ha and 314-ha scale), and 5) a combination of abiotic and biotic covariates (both field plot and remotely sensed; Table 3). After confirming an adequate fit (Hosmer and Lemeshow 2000) for the most highly parameterized model, we used information-theoretic model selection to rank candidate models by small-sample corrected Akaike's Information Criteria (AIC_c) and associated Akaike weights (Burnham and Anderson 2002). We evaluated the top competing model(s) within 4 AIC_c units of the highest ranked model. We used model-averaged coefficient estimates if >1 top model occurred, and evaluated coefficients of the top model(s) using 95% confidence intervals. We assessed estimated DSR from the top model(s) by varying covariates of interest while holding the remaining covariates at their mean observed values.

Reported nesting period for white-headed woodpeckers ranges from 40 (Garrett et al. 1996, Wightman et al. 2010) to 45 (Dudley and Saab 2003) days. We calculated nest success (probability that a nest will be successful) by raising the mean daily nest-survival rate of the constant survival model (intercept-only) by a nesting period of 40 days (i.e., DSR^{40}). Nest success for the constant survival model is analogous to a Mayfield estimate of nest success (Mayfield 1975) and allows for comparison with other published nest success values. We used the delta method to approximate 95% confidence limits for nest success (Powell 2007). We also evaluated nest success from the top-ranked model(s) by varying each model covariate while holding the remaining covariates at their mean observed value and plotting the resulting nest success values.

RESULTS

Habitat Suitability

Based on 382 nests monitored from 1997 to 2004, we selected the habitat suitability model containing slope, elevation, 314-ha scale canopy cover, IJI, QMD, and large-tree density covariates, at a partition of $k = 3$, as the best performing model for the study areas (Table 2). The median HSI for nest sites was 0.67 and the cross-validated median HSI was 0.66, suggesting that few outlier observations existed among the multivariate combinations at nest sites used to build the model. Covariates describing landscape canopy closure, QMD, and density of large trees were similar for nest locations and regional landscapes, whereas

Table 3. Candidate models and supporting hypotheses comparing random, biotic, or abiotic influences on nest survival of white-headed woodpeckers in unburned forests of central Oregon, 1997–2004.

Category and model(s)	Alternative hypotheses
Null	Nest survival is random; likely due to random predation events
Intercept-only	
Abiotic and temporal	More variation exists in abiotic factors than habitat characteristics at nest sites; thus, abiotic factors may have the stronger influence on nest survival
tavg + year	
precip + year	
Field plot-scale (nest tree/snag and immediate vicinity)	Nest tree characteristics have the strongest influence on nest survival
dbh + cav_hgt	
dbh + tph_large_fc	Factors influencing nest selection will be consistent with those influencing nest survival. Physical features may provide greater protection from predators
tph_snags + tph_trees + shrubcov	
tph_large_fc + shrubcov	
dbh + tph_snags + tph_trees + cav_hgt + shrubcov	
Remote sensed (1-ha and 314-ha scales)	Factors associated with nest occupancy will be similar to those associated with nest survival. A mosaic of high- and low-canopy cover of ponderosa pine will provide nesting and diverse foraging options
cosasp + LocCC + qmd + IJI	
cosasp + LocCC + tph_large + IJI	
Combination (abiotic, field plot, and remote sensed)	Abiotic and biotic factors (higher temperatures, lower precipitation, east-facing nest sites, large tree densities and diameters, and a landscape mosaic of high- and low-canopy cover of ponderosa pine) may increase nest survival because of good environmental conditions, protection from predators, and diverse nesting and foraging options
tavg + tph_large_fc	
tavg + cosasp + qmd + IJI	
tavg + cosasp + tph_large + IJI	
precip + cosasp + qmd + IJI	
precip + cosasp + tph_large + IJI	
cosasp + tph_large_fc + IJI	A combination of local and landscape characteristics provide the best conditions for nesting trees, protection from predators, and diverse foraging opportunities for high nest survival
cosasp + cav_hgt + dbh + LocCC + qmd + IJI + shrubcov	
tph_snags + tph_trees + LocCC + qmd + IJI + shrubcov	
tph_snags + tph_trees + LocCC + tph_large + shrubcov + IJI	

See Table 1 for acronym definitions.

lower slopes, lower elevations, and a higher IJI of ponderosa pine forest patches were found at nest locations compared to regional landscapes (see Table 4). However, Mahalanobis distance models use covariate combinations to characterize niche (habitat suitability), and extrication of individual covariates for interpretation is not appropriate (Griffin et al. 2010). Furthermore, samples of covariate values from presence locations and the landscape are not valid for statistical comparison related to habitat suitability.

Habitat suitability maps (predicted HSI values; Figs. 3 and 4) showed 30% of the study area (both regions) had an HSI $\geq$ median HSI of the selected model (nest-site median HSI $= 0.67$; study area [both regions] median HSI $= 0.21$). The maximum predictive gain (HSI value where the maximum number of nest locations [73%] occurred on the smallest proportion of the landscape [39%]) was 0.36 (Fig. 5). Maximum predictive gain may be used as an initial guide for coarse-scale identification of areas to be considered for habitat management activities. Areas with HSI values above maximum predictive gain are generally good habitat; areas with lower values might benefit from management actions.

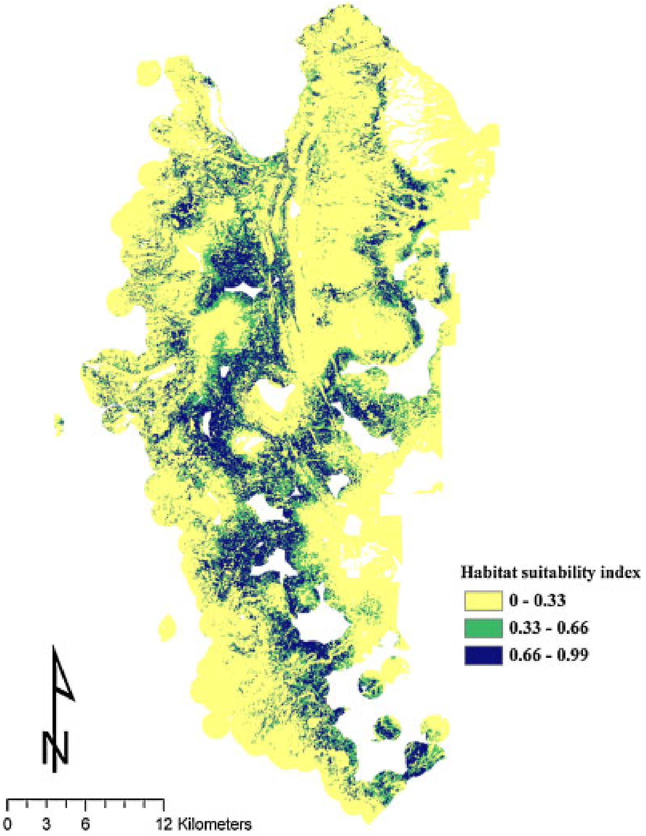

Figure 3. Habitat suitability map for nesting white-headed woodpeckers on Sisters Ranger District, Deschutes National Forest, central Oregon, 1997–2004.

Nest Survival

We analyzed 382 nests (effective sample size $= 6{,}821$; number of days nests survived plus number of failures) for daily nest-survival rate. We confirmed an adequate fit of our most highly parameterized model ($\hat{C} = 8.15$, $P = 0.42$). The top-ranked model included average maximum daily temperature and density of large-diameter trees (field-collected). This model accounted for >99% of the Akaike weights and had >100 times more support for describing nest survival than did the next competing model (Table 5). Both average maximum daily temperature (over nesting interval) and density of large trees (>50 cm dbh) had positive relationships with DSR, with temperature having the greater effect (Table 6).

Daily nest-survival rate for the top model at covariate means (large-tree-density and maximum-daily-temperature) was 0.977 (SE $= 0.002$). Plots of DSR over each covariate, with the remaining covariate held constant at its mean value, show the substantial effect of average maximum daily temperature at lower values (e.g., <20° C; Fig. 6a) and the lesser, linear effect of large tree density (Fig. 6b). Over the range of observed maximum daily temperatures, with large tree density held constant at its mean value, DSR ranged from 0.870 (SE $= 0.026$) to 0.996 (SE $= 0.001$) at 9.5° C and 27° C, respectively. Over the range of observed large tree densities, with maximum daily temperature held constant at its mean value, DSR ranged from 0.969 (SE $= 0.004$) to 0.992 (SE $= 0.003$) at 0.5 trees/ha and 69 trees/ha, respectively. Estimated nest success ranged from 0.002 (SE $= 0.003$) to 0.853 (SE $= 0.035$) over the range of observed maximum daily temperatures (large tree density held constant; Fig. 6c) and from 0.294 (SE $= 0.044$) to 0.727 (SE $= 0.083$) over the range of observed large tree densities (maximum daily temperature held constant; Fig. 6d).

Table 4. Characteristics of white-headed woodpecker nest sites and surrounding landscape associated with partitioned Mahalanobis model of nest-site habitat suitability in unburned forests on the Deschutes and Fremont-Winema national forests, Oregon, 1997–2004.

			Nests ($n = 382$)		Landscape ($n = 5{,}643{,}562$)	
Variable	Scale	Description	$\bar{x}$	SD	$\bar{x}$	SD
slope	1 ha	Slope (% slope)	7.04	7.26	11.39	12.34
elev	1 ha	Elevation (m)	1,123	244.32	1,476	265.83
LandCC	314 ha	Mean canopy cover (%)	42.97	6.78	42.27	14.87
IJI	314 ha	Interspersion–juxtaposition index	60.04	27.62	54.78	29.15
qmd	1 ha	Quadratic mean diameter (cm)	27.58	7.07	28.37	9.47
tph_large	1 ha	Tree density (trees >50 cm dbh/ha)	13.99	10.5	16.02	16.11

See Table 1 for acronym definitions.

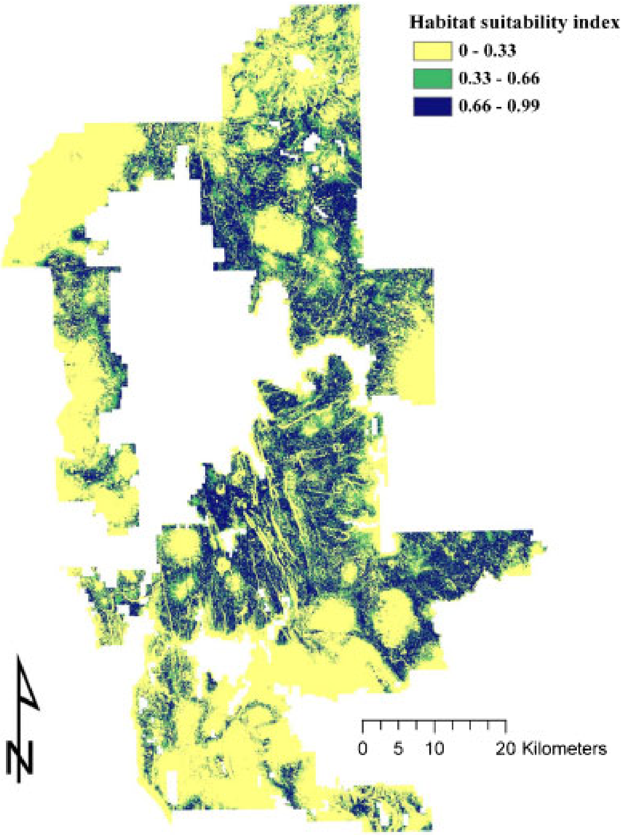

Figure 4. Habitat suitability map for white-headed woodpeckers on Chemult and Chiloquin ranger districts, Fremont-Winema National Forest, central Oregon, 1997–2004.

The intercept-only model (constant DSR) was not included in the top performing model set. However, we used the intercept-only model to estimate nest success for comparing with other studies that report this value. Daily nest-survival rate for the intercept-only model was 0.977 (SE = 0.002). We estimated nest success (intercept-only model) at 0.39 (95% CI: 0.33–0.45).

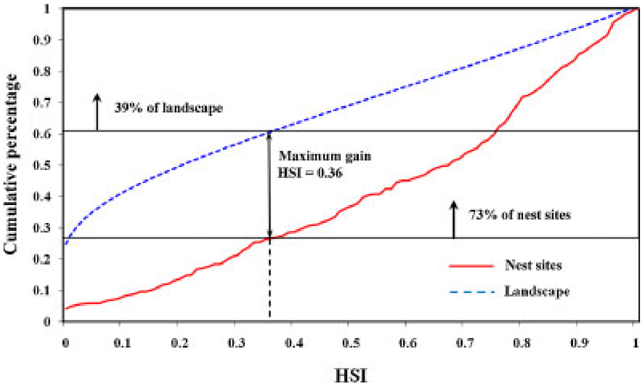

Figure 5. Maximum predictive gain for white-headed woodpecker nest-site habitat suitability in the Sisters, Chemult, and Chiloquin ranger districts, central Oregon, 1997–2004. Maximum separation (difference) between landscape (pixels) and nest-site curves occurs at a habitat suitability index (HSI) value of 0.36.

DISCUSSION

Nest Survival

Daily nest-survival rate was substantially influenced by the average maximum daily temperature during the nesting observation period (Fig. 6a). The positive relationship between temperature and nest survival might be related to increased activity of insects and subsequent foraging opportunities (cf. Neal et al. 1993, Newlon and Saab 2011, Saab et al. 2011) or within-cavity microclimate (cf. Conway and Martin 2000). During the breeding season white-headed woodpeckers rely on surface-bark inhabiting insects that likely become more available as the weather warms (cf. Kozma 2009). Daily nest-survival rate was also positively related to density of large-diameter trees surrounding the nest site (field-collected covariate; Fig. 6b). Although the method of collection differed (field-collected vs. remotely sensed), large tree density was the only covariate common to both nest survival and nesting habitat suitability models. Nearby large-diameter trees may present increased foraging opportunities (e.g., Jones and Hunt 1996) and consequently increase foraging efficiency and parental attentiveness. Large-diameter pine trees may also provide greater numbers of cones and seeds (Burns and Honkala 1990, Keyes and Maguire 2007). Large-cone pine seeds are an important winter food for white-headed woodpeckers that may influence breeding condition of birds and consequently nest survival (Ligon 1973, Martin 1987, Garrett et al. 1996). Furthermore, a higher density of large-diameter trees may reduce the search efficiency of predators (Martin and Roper 1988, Li and Martin 1991). Li and Martin (1991) found higher nest success for cavity-nesting species at sites with higher tree and snag density in mixed aspen-conifer habitat in central Arizona. However, our study area was primarily conifer forest and the effect of tree density on predation may differ. Common nest predators in our study area (yellow-pine chipmunk [*Neotamias amoenus*] and golden-mantled ground squirrel [*Spermophilus lateralis*]) are typically associated with live conifers (Wightman et al. 2010). A swamping effect (cf. Ims 1990) could occur for these nest predators searching for occupied cavities in conifer forests, where large trees and nest cavities are abundant relative to the surrounding forest.

Our constant (intercept-only) DSR of 0.976 was low compared to (constant DSR) values reported for other cavity-nesting birds (range 0.980–0.998; Saab et al. 2007, 2011) and our estimated nest success (0.39) was much lower than that reported for white-headed woodpeckers in nearby burned forests of central Oregon (0.76; Wightman et al. 2010) and unburned managed forest in central Washington (0.84; Kozma 2009). Our estimated nest success was also lower than nest success values generally reported for primary cavity-nesters (Martin and Li 1992).

Nests in unburned forests might be more vulnerable to predation compared with burned forests, where small mammalian predators are likely reduced after recent wildfire (Saab and Vierling 2001; Saab et al. 2007, 2011). Alternatively, nests in unburned forest may experience lower ambient

Table 5. Model selection for nest survival of white-headed woodpeckers in ponderosa pine forests of central Oregon, 1997–2004.[a]

Model	-2 logLik[b]	K[c]	ΔAIC_c[d]	w[e]
tavg + tph_large_fc	766	4	0.0	0.996
tavg + year	778	4	11.7	0.003
tavg + cosasp + qmd + IJI	777	6	14.9	0.001
tavg + cosasp + tph_large + IJI	778	6	15.3	0
tph_snags + tph_trees + LocCC + tph_large + shrubcov + IJI	818	8	59.7	0
tph_large_fc + shrubcov	826	4	59.9	0
tph_snags + tph_trees + LocCC + qmd + IJI + shrubcov	818	8	60.2	0
tph_snags + tph_trees + shrubcov	824	5	60.2	0
cosasp + cav_hgt + dbh + LocCC + qmd + IJI + shrubcov	820	9	64.0	0
dbh + tph_snags + tph_trees + cav_hgt + shrubcov	824	7	64.1	0
Constant survival (intercept-only)	836	2	65.9	0
precip + year	832	4	66.3	0
dbh + tph_large_fc	835	4	68.5	0
dbh + cav_hgt	836	4	69.5	0
cosasp + LocCC + tph_large + IJI	832	6	70.0	0
cosasp + LocCC + qmd + IJI	832	6	70.1	0
cosasp + tph_large_fc + IJI	835	5	70.4	0
precip + cosasp + qmd + IJI	836	6	73.3	0
precip + cosasp + tph_large + IJI	836	6	73.5	0

[a] See Table 1 for acronym definitions.
[b] 2 logLik = −2 (log likelihood).
[c] K = number of estimated parameters.
[d] ΔAIC_c = Akaike Information Criterion relative to highest-ranked model.
[e] w = Akaikeweight.

temperatures which may, in turn, affect incubation behavior and reproductive effort (Conway and Martin 2000). Regardless of the mechanism, considerable differences of nest survival in burned (high nest survival) and unburned (low nest survival) forests suggest source-sink dynamics (Connor et al. 2000, Saab and Vierling 2001, Runge et al. 2006, Nappi and Drapeau 2009, Saab et al. 2011). Adult and juvenile survival data are not available for white-headed woodpecker but are needed to confirm source-sink processes. Differences of nest success in burned and unburned forests, however, have implications for regional population dynamics and habitat management, as well as finer scale nest-site habitat management (e.g., open-canopied forests adjacent to large-diameter snags and trees in clumps for retention of nesting microhabitat and to increase foraging efficiency, respectively). Ultimately, white-headed woodpeckers may require dynamic landscapes of both burned and unburned habitat for long-term persistence of their populations (cf. Nappi and Drapeau 2009), which may have considerable implications for conservation planning and forest management.

Nesting Habitat Suitability

White-headed woodpeckers typically nest in open-canopied forests with mature, cone-producing ponderosa pine trees (Garrett et al. 1996) and our model confirms these characteristics as important for white-headed woodpecker nesting habitat in central Oregon. Our habitat suitability model for unburned forest identified habitat characterized by patches of open and closed canopied ponderosa pine forests, lower slopes, and lower elevations, compared with regional landscapes. A mosaic of crown closures, as measured by IJI, across the ponderosa pine landscape may benefit white-headed woodpeckers by providing more open habitats as potential nesting areas with nearby closed-canopied forests providing year-round foraging habitat with cone-producing trees and insects. The IJI of low- and high-severity burned patches was an important covariate in the habitat suitability model developed for nesting white-headed woodpeckers in burned forests of central Oregon (Wightman et al. 2010). Wightman et al. (2010) suggested that the mosaic of high- and low-severity burned patches of ponderosa pine facilitated placement of nests in large-diameter burned snags near low-severity burned or unburned patches containing live, cone-producing trees for foraging (both seeds and insects). In unburned forests, white-headed woodpeckers prefer nest sites with low-canopy cover (Raphael and White 1984, Garrett et al. 1996). Presence of nearby ponderosa pine with high-canopy cover may be equally important for year-round foraging, particularly outside of the breeding season (Garrett

Table 6. Estimated coefficients, standard errors, and 95% confidence intervals for the top performing nest survival model for white-headed woodpeckers in ponderosa pine forests of central Oregon, 1997–2004. Estimates are considered significant if the 95% confidence interval does not overlap zero.[a]

Model	w[b]	Covariate	Estimate	SE	95% lower CL	95% upper CL
tavg + tph_large_fc	0.996	Intercept	−0.516	0.524	−1.543	0.511
		tavg	0.212	0.027	0.159	0.265
		tph_large_fc	0.020	0.006	0.007	0.032

[a] See Table 1 for acronym definitions.
[b] w = Akaikeweight.

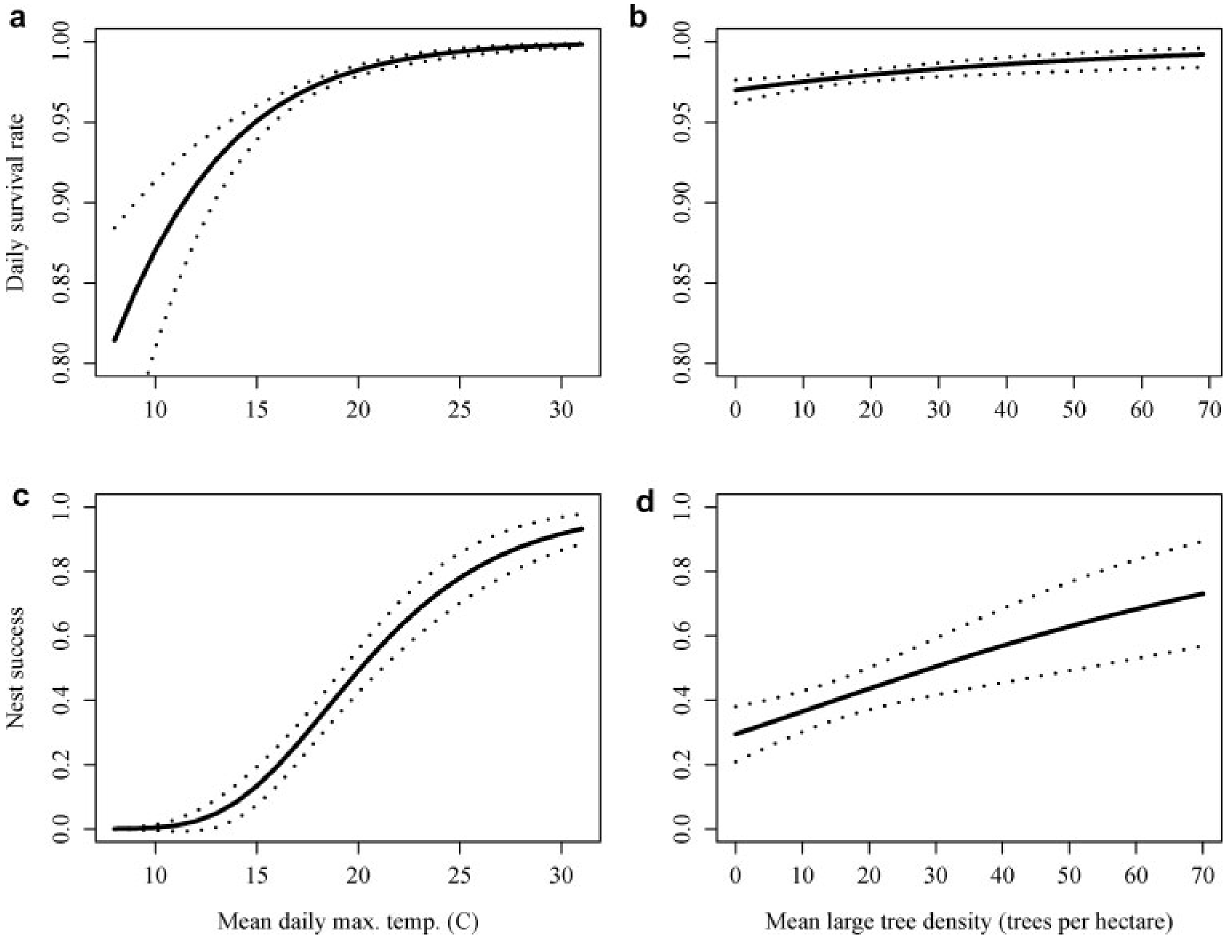

Figure 6. White-headed woodpecker daily survival rate and nest success by: average maximum temperature during nest interval, with density of large trees in nest vicinity held constant (a and c), and density of large trees in nest vicinity, with average maximum temperature held constant (b and d), central Oregon, 1997–2004.

et al. 1996). The IJI of ponderosa pine patches with high- and low-canopy cover reported in our selected model may reflect a hierarchical, multi-scale process of selecting sites with adequate nesting substrate and nearby year-round foraging resources (Morris 1987, Orians and Wittenberger 1991, Orrock et al. 2000). White-headed woodpeckers are residents of ponderosa pine forests and may benefit from selecting nest sites near habitats used during other seasons of the year. In particular, reliable cone seed availability during winter may improve adult condition and subsequent nesting success (Martin 1987).

Large tree density and QMD were present in each of the top performing models (Table 2) and exclusion of these covariates led to a substantial departure of the median cross-validated HSI value from the inclusive model HSI, supporting their inclusion in the model. However, evaluating the relative importance of these individual covariates is difficult because multivariate niche combinations are complex and classification accuracy for most GNN-derived covariates was <80% (QMD was approx. 50%; LEMMA 2009). This highlights a limitation of classified satellite imagery in niche models and that these data should be used at an appropriate scale (cf. Russell et al. 2007). Furthermore, because white-headed woodpeckers appear to select habitat at multiple spatial scales, we may have omitted habitat features unique to nesting habitat but rare on the landscape (e.g., mature ponderosa pine trees). However, because of limitations in remotely sensed data, such features are currently not practical for region-wide modeling.

Mahalanobis distance models are best suited for the region where they were developed (Knick and Rotenberry 1998). Partitioning may improve portability to other regions (Preston et al. 2008), but similar ranges of habitat conditions need to occur in both the model development and target areas. Furthermore, observations (e.g., habitat covariates at nest sites) used to construct the model should represent the range possible in the theoretical niche (Knick and Rotenberry 1998, Rotenberry et al. 2006), and these may vary over space or time (e.g., after large-scale disturbance). Therefore, caution should be exercised when using Mahalanobis distance models outside their region of origin.

Despite the limitations of niche modeling and remotely sensed data sources, our selected habitat suitability model predicted all nest locations and iterative subsets of nest locations (i.e., leave-one-out cross-validation) equally well. At the appropriate scale (>1 ha), the resulting habitat suitability map could be used to stratify survey areas for determining habitat occupancy of white-headed woodpeckers or to identify areas for woodpecker habitat improvement and for ponderosa pine forest restoration.

MANAGEMENT IMPLICATIONS

Our habitat suitability model identifies important habitat covariate combinations, but not individual features, for white-headed woodpeckers. Consequently, the model is most useful as a remote sensing-based tool for targeting management or surveying activities where the probability threshold and resulting search area can be adjusted according to management objectives. If a management goal is habitat restoration, the maximum predictive gain HSI (0.36; Fig. 5) may be used as an initial threshold (i.e., Figs. 3 and 4) and areas with lower values considered for treatment. If a management goal is to reserve high quality habitat, a higher threshold (0.5–0.7) may be used and areas at or above the threshold considered for reserves.

If managers have access to nest location data, constructing a partitioned Mahalanobis distance model, specific to a region of interest, is straightforward (see Supplementary Material Appendix B, available online at http://onlinelibrary.wiley.com). If nest location data are lacking, a model developed for a nearby region may be useful with a conservative approach to the results. Consequently, land managers could apply our model to regions within dry ponderosa pine and mixed-conifer forests of the Inland Northwest to identify habitat suitability, but the predictive ability is expected to be lower in areas outside the model origin. Model validation and refinement using nest locations from both ours and other study areas are necessary to improve the utility of our model.

ACKNOWLEDGMENTS

Funding was provided by United States Forest Service Pacific Northwest Region and the Rocky Mountain Research Station, National Fire Plan. Nest-site data collection was supported by United States Forest Service Pacific Northwest Region, Oregon Department of Fish and Wildlife, Audubon Society, M. Stern of The Nature Conservancy, and C. Carey of Oregon Department of Fish and Wildlife. J. Ohmann provided guidance on using GNN layers for modeling. K. Mellen-McLean, A. Markus, and B. Bresson were the impetus for our work, provided input on the covariates used in the modeling, and helped with data interpretation. We thank J. Kozma and K. Preston for thoughtful reviews.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Barrows, C. W., K. L. Preston, J. T. Rotenberry, and M. F. Allen. 2008. Using occurrence records to model historic distributions and estimate habitat losses for two psammophilic lizards. Biological Conservation 141:1885–1893.

Bartel, R. A., and J. O. Sexton. 2009. Monitoring habitat dynamics for rare and endangered species using satellite images and niche-based models. Ecography 32:888–896.

Browning, D. M., S. J. Beaupre, and L. Duncan. 2005. Using partitioned Mahalanobis $D^2(k)$ to formulate a GIS-based model of timber rattlesnake hibernacula. Journal of Wildlife Management 69:33–44.

Buchanan, J. B., R. E. Rogers, D. J. Pierce, and J. E. Jacobson. 2003. Nest-site habitat use by white-headed woodpeckers in the eastern Cascade mountains, Washington. Northwestern Naturalist 84:119–128.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Agricultural Handbook 654. USDA Forest Service, Madison, Wisconsin, USA.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519–526.

Connor, E. F., A. C. Courtney, and J. M. Yoder. 2000. Individuals-area relationships: the relationship between animal population density and area. Ecology 8:734–748.

Conway, C. J., and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670–685.

Cushman, S. A., K. McGarigal, and M. C. Neel. 2008. Parsimony in landscape metrics: strength, universality, and consistency. Ecological Indicators 8:691–703.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Dudley, J., and V. Saab. 2003. A field protocol to monitor cavity-nesting birds. USDA Forest Service. Report RMRS RP-44, Fort Collins, Colorado, USA.

Dudley, J. G., and V. A. Saab. 2007. Home range size of black-backed woodpeckers in burned forests of southwestern Idaho. Western North American Naturalist 67:593–600.

Duncan, L., and J. E. Dunn. 2001. Partitioned Mahalanobis D^2 to improve GIS classification. SAS User Group International 26, SAS Institute, Cary, North Carolina. Pages 198–226.

Environmental Research Systems Institute [ESRI]. 2004. ArcGIS 9: using ArcMap. ESRI, Redlands, California, USA.

Garrett, K. L., M. G. Raphael, and R. D. Dixon. 1996. White-headed woodpecker (*Picoides albolarvatus*). Birds of North America. Cornell Lab of Ornithology. Issue 252. <http://bna.birds.cornell.edu/bna/species/252/articles/introduction>. Accessed 13 May 2009.

Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck, and D. Tyler. 2002. The national elevation dataset. Photogrammetric Engineering and Remote Sensing 68:5–11.

Griffin, S. C., M. L. Taper, R. Hoffman, and L. S. Mills. 2010. Ranking Mahalanobis distance models for predictions of occupancy from presence-only data. Journal of Wildlife Management 74:1112–1121.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. Wiley and Sons, New York, New York, USA.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. American Naturalist 136:485–498.

Jones, C. M., and H. E. Hunt. 1996. Foraging habitat of the red-cockaded woodpecker on the D'Arbonne National Wildlife Refuge, Louisiana. Journal of Field Ornithology 67:511–518.

Keyes, C. R., and D. A. Maguire. 2007. Seed rain of ponderosa pine beneath partial overstories. New Forests 34:107–114.

Knick, S. T., and J. T. Rotenberry. 1998. Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. Journal of Agricultural, Biological, and Environmental Statistics 3:311–322.

Kozma, J. M. 2009. Nest-site attributes and reproductive success of white-headed and hairy woodpeckers along the east-slope Cascades of Washington state. Pages 52–61 *in* Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics. Partners in Flight, 13–16 February 2008, McAllen, Texas, USA

LEMMA (Landscape Ecology Mapping Modeling and Analysis). 2009. IMAP—Interagency Mapping and Assessment Project. <http://www.fsl.orst.edu/lemma/main.php?project=imap&id=home>. Accessed 16 May 2009.

Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

Ligon, J. D. 1973. Foraging behavior of the white-headed woodpecker in Idaho. Auk 90:862–869.

Lillesand, T. M., and R. W. Kiefer. 2000. Remote sensing and image analysis. Fourth edition. John Wiley and Sons, New York, New York, USA.

Lindstrand, L., and M. Humes. 2009. White-headed woodpecker occurrences in Sun Pass State Forest, south-central Oregon. Northwestern Naturalist 90:212–216.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18:453–487.

Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

Martin, T. E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73:579–592.

Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51–97.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 7:456–466.

McGarigal, K., and B. J. Marks. 1985. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service, GTR PNW-351, Portland, Oregon, USA.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362–369.

Nappi, A., and P. Drapeau. 2009. Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? Biological Conservation 142:1381–1391.

Neal, J. C., D. A. James, W. G. Montague, and J. E. Johnson. 1993. Effects of weather and helpers on survival of nestling red-cockaded woodpeckers. Wilson Bulletin 105:666–673.

Newlon, K. R., and V. A. Saab. 2011. Nest-site selection and nest survival of Lewis's woodpecker in aspen riparian woodlands. Condor 113:183–193.

Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. Canadian Journal of Forest Research 32:725–741.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist 137:S29–S49.

Orrock, J. L., J. F. Pagels, W. J. McShea, and E. K. Harper. 2000. Predicting presence and abundance of small mammal species: the effect of scale and resolution. Ecological Applications 10:1356–1366.

Podruzny, S. R., S. Cherry, C. C. Schwartz, and L. A. Landenburger. 2002. Grizzly bear denning and potential conflict areas in the greater Yellowstone ecosystem. Ursus 13:19–28.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:949–954.

Preston, K. L., J. T. Rotenberry, R. A. Redak, and M. F. Allen. 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. Global Change Biology 14:2501–2515.

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt, and T. C. Will. 2004. Partners in Flight North American Landbird Conservation Plan. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

Rotenberry, J. T., K. L. Preston, and S. T. Knick. 2006. GIS-based niche modeling for mapping species' habitat. Ecology 87:1458–1464.

Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. American Naturalist 167:925–938.

Russell, R. E., V. A. Saab, and J. G. Dudley. 2007. Habitat-suitability models for cavity-nesting birds in a postfire landscape. Journal of Wildlife Management 71:2600–2611.

Saab, V. A., J. Dudley, and W. L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106:20–36.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109:97–108.

Saab, V. A., R. E. Russell, J. J. Rotella, and J. Dudley. 2011. Modeling nest survival of cavity-nesting birds in relation to post-fire salvage logging. Journal of Wildlife Management 75 (in press).

Saab, V. A., and K. T. Vierling. 2001. Reproductive success of Lewis's woodpecker in burned pine and cottonwood riparian forests. Condor 103:491–501.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience 54:661–676.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

US Geological Survey. The National Map Seamless Server. <http://seamless.usgs.gov/index.php>. Accessed 1 Jun 2009.

USDA Natural Resources Conservation Service. National Water and Climate Center, SNOTEL Data collection network. <http://www.wcc.nrcs.usda.gov/snow>. Accessed 8 Aug 2009.

Vierling, K. T., L. A. Vierling, W. A. Gould, S. Martinuzzi, and R. M. Clawges. 2008. Lidar: shedding new light on habitat characterization and modeling. Frontiers in Ecology and the Environment 6:90–98.

Wiebe, K. L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk 118:412–421.

Wightman, C. S., V. A. Saab, C. Forristal, K. Mellen-McLean, and A. Markus. 2010. White-headed woodpecker nesting ecology after wildfire. Journal of Wildlife Management 74:1098–1106.

Associate Editor: David King.