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White-headed woodpecker nesting habitat at multiple spatial scales: Are habitat preferences adaptive?

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ABSTRACT

Ecological theory predicts that animals will select habitats for breeding that confer an adaptive advantage through increased reproductive success. We therefore expect to see congruence between habitat preferences and measures of fitness. We studied abundance, nest site selection, and nest survival in white-headed woodpeckers (*Picoides albolarvatus*) in four forest types along an elevational gradient in the southern Sierra Nevada, California. Our primary objective was to ascertain what habitat features white-headed woodpeckers were selecting for nesting and at what scale, and whether those choices translated into increased reproductive success. We examined sets of models that included abiotic factors and habitat at three spatial scales: nest site (0.04 ha), local (~1 ha), and home range (~125 ha). White-headed woodpeckers were more abundant at higher elevations, with low abundance in low-elevation ponderosa pine forest, moderate abundance in mid-elevation mixed conifer forest, and reached their highest abundance in true fir habitat before becoming rare in high-elevation lodgepole pine forest. They both selected for and nested more successfully at higher elevations in true fir forest. White-headed woodpecker nesting ecology in the Sierra Nevada demonstrated a mixed pattern of congruence between characteristics important to nest habitat selection and nest survival. We found congruence for abiotic and home range scale models (agreement between preferences and nest survival), indicating adaptive selection. At the landscape scale, White-headed woodpeckers selected closed-canopy conifer forests with abundant edges. Habitat preferences at the nest site scale were negatively related to nest survival, suggesting maladaptive habitat selection at this scale. White-headed woodpeckers selected open forest with higher basal area of snags compared to available sites, but nest survival was higher in forest with higher canopy closure and lower basal area of snags. Local scale models were weak and did not help clarify habitat relationships. Our results highlight the importance of considering multiple spatial scales when examining habitat preferences. The primary management considerations for white-headed woodpecker habitat include retention of large, suitable snags and the need to consider forest heterogeneity. The close association with ponderosa pine forests and large-seeded pines found over most of their range did not hold in the Sierra Nevada, where white-headed woodpeckers were most abundant in true fir forests and selected and nested more successfully in true fir forests. Habitat models developed outside the area for which they were developed should be validated before they are applied to other locations.

1. Introduction

Ecological theory predicts that the habitat preferences of animals should be adaptive and that fitness should be higher in preferred habitats (Hildén, 1965; Southwood, 1977; Martin, 1998; Chalfoun and Martin, 2007). Accordingly, animals should choose environments where they are more likely to survive and produce offspring (Hildén, 1965; Martin, 1998; Chalfoun and Martin, 2007). In birds, nest sites provide shelter from the elements and protection from predators and choices related to nest site selection often have fitness consequences (Hildén, 1965; Cody, 1985). Because nest predation is the primary cause of nest failure, typically resulting in the loss of the entire nesting attempt, and is a limiting factor on fitness, we expect birds to favor nest sites that minimize predation risk. As a result, we expect to see congruence between evolved habitat preferences and nest success, however nest site selection is not always positively associated with nest success (Chalfoun and Schmidt, 2012). Nest site preferences can be neutral or negative, where variables important to nest site preferences are not related to

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(neutral congruence) or negatively related to nest success. This might happen, for example, when habitat edges have structural cues indicative of suitable habitat but function as an 'ecological trap' (Gates and Gysel, 1978).

Habitat preferences can encompass multiple biological and abiotic factors that operate across multiple spatial scales (Wiens, 1989; Chalfoun and Martin, 2007; Mayor et al., 2009). Not all scales are equally informative, and the scale of analysis must be matched to the species being studied (Wiens, 1989). Concentrating on a single spatial scale may miss relationships and tradeoffs that occur across scales (Wiens, 1989; Mayor et al., 2009; Chalfoun and Schmidt, 2012). Understanding whether the behavioral choices birds make when selecting habitat are adaptive requires an assessment of their consequences on survival and productivity and, by extension, fitness. Identifying habitat features that influence habitat selection and enhance fitness is critical for effective management (Battin, 2004; Chalfoun and Martin, 2007; Chalfoun and Schmidt, 2012).

White-headed woodpeckers (*Picoides albolarvatus*) are found only in the mountains of western North America, from southern California to south-central British Columbia (Garrett et al., 1996). They are declining in the northern portion of their range but are locally common in California (Garrett et al., 1996). State agencies in Washington, Idaho, and Oregon, and in the province of British Columbia have classified the species into various categories of conservation concern. Declines have been attributed to logging of large-diameter trees and snags, especially pines, and conversion of pine-dominated forests to other forest types (Garrett et al., 1996). Throughout much of its range, the white-headed woodpecker is closely associated with large-seeded pines, especially ponderosa pine (*Pinus ponderosa*), and reaches its greatest abundance where two or more pine species with large seeds occur. The species is considered dependent on pine or mixed pine-fir forests throughout its range in western North America (Garrett et al., 1996).

Recent work has provided information on habitat requirements of white-headed woodpeckers in the Pacific Northwest (Wightman et al., 2010; Hollenbeck et al., 2011; Kozma, 2011, 2012; Latif et al., 2015) but the species is poorly studied in California. Because habitat models developed in other geographic locations and forest types are likely to perform poorly when applied outside of the area for which they were developed (Latif et al., 2015), models specific to California forests are needed. Raphael (1980) stressed the need to study habitat requirements over a variety of forest types to reveal the range of nesting habitats used, the key habitat elements, and the flexibility of bird preferences. Information and results collected across a broader portion of their range will help reveal differences among populations, suggest essential habitat requirements across their range, and help synthesize patterns across study areas and populations (Mayor et al., 2009).

Our primary objective was to assess whether habitat selection was adaptive for white-headed woodpeckers occurring along an elevational gradient in the southern Sierra Nevada, California. In other words, we examined whether factors important to nest site selection were positively associated with those important for nest success. We approached this question by modeling nest habitat selection and daily nest survival at multiple spatial scales and evaluating whether there was congruence between habitat preferences and components of fitness. We examined sets of models that included abiotic factors and habitat features at three spatial scales: the nest site scale, the local scale, and the home range scale. When models for nest site selection and nest survival were associated with the same variables, we concluded that nest site selection was adaptive. Our goal was to identify key habitat elements selected for nesting and to examine whether these features influenced nest survival and at what spatial scales. We also examined patterns of relative abundance in four forest types along the elevational range to test the hypothesis that greater abundance was positively correlated with nesting success (Van Horne, 1983. Finally, we also wished to compare habitat associations found for white-headed woodpeckers in this relatively unstudied portion of their range with those found in other areas.

2. Materials and methods

2.1. Study areas

We studied white-headed woodpeckers in four forest types along an elevational gradient in the High Sierra Ranger District of Sierra National Forest on the western slope of the southern Sierra Nevada, California (Fig. 1, 37.04°N, 119.11°W). The forest types in order of increasing elevation were ponderosa pine (elevation 1024–1372 m), mixed conifer (elevation 1707–2012 m), true fir (elevation 2170–2347 m), and lodgepole pine (elevation 2469–2774 m). Dominant tree species in ponderosa pine sites included ponderosa pine (*Pinus ponderosa*) and incense cedar (*Calocedrus decurrens*). Mixed conifer sites were dominated by white fir (*Abies concolor*) and incense cedar, true fir sites were dominated by white fir and red fir (*Abies magnifica*), and lodgepole pine sites were lodgepole pine (*Pinus contorta*).

As part of a larger study examining the abundance and productivity of forest birds, we established 18 study sites, including four sites in each forest type except for mixed conifer, where there were six. Of the six mixed conifer sites, four were sampled each year on a rotating schedule, such that each site was sampled an equal number of years during the eight years of the study. All sites consisted of at least 60 ha of mature forest with large trees and relatively extensive canopy cover (range 61–85% across all 18 study sites). A 40-ha plot was established within this target habitat and gridded at 50 m intervals within each of the sites to facilitate bird surveys and mapping and relocation of nests. A 1000 m transect within the 40-ha plot was established to facilitate bird surveys. While sites within a forest type were intended to be replicates, natural heterogeneity resulted in all sites having some open rocky or brushy areas and small meadows or streams. No site had experienced recent major disturbance due to logging, fire, or other forest management, and all sites were protected from major disturbance for 10 years per a Memorandum of Understanding with the High Sierra Ranger District of the Sierra National Forest.

2.2. Fieldwork and data collection

2.2.1. Bird Surveys

From 1995 through 2002, we surveyed birds on eight (1995) or 16 (1996–2002) sites each year using a timed transect method. Observers walked the transect at a rate of 50 m per 3 min, recording all birds seen or heard within 50 m of the transect line and those detected at unlimited distance but still within the study site and in similar habitat. Each site was visited 6 times per season by three to four observers each year. Efforts were taken to control for observer variability. Observers were carefully selected for proficiency in bird identification by sight and sound. Observers completed two weeks of training prior to the beginning of the field season, with additional training as they moved into higher forest types and encountered new species. All observers visited each site an equal number of times each year. Observers were retained for as many years as possible to help control for observer variability. A total of seven observers surveyed birds over the eight years of the study, so that most observers were repeat observers for several years of the study. Surveys were completed during the peak singing period for each forest type: April 17 through May 16 in ponderosa pine sites, May 22 through June 15 in mixed conifer sites, June 5 through July 6 in true fir sites, and June 21 through July 25 in lodgepole pine sites. The order of visits to sites and starting points were randomly selected, with the constraint that visits were evenly divided between the two starting points. Recording of birds began at 0700 PDT in all forest types except ponderosa pine, where counting began at 0730 PDT to account for shorter day lengths earlier in the season.

2.2.2. Nest monitoring

We searched for nests on all sites each year and monitored nests until the nest failed or fledged young. During the early stages of nesting and

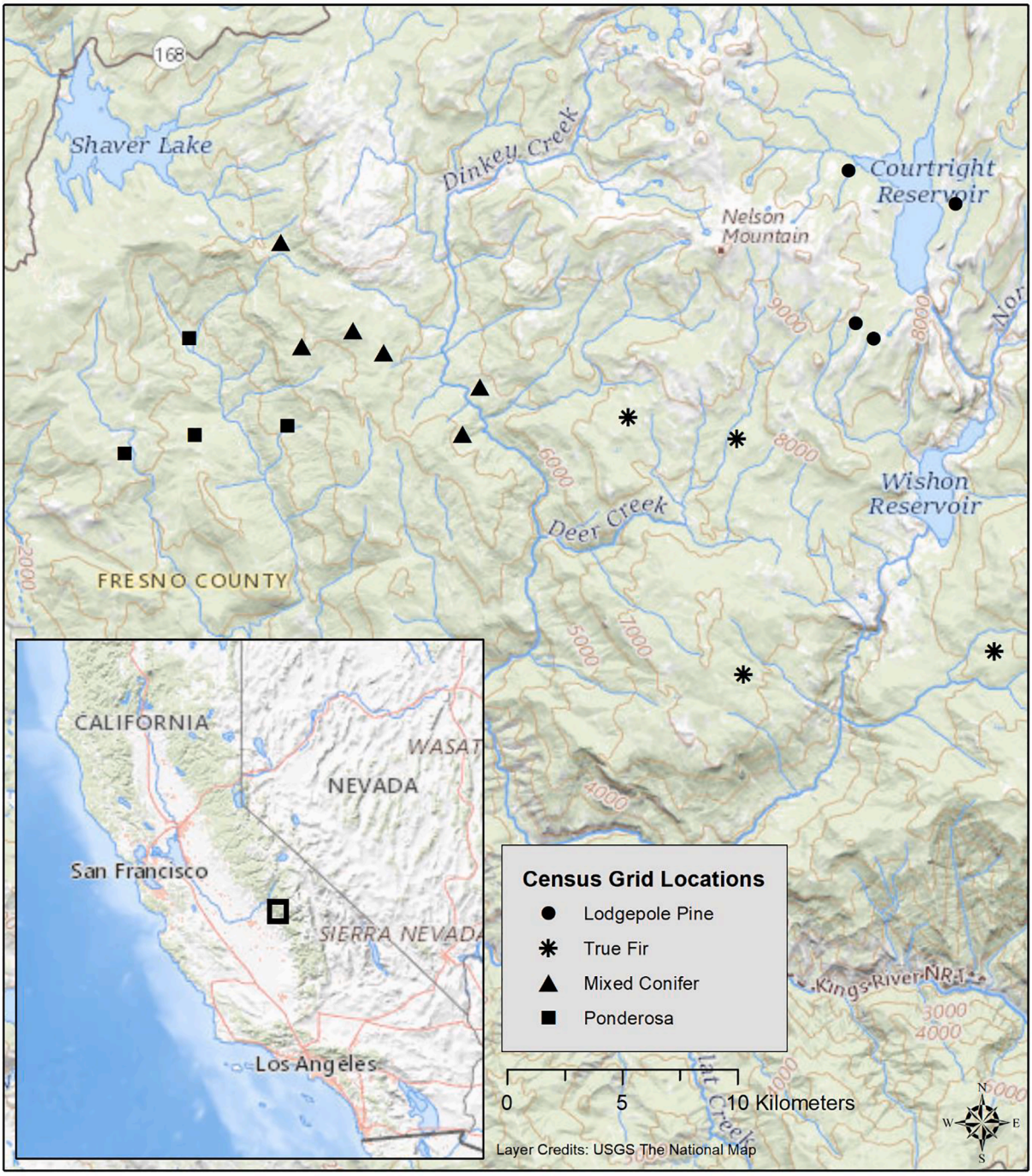


Fig. 1. Location of study sites (N = 18) across an elevational gradient in the Sierra National Forest, California, showing the four forest types.

when nests were too high to check from the ground or in unstable substrates that were hazardous to climb, we observed nests from a distance, noting the presence and behavior of adults. We checked nests twice a week, and, where possible, we checked nest contents once a week using a fiberscope to view nest contents (Purcell, 1997), recording the number of eggs and nestlings and noting the appearance and age of the nestlings.

2.2.3. Field-collected habitat data

We collected data on nesting substrates and the habitat patch surrounding the nest. We measured diameter at breast height (dbh) for nest trees and snags. We recorded the number of woodpecker cavities and the decay class of the nest substrate using five categories for snags (1–5 sensu Cline et al., 1980); nests in live trees were scored as 0 decay. We used a concave spherical densiometer to measure canopy closure, averaging four readings taken under the nest at right angles to each other. Basal area of snags (m^2 ha^{-1}) was measured with a basal area prism. We recorded the number of large trees (≥23 cm dbh) in an 11.3 m radius circle (0.04 ha) centered on the nest. Percent slope of the nesting area was measured with a clinometer and aspect was measured with a compass.

We recorded the same habitat variables at 35 random plots on each of the 18 study sites. Plot centers were located a random distance and direction from randomly selected grid points, with random points at least 100 m apart and within 50 m of the edge of the gridded plot. In 1996 and 1998–1999 we recorded dbh and decay class of the snag

(defined as ≥12 cm dbh) closest to the plot center. In 1997, we recorded these two variables for the nearest snag in each of four quadrants centered at the random point, only one of which was used in analyses.

We collected data on ambient temperature using Hobotemp temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) on 6–12 sites each year, except for 1996 when five of the data loggers failed to launch and we obtained data from only three sites. On our first visit to each site each year we placed a temperature logger in a weatherproof case with a temperature probe threaded out the end of the case, which was then placed inside a small vented wooden box painted white. The box was mounted on a t-post ~1 m above ground in an open area. Daily maximum temperatures were calculated from the hourly data. Following Hollenbeck et al. (2011), we calculated the average maximum daily temperature for each nest for the period from the date of the first observation through the date the nest either fledged or failed. Where data were missing for more than one day of the interval we calibrated temperatures using data for that year from sites in the same forest type at similar elevations, comparing as many years as possible where data from both sites were available. Where we had no similar sites for a particular year, we calibrated data from local weather stations at similar elevations (www.ncdc.noaa.gov; Wishon Dam and Balch Power House).

2.2.4. Remotely sensed habitat data

We identified an equal number of random sites as nest locations, however, due to missing values for some nest variables, the number of nests used in the analyses was lower. Random sites for each forest type were selected from the corresponding elevation band within the Sierra National Forest and were at least 200 m from nest sites and at least 100 m from other random sites. There was no overlap between random sites at the 1-ha scale. At the 125-ha scale random sites overlapped on average by 19.5 ha (~15%), and 40% of sites had no overlap. For both nest and random sites we characterized local scale habitat characteristics within a ~1 ha plot following Wightman et al. (2010), Hollenbeck et al. (2011), and Latif et al. (2015) and at the home range scale within a ~125 ha plot based on the 99% kernel home range size found by Lorenz et al. (2015a). We used forest structure and composition data from Gradient Nearest Neighbor (GNN) models (Ohmann and Gregory, 2002; LEMMA, 2014) for the year 1999 (approximate mid-point of the study period). These satellite-derived products are delivered as raster maps with 30 × 30-m pixel resolution.

We summarized variable values around each nest and random site using either circular buffers or moving window techniques for both spatial scales. Local scale variables include mean values within a 3 × 3 pixel (0.81 ha) moving window for snag density (snags/ha, includes snags ≥25 cm dbh and ≥2 m tall), canopy cover, canopy cover of conifer species, basal area of live trees, and basal area of conifer species. Additionally, within a 56 m radius (~1 ha) circular buffer around each site, we calculated the proportion covered by large trees (quadratic mean diameter ≥50 cm) and the proportion covered by >40% canopy cover. We used circular buffers for proportion calculations as this was more practical than a moving window approach. For home range scale variables, we used the same moving window and buffering techniques. We used a 37 × 37 pixel (123.2 ha) moving window to calculate mean values for snag density, canopy cover, canopy cover of conifer species, basal area of pine species, and basal area of ponderosa pine. We also measured the proportion of each site covered by >40% canopy cover within a 630 m radius (~125 ha) circular buffer. We included two edge-related variables at the home range scale, edge density and distance to nearest edge. We delineated edges by first smoothing the canopy cover layer using a 3x3 moving window average; this helps reduce the occurrence of isolated, anomalous pixel values (i.e., noise). We then reclassified the layer into two classes: ≤40% and >40% canopy cover, to distinguish more open areas from moderate- to high-cover forests. We calculated edge density within each circular buffer using FRAGSTATS software (McGarigal et al., 2012) and distance to nearest edge was measured in ArcGIS 10.3 (ESRI, 2011). Moving window calculations were made using the focal function in the raster package in R (Hijmans, 2019; R Core Team, 2019).

2.3. Statistical analysis

We assessed relative abundance of white-headed woodpeckers as the total count per plot averaged over the number of years each plot was surveyed. We examined detections within 50 m of the transect line and unlimited distance. We tested for differences among the relative abundance estimates for each forest type using Tukey's honest significance difference test. We tested all possible comparisons using t-tests, adjusting the significance level to control for Type I experimentwise error rates, with an overall significance level of 0.05. We tested for differences in clutch size and number of young fledged among habitats with two-sample t-tests assuming unequal variances (Welch's test; Welch, 1947) using Proc Mixed (SAS Institute, Inc 2012). Multiple comparisons used the Tukey Honestly Significant Difference adjustment (Tukey, 1949).

We used logistic regression to examine nesting habitat selection by comparing attributes of white-headed woodpecker nests with random sites. We included variables in our models found to be important to white-headed woodpecker habitat selection in previous studies (Table 1). Forest type (ponderosa pine, mixed conifer, or true fir) was included as a covariate in all models (class variable) and the single nest found in the lodgepole pine forest type was dropped from analysis. We evaluated candidate models using second order AIC corrected for small sample sizes (AIC_c), AIC differences (ΔAIC_c), and Akaike weights (w) (Burnham and Anderson, 2002). To assess the predictive power of models, we used both the receiver operating characteristic (ROC) and the coefficient of discrimination (Tjur, 2009). We generated ROC curves and calculated percent area under the curve (AUC) for the top model. An AUC value of 0.5 indicates no discrimination and an AUC value of 1.0 indicates perfect discrimination; AUC values of 0.7 reflect moderately good discriminatory power (Swets, 1988). The coefficient of discrimination has intuitive appeal and is interpreted similarly to an R^2 statistic, with an upper bound of 1.0. We used SAS Proc Logistic (SAS Institute, Inc 2012) for analysis. All model sets tested the same sample of nests; a nest with missing data for any of the variables used across model sets was dropped.

To examine nest survival, we used the logistic exposure method (Shaffer, 2004) to evaluate the influence of nesting habitat characteristics on nest survival. We evaluated candidate models using AIC_c (Burnham and Anderson, 2002). Analyses were conducted using Proc NLMixed (SAS Institute, Inc 2012). The usual ROC and the coefficient of discrimination were not calculated for nest survival models as there are multiple responses for an individual nest based on survival during distinct time intervals, rather than a single response variable as used in logistic regression.

We first evaluated whether nest age, date, and year were important in explaining variability in nest survival to control for their potentially confounding influence. We examined 24 models that included linear, quadratic, and cubic effects of nest age, linear and quadratic effects of date, and year. Quadratic and cubic effects included all lower order terms. The most supported time-specific model was used as the base model in subsequent analyses.

We examined nest habitat selection and nest survival using models looking at abiotic variables and data collected at three spatial scales (Table 1). The nest site scale represented fine-scale habitat around the nest (0.04 ha) and characteristics of the nest substrate. We summarized data at the ~1-ha scale to represent local habitat characteristics and the 125-ha scale to represent home range habitat. We evaluated the same sets of models in both the nest site and nest survival analyses with the exception of one abiotic variable added in the nest survival analysis.

To calculate period nest success, we raised the daily survival rate based on the constant survival model to the power of the number of days in the nesting period (Shaffer and Thompson, 2007). We used data from

Table 1
Description of variables included in models, abbreviations used in tables, and hypothesized effects on white-headed woodpecker nest habitat preferences and nest survival. Abiotic and nest site variables were field collected at nest and random sites. Remotely-measured variables were measured within a 1 ha buffer (local scale) or 125 ha buffer (home range scale) surrounding the nest location and at random sites.

Variable	Model set	Abbreviation	Hypothesized preference
Cosine aspect (measure of northness/southness)	Abiotic	Cosaspect	South-facing[a]
Slope (%)	Abiotic	Slope	Low[b]
Elevation, linear, quadratic and cubic forms (m)	Abiotic	Elev, Elev^2, Elev^3	Lower elevation[c]
Average maximum daily temperature during the nesting period (ºC)	Abiotic; nest survival only	Maxtemp	Higher temperatures[d]
Diameter at breast height (DBH) of nest substrate or nearest snag (cm)	Nest site	Subdia	Large diameter[e]
Decay class (0–5; Cline et al. 1980)	Nest site	Decay	More decayed[f]
Canopy cover (%)	Nest site	CC	Low[g]
Basal area of snags > 50 cm dbh (m^2 ha^{-1})	Nest site	BAsnag	High[h]
Number of large trees (0.04 ha circle)	Nest site	Nolgtrees	More[i]
Mean canopy cover (%)	Local, Home range	MeanCC	Low[g]
Mean canopy cover of conifers (%)	Local, Home range	CCconifer	Low[g]
% of area with canopy cover > 40% (%)	Local, Home range	CCabove40	Low[j]
Mean snag density (number per ha)	Local, Home range	Snagdensity	High[k]
Mean basal area live trees (m^2 ha^{-1})	Local	BAlive	High[l]
Mean basal area of conifer species (m^2 ha^{-1})	Local	BAconifer	High[m]
% of area with large trees (QMD ≥ 50 cm)	Local	PCarealgtrees	High[n]
Mean basal area of pine species (m^2 ha^{-1})	Home range	BApine	High[o]
Edge density (m ha^{-1}; calculated in Fragstats)	Home range	Edgedensity	High[p]
Distance to edge (m; calculated in Fragstats)	Home range	Edgedistance	Low[p]

[a] Milne and Hejl (1989; more nests had southern than northern exposures), Buchanan et al. (2003; selection for south-facing slopes), but see Latif et al. (2015; nests occurred in pixels with more north-facing aspects).
[b] Buchanan et al. (2003), Hollenbeck et al. (2011), Latif et al. (2015).
[c] Wightman et al. (2010), Hollenbecket al. (2011).
[d] Hollenbeck et al. (2011).
[e] Raphael and White (1984), Wightman et al. (2010).
[f] Raphael and White (1984), Buchanan et al. (2003), Wightman et al. (2010).
[g] Milne and Hejl (1989), Garrett et al. (1996), Wightman et al. (2010), Latif et al. (2015).
[h] Buchanan et al. (2003), Wightman et al. (2010), Lorenz et al. (2016).
[i] Buchanan et al. (2003), Hollenbeck et al (2011).
[j] Latif et al. (2015).
[k] Buchanan et al (2003), Wightman et al. (2010), Lorenz et al. (2016).
[l] Buchanan et al. (2003), but see Wightman et al. (2010; low basal area at 1-ha scale).
[m] Buchanan et al. (2003; basal large ponderosa pine), Latif et al. (2015; high % of ponderosa pine).
[n] Buchanan et al. (2003), Hollenbeck et al. (2011).
[o] Latif et al. (2015; high % of ponderosa pine).
[p] Milne and Hejl (1989), Latif et al. (2015).

this study to determine the length of the nesting period, employing data from nests with complete information for a particular period rather than published values. The average length of the incubation period was 12.4 days (n = 26) and the nestling period averaged 26 days (n = 12). Average clutch size was 4.5 (n = 77), yielding a laying period of 3.5 days. The number of days to complete a nesting cycle was 42 days, slightly longer than published values (Garrett et al., 1996).

2.3.1. Abiotic models

We examined models containing abiotic variables separately from those with habitat variables because abiotic variables may be more variable and have a stronger influence on nest site selection and nest survival than habitat variables, especially when there is neutral congruence between habitats and nest survival (Hollenbeck et al., 2011; Stillman et al., 2019). Abiotic variables examined for nest site selection included % slope, cosine aspect (to represent north–south orientation of nest sites), and linear, quadratic, and cubic forms of elevation (Table 1). For the elevation variables, only the linear, quadratic, or cubic form was included in any one model and all higher order models included the lower order terms. Including a null model (intercept and forest type only), we tested a total of 16 models to examine nest site selection. For the nest survival models we added an additional abiotic variable — maximum daily temperature during the nesting interval. We tested all possible subsets of these six variables, including a null model, for a total of 32 models examined.

2.3.2. Nest-site scale models

We examined five variables measured at the nest site scale for both nest site selection and nest survival models (Table 1). These included substrate dbh and decay class of the nest substrate, canopy closure, basal area of snags, and the number of large trees (>50 cm dbh). We tested all possible combinations of these five variables, excluding models with only one variable as we expected more than one variable would be needed to describe variability. Including a null model, we tested a total of 27 models.

2.3.3. Local scale models

We examined seven variables measured within the local area surrounding the nest or random point (Table 1). These included mean canopy cover, mean canopy cover of conifers, the % of area with canopy cover >40%, basal area of live trees, basal area of conifers, snag density (≥25 cm dbh and ≥2 m tall), and the % of area with large trees (quadratic mean diameter ≥50 cm). Mean canopy cover, mean canopy cover of conifers, the % of area with canopy cover >40%, basal area of live trees, and basal area of conifers were highly correlated ($r > 0.7$) and thus were not included in the same model. Excluding single-variable models, we tested a total of 16 models, including a null model.

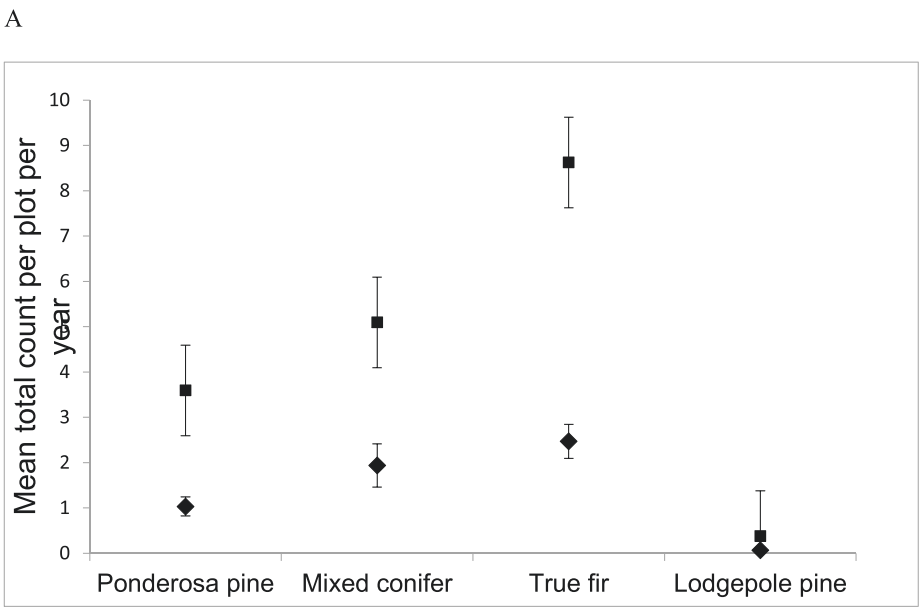
2.3.4. Home range scale models

At the 125-ha scale we again examined seven variables, including the three canopy cover variables and snag density from the local (1 ha) scale (Table 1). In addition, we included basal area of pines, edge density, and distance to nearest edge. The three canopy cover variables and snag density were all correlated ($r > 0.70$) so only one of these variables was used in any model. We tested a total of 33 models, again excluding single-variable models and including a null model.

3. Results

3.1. Abundance

White-headed woodpeckers were detected from 1080 to 2690 m elevation. Patterns based on detections within 50 m and unlimited distance detections were similar (Fig. 2a). The adjusted P values for comparisons of detections within 50 m across forest types indicated that relative abundance was greater in true fir and mixed conifer sites than in lodgepole pine sites ($P < 0.001$. df = 28 for true fir, and $P = 0.002$, df = 28 for mixed conifer) and greater in true fir compared to ponderosa pine sites ($P = 0.019$, df = 28; PP < TF and MC = TF > LP). Comparisons based on unlimited distance detections revealed that relative abundance in true fir was significantly greater than all other forest types ($P < 0.001$,



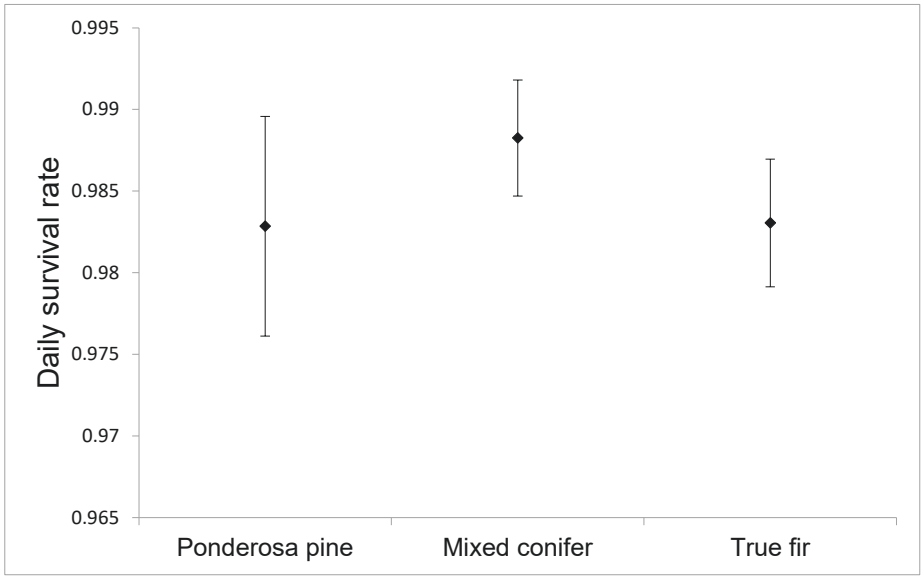


Fig. 2. (A) Relative abundance of white-headed woodpeckers (*Picoides albolarvatus*) in four forest types over an elevational gradient in the southern Sierra Nevada, CA, shown from low to high elevation. Relative abundance was calculated as the total count per plot averaged over the eight years of the study as plots were visited different numbers of years and is shown for detections within 50 m (diamonds) and unlimited distance (squares). Error bars represent 1 standard error. (B) Daily survival rates of white-headed woodpeckers in three forest types calculated using the logistic exposure method without explanatory variables. Sample sizes for nests were 22, 55, and 81 for ponderosa pine, mixed conifer, and true fir, respectively. Error bars represent 1 standard error.

df = 28 for all) and that of lodgepole pine was less than all other forest types ($P < 0.001$, df = 28 for all), with ponderosa pine and mixed conifer not differing ($P = 0.193$, df = 28; PP = MC < TF > LP).

3.2. Nest sites

We located and monitored 159 nests from 1995 through 2002 and the number of nests found mirrored abundance patterns (n = 22, 55, 81, and 1 in ponderosa pine, mixed conifer, true fir, and lodgepole pine, respectively).

Most nests were in snags (82%). Substrates tended to be large (mean diameter = 77.8 cm, SD = 47.4, range = 15–345, n = 136) and nest snags were larger in true fir sites (adj $P < 0.001$, df = 130 for true fir vs. ponderosa pine and adj $P = 0.013$, df = 139 for true fir vs. mixed conifer). Live trees and logs were each used 7% of the time, stumps were used 2% of the time and one nest was excavated in a root ball. Across all forest types, red fir, white fir, and pines (ponderosa, Jeffrey, lodgepole, and unidentified pines) were the most common tree species used (including both snags and trees) but tree species used were more diverse in mixed conifer (7 species used) compared to ponderosa pine and true fir (4 species each). Half of the 10 nests found in live trees were in California black oaks (*Quercus kelloggii*). Half of the 10 nests found in logs were in Jeffrey pine logs. Average decay class for snags was 2.84 (SD = 1.15, n = 105).

3.3. Nest site selection

3.3.1. Abiotic models

The most supported model for abiotic variables included the cubic form of elevation (Table 2). Two other models were competitive, one adding slope and the other the cosine of aspect, however the 95% confidence intervals for both variables included zero, suggesting negligible contribution. The probability of nesting was maximized in true fir forest at 2200 m and then dropped off sharply at higher elevations. Forest type effects were important, with the probability of use lower for mixed conifer compared to true fir forest ($P < 0.000$). The coefficient of

Table 2
Model selection results for nest site selection of white-headed woodpeckers nesting in the southern Sierra Nevada, CA. ΔAIC_c is the difference between Akaike's information criterion corrected for small sample size for each candidate model and the top-ranking model., K is the number of parameters and *w* is the Akaike weight. Only models with $\Delta AIC_c < 2$ are shown. See Table 1 for variable name abbreviations. Sample sizes were 118 for nests and 481 for random sites for the nest site scale model and 160 random sites for the local and home range scale models.

Model	ΔAIC_c	K	*w*
Abiotic models			
Elev^3 [1]	0	6	0.40
Elev^3 Slope	1.915	7	0.15
Elev^3 Cosaspect	1.930	7	0.15
Nest site scale models			
CC Basnag Decay Nolgtrees Subdia[1]	0	8	0.51
CC Basnag Decay Nolgtrees	0.050	7	0.49
Local scale models			
BAconifer Snagdensity[2]	0	5	0.43
BAconifer Snagdensity PCarealgtrees	0.885	6	0.27
Home range scale models			
CCconifer Edgedensity[2]	0	5	0.40
CCconifer Edgedensity Edgedistance	0.600	6	0.29
CCconifer Edgedensity BApine	0.598	6	0.18

[1] ΔAIC_c for the null model was 573.697.
[2] ΔAIC_c for the null model was 449.614.

discrimination was 0.100 and AUC of the most-supported model was 0.662, suggesting low support for the model.

3.3.2. Nest site scale models

The top model at the nest site scale was the global model (Table 2) and a second model, lacking substrate diameter, was nearly as competitive. The combined Akaike weights of the top two models was 0.998. Confidence intervals around the parameter estimate for substrate diameter overlapped zero, suggesting little or no ecological insight from this variable. Forest type effects were not important in nest scale models. White-headed woodpecker nests were found in areas with open canopy, with fewer large trees, higher basal area of snags, and in more decayed substrates. Mean canopy closure at nest sites was only half that for random sites ($\bar{x}$ = 42%, SD = 27 for nests sites vs. 81%, SD = 19, at available sites). The average number of large trees (≥23 cm dbh) per 0.04 ha was only 2.6 (SD = 2.5) at used sites compared to 14.8 (SD = 13.5) at random sites. Basal area of snags at nest sites was 8.5 m^2 ha^{-1} (SD = 7.6) vs. 6.1 (SD = 9.0) at random sites, and the average decay class of snags at nest sites was 2.8 (SD = 1.1) vs 1.9 (SD = 1.1) for random sites. Forest type was not important in the nest site scale models (P = 0.22). The coefficient of discrimination was 0.558 and the AUC of the most-supported model was 0.948, suggesting excellent discrimination between nests and random sites.

3.3.3. Local scale models

The most-supported model at the local scale included basal area of conifers and snag density (Table 2). An additional competitive model also included the % area with large trees but this variable did not appear to be important (95% CI overlapped 0). White-headed woodpecker nests tended to have greater basal area of conifers and lower density of snags compared to random sites at this scale. Forest type was not important in the local scale models (P = 0.24). The coefficient of discrimination was 0.08 and the AUC of the top model was 0.67 and, suggesting poor discrimination at this scale. The poor predictive power of the top model was revealed by small differences in the parameters between nests and random sites. The mean basal area of conifers at nests was 16.4 m^2 ha^{-1} (SD = 15.7) vs. 17.4 (SD = 18.2) for random sites. Mean snag density at nests was 37.6 (SD = 21.6) vs. 29.5 (SD = 21.8) for random sites.

3.3.4. Home range scale models

The most-supported model at the 125-ha scale included canopy cover of conifers and edge density (Table 2). Two other models were competitive, adding distance to edge or basal area of pines to the top model. The 95% confidence intervals for these two variables all overlapped zero and thus were not considered important. The coefficient of discrimination for the top model was 0.333 and the AUC for the top model was 0.820, suggesting good predictive power. In addition, the null model was the least-supported model, suggesting that the variables considered were able to discriminate nests from random sites. Based on positive parameter estimates for both variables, we conclude that habitat surrounding White-headed woodpecker nests had greater cover of conifers and greater edge density at the home range scale. Percent cover of conifers at white-headed woodpecker nests was 55% (SD = 14) vs. 42% (SD = 17) at random sites. Forest type was significant for all contrasts (all $P < 0.000$). Edge density was highest in ponderosa pine habitat (94.4 m ha^{-1}, SD = 13.7, n = 22), intermediate in mixed conifer (78.7 m ha^{-1}, SD = 18.2, n = 56), and lowest in true fir forest (34.3 m ha^{-1}, SD = 25.1, n = 82).

3.4. Nest survival

Period nest success was 42%, 55%, and 43% for ponderosa pine, mixed conifer, and true fir, respectively and daily survival rates did not differ across these three forest types (Fig. 2b). Most nests that failed were lost due to predation (65%), 13% were abandoned, one nest was lost due to infertility, the death of the female, and weather (2% each), and the cause of failure of the remaining failed nests was undetermined (17%). Clutch size showed a tendency to decrease with elevation (mean clutch size was 4.53, 4.46, and 4.41 for ponderosa pine, mixed conifer, and true fir, respectively) but none of the comparisons was significant (all *Adj P* > 0.77). The number of young fledged from successful nests showed the same pattern (mean number fledged was 3.75, 3.33, and 2.97 for ponderosa pine, mixed conifer, and true fir, respectively). The comparisons for ponderosa pine and mixed conifer and for mixed conifer and lodgepole pine were not significant (*Adj P* > 0.39) but the number of young fledged was significantly higher in ponderosa pine compared to lodgepole pine (*Adj P* = 0.046).

3.4.1. Time-specific models

Of the 24 models tested, the most supported model included quadratic effects of both age and date and was the only competitive model (Table 3; parameter estimates are provided for all models in Appendix A). Nest survival was lowest at ~20 days (early nestling period) and early in the nesting season.

3.4.2. Abiotic models

The most-supported abiotic model for nest survival included average maximum temperature (Table 3). Three other models were competitive ($\Delta AIC_c \leq 2$), each adding cosine aspect, slope, or linear elevation to average maximum temperature, although confidence intervals for the parameter estimates of these three variables overlapped zero, suggesting they were not important. Nest survival increased with higher average daily maximum temperatures. Forest type effects were important and suggested that nest survival was lower in ponderosa pine compared to mixed conifer forest ($F_{1,144}$ = 3.72, P = 0.055) and compared to true fir (($F_{1,144}$ = 7.36, P = 0.007). In addition, average temperatures during nesting were lower in ponderosa pine compared to true fir (*Adj P* = 0.029). Especially at cooler temperatures, daily survival rates differed among the forest types, and because habitat is correlated with elevation, daily survival rates are lower at lower elevations (Fig. 3).

3.4.3. Nest site scale models

The most-supported nest site scale model included canopy closure, substrate diameter, and basal area of snags (Table 3). The one other competitive model dropped basal area of snags. Nest survival was higher in areas with greater canopy closure, lower basal area of snags and in smaller diameter nest snags and trees. Forest type effects were important

Table 3
Model selection results for daily nest survival of white-headed woodpeckers nesting in the southern Sierra Nevada, CA. Only models with $\Delta AIC_c < 2$ are shown. See Table 1 for variable name abbreviations except for Age[2] and Date[2], which were the quadratic forms of nest age and date. Effective sample size for all models was 3329 exposure days.

Model	ΔAIC_c	K	*w*
Time-specific models			
Age[2] Date[2]	0	7	0.56
Abiotic models			
Maxtemp [1]	0	8	0.26
Cosaspect Maxtemp	0.681	9	0.18
Elev Maxtemp	1.545	9	0.12
Slope Maxtemp	1.936	9	0.10
Nest site scale models			
Subdia CC BAsnag [1]	0	10	0.25
Subdia CC	1.757	9	0.11
Local scale models			
Null [3]	0	7	0.23
BAconifer Snagdensity	0.836	9	0.15
BAllive Snagdensity	1.273	9	0.12
Home range scale models			
Edgedensity Edgedistance [2]	0	9	0.09
MeanCC Edgedensity	0.092	9	0.09
CCabove40 Edgedensity	0.398	9	0.08
BApine Edgedensity	0.787	9	0.06
Snagdensity Edgedensity	0.834	9	0.06
CCconifer Edgedensity	0.907	9	0.5
Null	1.183	7	0.05
MeanCC Edgedensity Edgedistance	1.348	10	0.047
CCabove40 Edgedensity Edgedistance	1.559	9	0.042
Snagdensity Edgedistance	1.588	9	0.041
Snagdensity BApine	1.920	9	0.035

[1] ΔAIC_c for the null model was 348.690.
[2] ΔAIC_c for the null model was 357.179.

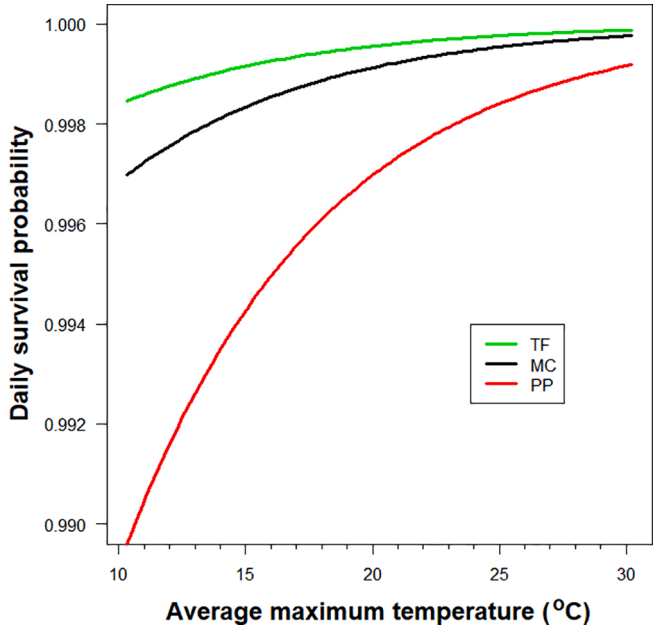


Fig. 3. Daily survival rates of white-headed woodpecker nests as a function of average maximum daily temperature during the nesting interval. Nest date was held constant at 130, a value common to all three forest types and nest age was set to 0.

and suggested that nest survival was lower in ponderosa pine compared to mixed conifer forest ($F_{1,144} = 8.39$, $P = 0.004$) and compared to true fir forest (($F_{1,144} = 13.96$, $P < 0.000$). Differences between successful and failed nests were small. Mean canopy closure at successful nests was 41.1% (SD = 27.8) compared to 44.4% (SD = 25.6) for failed nests. Mean basal area of snags was 7.3 m^2 ha^{-1} (SD = 6.5) at successful nests compared to 10.0 m^2 ha^{-1} (SD = 9.8) at failed nests.

3.4.4. Local scale models

The null model was the most-supported model for nest survival at the local scale (Table 3). Two other models were competitive but the 95% confidence intervals for the parameter estimates included zero for all variables in these models, suggesting none of the variables were important for explaining variation in daily survival rate. Forest type effects were important and suggested that nest survival was lower in ponderosa pine compared to mixed conifer forest ($F_{1,144} = 4.17$, $P = 0.042$) and compared to true fir forest ($F_{1,144} = 6.47$, $P = 0.011$).

3.4.5. Home range scale models

There were 11 competitive models at the home range scale (Table 3). Of the variables included in these models, only edge density was important and edge density appeared in 8 of the 11 models. Daily nest survival increased with increasing edge density.

4. Discussion

Understanding the habitat requirements that help species meet their life history needs and that influence fitness and survival is important for conservation and management of species. This is especially true when habitat selection does not correspond with quality habitat. When habitat selection is maladaptive, the use of non-preferred sites may have substantial fitness costs (Martin, 1998). These habitat requirements are likely to operate at different scales as animals may select different habitat components at different scales (Mayor et al., 2009). At smaller spatial scales, nest predation may be the primary selection pressure whereas landscapes may be chosen on the basis of food availability (Chalfoun and Martin, 2007). Fortunately, new technologies are helping facilitate analysis across scales (Mayor et al., 2009).

Our results show that white-headed woodpecker nesting ecology in the Sierra Nevada demonstrated a mixed pattern of congruence between characteristics important to nest habitat selection and nest survival. Nest survival was higher at preferred sites for abiotic variables and at the home range scale (Table 4), indicating that abiotic and larger landscape scale preferences were adaptive. However at the nest site scale, we found negative congruence between habitat selection and nest survival, with white-headed woodpeckers selecting open forest with higher basal area of snags for nesting compared to available sites, but nest survival was higher in forest with higher canopy closure and lower basal area of snags (Table 4). At the local scale, the model for nest site selection was weak and no variables were important for nest survival.

We found negative congruence at the nest site scale, suggesting maladaptive habitat selection. Other studies have found little evidence for an association between white-headed woodpecker nest survival and habitat variables, either positive or negative. Wightman et al. (2010) found that white-headed woodpeckers nested in open-canopied forest, but no habitat variables were associated with nest survival. They attributed this to the fact that nest success was high and there was little variation within habitat features among nest locations. Kozma and Kroll (2012) found little evidence for an association between nest survival and habitat variables, with temporal covariates explaining most of the variation in nest survival. The predictive power of our nest site selection model was excellent, and the differences in canopy closure and snag basal area for nest site selection were not trivial. For nest survival, differences between successful and failed nests were small for canopy closure but larger for snag basal area.

Numerous mechanisms have been proposed for a lack of linkage between fitness and habitat selection (see Chalfoun and Schmidt, 2012 for a review). We focus on five potential explanations that may apply in our case. First, perhaps critical habitat features were not quantified or birds were responding to fitness components not measured such as adult survival, clutch size, fledgling survival, or lifetime reproductive success.

Table 4
Summary of results of models for abiotic variables and three scales for white-headed woodpecker and comparison of effects on nest site selection and daily nest survival in the southern Sierra Nevada (1995–2002). ↑denotes that the variable is greater at nest sites compared to random sites or that higher values are associated with increased nest survival; ↓ denotes association with decreased nest survival.

Model (Scale)	Nest site selection	Nest survival	Conclusion
Abiotic	↑cubic elevation	↑ elevation ↑ maximum temperature	Congruence
Nest site (0.04 ha)	↓ closed canopy ↑ snag basal area ↓ large trees ↑ decay class	↑ closed canopy ↓ snag basal area ↓ nest substrate diameter	Negative congruence
Local (1 ha)	↑ conifer basal area ↓ snag density	Null model most supported	Both models were weak
Home range (125 ha)	↑ conifer cover ↑ edge density	↑ edge density	~ Congruence

Our primary measure of fitness, nest success, is the probability that at least one nestling fledges and does not take into account the number of nestlings that fledge and their subsequent survival (see below for discussion of clutch size and number of young fledged). Increased productivity per successful nest can be related to food availability (Chalfoun and Martin, 2007).

Second, selection pressures, in particular those related to food availability or nest predation, may vary across spatial scales (Orians and Wittenberger, 1991; Chalfoun and Martin, 2007; Mayor et al., 2009). While our findings and those of Latif et al. (2015) suggest that white-headed woodpeckers nest adjacent to closed-canopied forest that presumably provides critical food resources during the nesting period, nest predation may be the primary influence on habitat selection at smaller scales.

Third, nest predators may be more abundant at forest edges, leading to higher nest predation (Gates and Gysel, 1978; Andrén, 1995). We found selection for high edge density at white-headed woodpecker nests at the home range scale, as did Latif et al. (2015), and nest survival was also higher with greater edge density, with congruence in model results at the landscape scale. We were unable to examine edge effects at the nest site scale.

Fourth, nest survival may primarily be driven by abiotic and/or temporal variables (Stillman et al., 2019). As discussed below, temperature and elevation were important to both nest site selection and nest survival and time-specific variables were important at all scales (Appendix A). Nests were less successful early in the nesting season and in the early nestling period, when young nestlings need to be fed frequently, necessitating more feeding trips by the adults that can draw the attention of predators.

Finally, Chalfoun and Schmidt (2012) found that tests of congruence between evolved habitat preferences and measures of fitness were lowest in forest habitats, and especially so in cavity nesters. Cavity nesters generally have relatively high nest survival, which could relax selection for nest predation. When birds nest almost exclusively in habitats with low predation, with birds occupying 'adaptive peaks', nest predation may no longer be acting on nest site selection, even though it shaped it in the past (Latif et al., 2012). However, nest success was low in our study (see below), and we might expect selection for nesting habitat to be important if nest predation is a limiting factor on fitness.

Similar to other studies, we found that abiotic factors were important to white-headed woodpecker habitat selection and reproductive success (Hollenbeck et al., 2011; Latif et al., 2015). Elevation was important to both nest site selection and nest survival, temperature was important to nest survival, and time-specific variables were important at all scales (Appendix A). Nest survival increased with warmer temperatures, as hypothesized, however contrary to our hypotheses, both nest site selection and nest survival increased with increasing elevation and white-headed woodpeckers were most abundant in higher elevation true fir forests. Taken together, these results are surprising because, on a given date, temperatures are cooler at higher elevations and generally warm as the season progresses. However, temperatures during nesting were cooler in ponderosa pine forests, suggesting the timing of nesting occurred relatively earlier in the season at lower elevations.

We examined the local (~1 ha) scale to emulate a common scale used to characterize the habitat surrounding nest sites in other studies of white-headed woodpecker habitat selection. Variables found important at this scale in previous work include lower density of live trees (Wightman et al., 2010), greater density of large trees (Hollenbeck et al., 2011), larger and more decayed snags (Wightman et al., 2010), and moderate (~40%) canopy cover (Latif et al., 2015). These results are consistent with ours, but only at the nest site scale. Because we found contrasting results at finer (nest site) and broader (home range) scales, with white-headed woodpeckers using open habitat with few large trees and abundant decayed snags at the nest site scale versus fragmented dense conifer forests at the home range scale, the local scale does not appear relevant to white-headed woodpecker ecology and habitat selection in our study area or help clarify habitat relationships.

At the home range scale, white-headed woodpeckers both selected and had higher nest survival in forests with high edge density. High edge density arises from the interspersion of openings at nest sites surrounded by closed-canopied forest at the landscape scale and is consistent with heterogeneity in forest structure. Differences in edge density between nests and random sites at the home range scale were greatest in ponderosa pine habitat. Because we defined edge as the length of edge between open forests (≤40% canopy cover) and forests with moderate to high canopy cover (≥40% canopy cover; per Latif et al., 2015), this suggests that birds in ponderosa pine forests are selecting more mixed density forest compared to the available forest. Landscape heterogeneity may benefit white-headed woodpeckers by providing them with open habitats for nesting and nearby closed-canopy forests that provide year-round foraging opportunities (Hollenbeck et al., 2011; Latif et al; 2015).

White-headed woodpeckers selected landscapes with high canopy cover of conifers, in agreement with our hypotheses and previous work (Hollenbeck et al., 2011; Latif et al., 2015). Conifer forest with high canopy cover is likely important to meet year-round foraging needs. White-headed woodpeckers feed on conifer seeds and invertebrates, which they obtain by flaking and gleaning the bark of living conifers (Garrett et al., 1996; but see Lorenz et al., 2016).

Nesting success in our study was low compared to other studies, with an overall rate of 52% across all forest types. Kozma (2009) and Kozma and Kroll (2012) found overall Mayfield nesting success rates of 85% (n = 22 nests) and 70% (n = 55) in managed ponderosa pine forests in eastern Washington, and Wightman et al. (2010) found 76% nesting success (n = 45) in burn areas in south central Oregon. However, based on a large sample size, Hollenbeck et al. (2011) estimated nesting success at 39% (n = 382) in unburned forests in central Oregon. Clutch sizes in our study are the highest reported, as are the number of young fledged per successful nest (Garrett et al., 1996; Kozma, 2009; Kozma and Kroll, 2012; Lorenz et al., 2016). Despite the relatively low nesting success observed in the southern Sierra Nevada, the population appears to be

increasing over the time period from 1966 to 2018 based on Breeding Bird Survey data, with a positive annual percentage change of 1.12 (Sauer et al., 2020). Because nest survival reflects only the probability that at least one nestling fledges, we hypothesize that average higher productivity per nest helps offset the lower success rate (Garrett et al., 1996; Flashpoler et al., 2001).

The largest differences between our study and previous work center around dependence on ponderosa pine forests and large-seeded pines as a food source (Ligon, 1973; Bull, 1978; Bull et al., 1986; Garrett et al., 1996; Kozma, 2009; Hollenbeck et al.; 2011). We found white-headed woodpeckers to be most abundant in areas dominated by true fir. This is contrary to their close association with ponderosa pines over most of their range and the conclusions of Garrett et al. (1996) that white-headed woodpeckers are found at highest densities in the southern portion of their range (southern Oregon and California) where more than one species of pine is present. The preponderance of work to date on white-headed woodpeckers has been done in low-elevation ponderosa pine and mixed conifer forests in the Pacific Northwest where the association with ponderosa pine has been found to be strong (Bull, 1978; Bull et al., 1986; Wightman et al., 2010; Hollenbeck et al., 2011; Kozma 2011, 2012; Latif et al., 2015). In northeastern Oregon, Bull (1978) found white-headed woodpeckers in ponderosa pine and mixed conifer forests but did not find them in white fir or lodgepole pine forest types. However, in northern California, Linden and Roloff (2015) studied white-headed woodpeckers nesting in historically ponderosa pine-dominated stands that are now mostly white fir as a result of selective logging and fire suppression where they nested mostly in white fir snags. The association with ponderosa pine forests clearly does not hold in California, where white-headed woodpeckers were found across a range of forest types and elevations, but they both selected and were more successful in true fir forests.

Where ponderosa pine seeds are an important food source, their use is limited to seasonal availability, primarily fall and winter, because pine seeds are not cached, and other food sources are important at other times of the year (Ligon, 1973; Otvos and Stark, 1985; Bull et al., 1986; Garrett et al., 1996). In the Sierra Nevada, Otvos and Stark (1985) found that white-headed woodpeckers eat conifer seeds only in the fall. Arthropods are important food items throughout the year (Raphael and White, 1984; Garrett et al., 1996), with invertebrates accounting for 74% (males to 85% (females) of the total year-round food volume based on stomach contents (Otvos and Stark, 1985). Lorenz et al. (2016) found that white-headed woodpeckers were plastic in their foraging, with seasonal variation in substrates used. Large-seeded pines could still be important as winter food resources at higher elevations as sugar pines and Jeffrey pines can be found well up into the elevation range of the true fir zone in the southern Sierra Nevada (Kricher, 1993; Lanner, 2002). In addition, while they are considered sedentary, white-headed woodpeckers nesting in true fir may make short downslope movements in winter to forage on pine species (Garrett et al., 1996). The feeding ecology of white-headed woodpeckers warrants additional study. Corresponding to our results on the lack of association with ponderosa pine forests are our results related to elevation, with higher elevations selected for and important for nest survival. We observed white-headed woodpeckers nesting at higher elevations compared to other studies (Bull et al., 1986; Buchanan et al., 2003; Hollenbeck et al., 2011; Kozma, 2012, Latif et al., 2015; Linden and Roloff, 2015). We also found them breeding across a broader range of elevations, with a range of 1500 m in this study compared to 700–750 m in other studies (Kozma, 2012; Buchanan et al., 2003; Linden and Roloff, 2015). Elevation and forest type are correlated and, despite the preference for true fir habitat, the broad elevation range and the diversity of habitats used in the southern Sierra Nevada demonstrate the plasticity of white-headed woodpecker habitat selection.

A limitation of this study is that the assessment of habitat quality was limited to a few demographic variables—those related to abundance and annual reproductive success. Ideally, density, survival, and multiple measures of reproduction, including lifetime reproductive success would be measured at multiple spatial scales, but this is often not feasible (Arlt and Pärt, 2007; Chalfoun and Martin, 2007; Johnson, 2007). Low nesting success may be counterbalanced by higher clutch sizes (Flashpoler et al., 2001) and multiple breeding attempts (Chalfoun and Martin, 2007), leading to similar rates of young production (Battin, 2004). We found that nests at low elevations fledged more young compared to nests at high elevations, suggesting compensation for lower nesting success at low elevations.

4.1. Management and conservation implications

The identification of the habitat features that influence habitat preferences and enhance fitness is essential to effective management and conservation of species (Chalfoun and Martin, 2007). Wildlife habitat relationship models fail if the relationship between habitat selection and measures of fitness and survival differ. Management actions designed to benefit species could be detrimental to the species whose populations we are endeavoring to safeguard.

Because white-headed woodpeckers use heterogeneous landscapes and habitat preferences differ across spatial scales, we need to consider both fine scale habitat and the surrounding landscape when managing for them. These complex habitat requirements complicate recommendations for forest management. At the landscape scale, white-headed woodpeckers need conifer forests with high canopy cover in areas with abundant edges. Fortunately, western conifer forests are naturally patchy due to the steep topography of rugged, young mountain ranges and periodic disturbance from fire, disease, and other natural processes. Forest management practices and anthropogenic fragmentation can also be important in maintaining landscape heterogeneity and the amount of edge.

Snags, especially large, decayed snags, are important as nesting and foraging substrates for white-headed woodpecker (this study; Bull, 1978; Raphael and White, 1984; Wightman et al., 2010; Kozma, 2012). Snags used as nesting substrates were typically large, with 75% of nest snags greater than 44 cm. Both fir and pine species were used, with use related to the availability of species found in the area. Lorenz et al. (2015b) found that most woodpecker species are constrained by interior wood hardness. White-headed woodpeckers are weak excavators (Bunnell, 2013) and wood hardness was important to nest site selection (Lorenz et al., 2015b). Lorenz et al. (2015b) demonstrated that decay classes are poor predictors of wood hardness and concluded that the suitability of snags for nesting is likely overestimated. They advised that higher densities of snags should be provided than generally recommended. Management prescriptions that specify snag retention should take into account that many snags are not suitable or do not provide ideal nesting sites. The retention of large, decayed snags is important (Buchanan et al., 2003; Wightman et al., 2010; Bunnell, 2013; Lorenz et al., 2015b), and protection of preferred snags prior to application of prescribed fire is recommended (Bagne et al., 2008).

Similar to Raphael and White (1984) and Milne and Hejl (1989), we found that logs were relatively important nesting substrates in the Sierra Nevada. Nesting in fallen logs or leaning snags has been noted only rarely in other study areas but appears to be a fairly common behavior in the southern portion of their range. While fallen logs contribute to fuel loading and fire risk, leaving some large logs in an area would likely be beneficial for white-headed woodpeckers.

Our results on habitat preferences of white-headed woodpeckers are largely consistent with the findings of others working in other parts of their range (Wightman et al., 2010; Hollenbeck et al., 2011; Latif et al., 2015), however, before making recommendations on local forest management activities, habitat models should be validated in those landscapes. Latif et al. (2015) found that models performed poorly outside the area for which they were developed. In particular, in areas where ponderosa pine is not the dominant tree species and where pine species diversity, as well as overall tree species diversity, is greater, models from

outside the study area should be applied with caution (Latif et al., 2015).

Finally, while white-headed woodpeckers nested across a broad elevational range, habitat suitability was associated with higher elevations and true fir forest. Management considerations implemented with an eye to maintaining populations of white-headed woodpeckers can take these results into account when making management decisions.

Because habitat loss is the primary driver of species extinctions and habitat loss and degradation is the greatest threat to native bird species, understanding habitat needs of species is crucial to their conservation (Wilcove et al., 1998; Johnson, 2007). Drought, bark beetle infestations, and wildfires will continue to compromise the amount and quality of suitable habitat in California (Fettig et al., 2019), leading to changes in stand age structure and tree species composition. These disturbances can take place over large landscapes, driving rapid and often persistent changes that reduce resiliency and forest heterogeneity (Fettig et al., 2019). Studies of the impacts on wildlife resulting from these disturbances are needed (Garrett et al., 1996) as forests are altered by factors related to climate change.

CRediT authorship contribution statement

Kathryn L. Purcell: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. **Eric L. McGregor:** Methodology, Data curation, Writing - review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Kathryn Purcell reports financial support was provided by USDA Forest Service, Pacific Southwest Research Station.

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Appendix A. Parameter estimates and 95% confidence intervals for the most-supported models explaining variation in nest site selection and nest survival for models with abiotic variables and three spatial scales for white-headed woodpeckers nesting in the Sierra Nevada. See Table 1 for definitions of variables. PP = ponderosa pine, MC = mixed conifer, TF = true fir, Day = linear date, Day^2 = quadratic date, Age = linear nest age, Age^2 = quadratic nest age. NA means the variable was not included in the most-supported model

Model (Scale)	Variables	Nest site selection			Daily survival rate		
		Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI
Time dependent	Day	NA			−25.36	−41.30	−9.41
	Day^2	NA			61.3	26.4	96.3
	Age	NA			36.9	12.5	61.3
	Age^2	NA			−11.84	−19.13	−4.56
Abiotic	Elev	−0.05	−0.13	0.02	NA		
	Elev^2	0	0	0	NA		
	Elev^3	0	0	0	NA		
	Max temp	NA			0.07		
	PP	−0.42			−10.37	0.03	0.12
	MC	−1.68	−2.28	1.44	−9.12	−34.72	14
	TF	NA	−2.60	−0.77	−8.45	−34.17	15.9
	Day	NA	NA	NA	18.1	−33.50	16.6
	Day^2	NA			−7.22	−11.68	47.9
	Age	NA			−21.51	−15.88	1.45
	Age^2	NA			60.5	−38.34	−4.67
						23.3	97.8
Nest site (0.04 ha)	CC	−0.04	−0.05	−0.03	0.01	0	0.03
	BAsnag	0.08	0.05	0.12	NA		
	Nolgtrees	−0.30	−0.40	−0.19	NA		
	Decay	0.51	0.23	0.79	NA		
	Subdia	0.01	−0.00	0.01	−0.01	−0.01	−0.00
	PP	−0.42	−0.98	0.14	−3.24	−26.26	19.8
	MC	0.4	−0.08	0.87	−1.33	−25.09	22.4
	TF	NA			−0.54	−24.32	23.3
	Day	NA			15.2	−13.12	43.5
	Day^2	NA			−6.30	−14.53	1.93
	Age	NA			−20.13	−36.09	−4.18
	Age^2	NA			55	20.2	89.7
Local	BAconifer	0.04	0.02	0.05	NA		
(1 ha)	Snagdensity	−0.03	−0.05	−0.01	NA		
	PP	0.41	−0.07	0.89	−1.05	−26.70	24.6
	MC	−0.19	−0.54	0.17	0.27	−26.06	26.6
	TF	NA			0.73	−25.63	27.1
	Day	NA			12	−19.31	43.4
	Day^2	NA			−5.18	−14.25	−3.90
	Age	NA			−17.46	−33.35	−1.57
	Age^2	NA			48	13.7	82.4
Home range	CCconifer	0.21	0.15	0.28	NA		

(continued on next page)

(*continued*)

Model (Scale)	Variables	Nest site selection			Daily survival rate		
		Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI
(125 ha)	Edgedensity	0.04	0.02	0.06	0.02	0	0.04
	Edgedistance	NA	NA	NA	0	−0.00	0.01
	PP	3.21	2.19	4.23	−1.83	−27.23	23.6
	MC	−1.09	−1,61	−0.57	−0.05	−26.06	26
	TF	NA			1.22	−24.84	27.3
	Day	NA			10.4	−20.57	41.4
	Day^2	NA			−4.74	−13,74	4.26
	Age	NA			−17.04	−32.79	−1.30
	Age^2	NA			46.6	12.4	80.7

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