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Nesting habitat of Warbling Vireos across an elevational gradient in the southern Sierra Nevada

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ABSTRACT. Populations of Warbling Vireos (*Vireo gilvus*) are declining in California, apparently due to low reproductive success. From 1989–2002, I studied the nest-site selection and reproductive success of Warbling Vireos across an elevational gradient in the southern Sierra Nevada. Warbling Vireos regularly nested in upland coniferous forests with few or no deciduous trees, and tree species used by nesting vireos included five species of conifers and four species of deciduous trees. Overall, hardwoods were used more than expected based on their availability, but 69% of all nests were in conifers. Hardwood trees were found only in low and mid-elevation ponderosa pine (*Pinus ponderosa*) and mixed-conifer sites. In low-elevation ponderosa pine habitat, 87% of nests were in hardwoods, with 67% in California black oaks (*Quercus kelloggii*), a species that typically occupies upland sites. In mixed-conifer sites where reproductive success was high, 65% of nests were in incense cedar (*Calocedrus decurrens*) and California black oak was the next most commonly used species. Because fire suppression has likely increased numbers of shade-tolerant tree species like incense cedar, shade-intolerant species like black oaks may have been more important as a nest substrate for vireos in the past. Only conifers were used as nesting substrates at higher elevations. Nest success was greater for Warbling Vireos that nested in tall trees in areas with high basal area. My results suggest that Warbling Vireos in the Sierra Nevada would benefit from management activities that encourage retention and recruitment of California black oaks at lower elevations, and development of stands with large trees, dense foliage, and semi-open canopy throughout their elevation range.

SINOPSIS. **Habitat de anidamiento de *Vireo gilvus* a lo largo de un gradiente altitudinal en el sur de la Sierra Nevada**

Las poblaciones del vireo (*Vireo gilvus*) se están reduciendo en California, aparentemente, debido al bajo éxito reproductivo. De 1989-2002, estudie la selección del lugar de anidamiento y determiné el éxito reproductivo del vireo a través de una serie de gradientes altitudinales en la parte sur de la Sierra Nevada. Estas aves por lo general anidan en bosques de coníferos de alturas y en contadas ocasiones en árboles deciduos. Las plantas utilizadas para anidar incluyen cinco especies de coníferos y cuatro especies de deciduos. Basándonos en su disponibilidad, las especies de maderas duras fueron utilizadas en mayor grado que lo esperado, pero el 69% de los nidos fueron construidos en coníferos. Se encontraron maderas duras solamente en elevaciones medias y bajas de bosque de Pino Ponderosa (*Pinus ponderosa*) y lugares mixtos de coníferos. En lugares de baja elevación con habitat de Pino Ponderosa el 87% de los nidos fueron encontrados en maderas duras, con el 67% de estos en Robles Negros de California (*Quercus kelloggii*), una especie comunmente encontrada en lugares elevados. Dado el caso que el control de incendios forestales ha incrementado el número de especies tolerantes a la sombra como el Cedro Oloroso, las especies intolerantes a la sombra, como el Roble Negro, muy bién pudieran haberse sido especies importantes para el anidamiento de los vireos en el pasado. En lugares elevados, sólo los coníferos fueron utilizados para anidar. El éxito de anidamiento fue mayor para las aves que anidaron en vegetación de gran altura con una buena área basal. Mis resultados sugieren que el vireo de la Sierra Nevada se beneficiaría de actividades de manejo que favorezcan la retención y el reclutamiento de Robles Negros de California a bajas elevaciones, y el desarrollo de rodales con árboles grandes, de denso follaje y un docel semi-abierto a través de diferentes elevaciones. de rodales con árboles grandes, de denso follaje y un docel semi-abierto a través de diferentes elevaciones.

Key words: elevational gradient, habitat selection, nesting habitat, nest-site selection, *Vireo gilvus*, Warbling Vireo

Populations of Warbling Vireos (*Vireo gilvus*) in California have been declining over the past several decades, with Breeding Bird Survey data from 1966 to 2004 showing a significant decline of 1.32% per year (Sauer et al. 2005). Declines of 9%–12% per year in coastal California have been found for both breeding populations (Gardali et al. 2000) and fall migrants (Gardali et al. 2000, Gardali and Jaramillo 2001, Ballard et al. 2003), indicating possible declines over a

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larger area. These declines are believed to be due to low reproductive success. Most previous studies of Warbling Vireos in California have revealed low nest success (10–30%; Gardali and Ballard 2000, Gardali et al. 2000, Smith et al. 2005). In contrast, Purcell (2006) found high nest success rates (60%) in mixed conifer forests in the southern Sierra Nevada where vireos were abundant, and lower success in ponderosa pine (30%) and true fir (32%) forests where vireos were less abundant.

Warbling Vireos are typically associated with moist deciduous woodlands at elevations from sea level to 3200 m and avoid dry habitats and high elevations (Gaines 1988, Gardali and Ballard 2000). Although partial to deciduous trees and moist habitats, Warbling Vireos are occasionally found in clumps of deciduous trees or even single deciduous trees in upland coniferous forests (Grinnell and Storer 1924, Grinnell and Miller 1944, Gardali and Ballard 2000). Because habitat features can influence nest-site quality and reproductive success (Martin and Roper 1988), examination of nest-site selection by Warbling Vireos may provide insight into the factors that influence nesting success. My objective was to examine nest site selection by Warbling Vireos breeding in coniferous forests across an elevational gradient in the southern Sierra Nevada where nesting success was high compared to other populations in California (Purcell 2006). Based on previous studies, I hypothesized that nests and successful nests would be located in larger deciduous trees with sparser foliage, in areas with lower canopy cover and basal area, and closer to water than available trees and habitat and unsuccessful nests.

METHODS

Study areas. I studied Warbling Vireos in four forest types in the High Sierra Ranger District of the Sierra National Forest on the western slope of the southern Sierra Nevada, California (Fig. 1). The four forest types included ponderosa pine (*Pinus ponderosa*) at low elevations (1024–1372 m), mixed conifer at middle elevations (1707–2012 m), and true fir and lodgepole pine forests at upper elevations (2170–2347 m and 2469–2774 m, respectively). I selected 18 study sites consisting of four replicate sites in each forest type, except for mixed conifer, where there were six. Dominant tree species in ponderosa pine sites were ponderosa pine and incense cedar (*Calocedrus decurrens*), with several hardwood species, most notably California black oak (*Quercus kelloggii*) and canyon live oak (*Quercus chrysolepsis*), also present. Mixed-conifer sites included a mixture of primarily white fir (*Abies concolor*), incense cedar, sugar pine (*Pinus lambertiana*), ponderosa pine, and California black oak. True fir sites were dominated by white fir and red fir (*Abies magnifica*), and lodgepole pine sites consisted of nearly pure stands of lodgepole pine with a few red fir. All sites consisted of $\geq$60 ha of mature forest with relatively high canopy cover, and all included small meadows or creeks, and open, rocky, or brushy areas. All sites were protected from major disturbance for the duration of the study. A 40-ha gridded plot was established within each of the sites to facilitate mapping and relocation of nests.

Field methods. From 1995 to 2002, nests of all bird species were located, including those of Warbling Vireos, on eight (1995) or 16 (1996–2002) of the 18 study sites each year. Four of the six sites in the mixed conifer forest type were searched for nests each year on a rotating schedule so that each site was sampled an equal number of years during the 8-year study.

Nests were monitored twice a week. Where possible, nests were checked once a week using a mirror on a pole or a small video camera mounted on an extendable fiberglass pole. When too high to reach from the ground, field crews climbed to nests. During early nesting stages and when nests could not be monitored using other methods, we observed nests from the ground and noted the presence and behavior of adults and the appearance of nests. For nests checked directly, the number of eggs and nestlings and the appearance of the nestlings (size, whether the eyes were closed, slits, or open, presence and extent of down and pin feathers, and the extent of emergence of the remiges and rectrices) were recorded.

Descriptions of known-aged nestlings from this study were helpful in ageing nestlings and determining nest fate. I determined nest age by extrapolating from identified events such as the beginning of incubation, hatching, or fledging. Because the duration of nesting stages can differ over a species' range, I used data from nests with complete information for a particular nesting stage to determine the laying, incubation, and

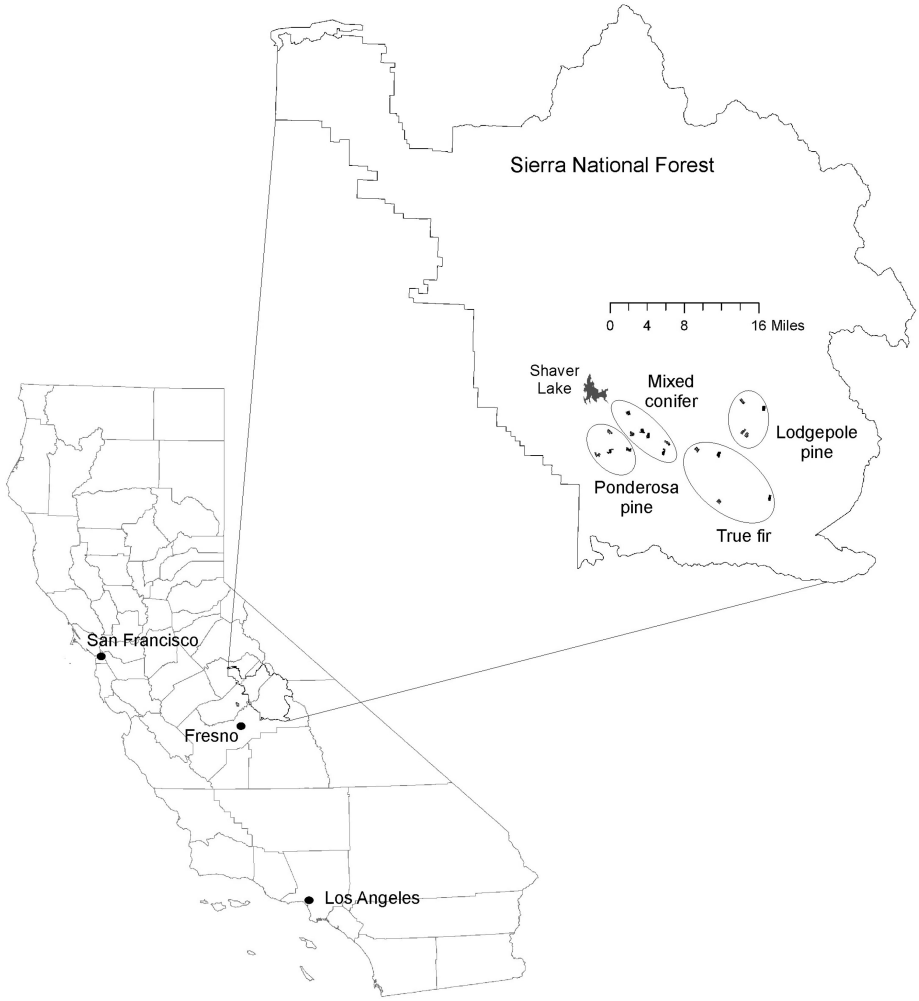

Fig. 1. Location of study sites ($N = 18$) across an elevational gradient in the Sierra National Forest, California, showing the four forest types.

nestling periods. The average laying, incubation, and nestling periods were 3, 12, and 16 d, respectively. Nests were aged when they could be reasonably assigned to within ±1 d. I was not able to determine the age of six nests that failed soon after they were found or before a transition that would allow backdating.

In addition, Warbling Vireo nests were located and monitored from 1989 to 1993 on one of the mixed conifer sites as part of an earlier study. Because they were monitored less regularly and by observation from the ground, these nests were included in analyses examining habitat use but were not used in nest survival models.

Habitat measurements were taken at the nest site and included nest height (measured with a clinometer and meter tape or a hypsometer), substrate species, substrate height, diameter at breast height (dbh), nest orientation, foliage density of the nest tree, percent canopy cover, and basal area of live trees. Nest orientation was measured as the compass direction from the main stem to the nest. Foliage density of the nest tree was estimated based on a scale of 0–5, with 0 for snags (no live foliage), 1 for sparse foliage, 2 for medium-low foliage density, 3 for medium density, 4 for medium-high foliage, and 5 for dense foliage. Canopy cover was based

on four spherical densiometer readings taken under the nest at right angles to each other. Basal area (m^2/ha) was measured with a basal area prism. The presence of water within 30 m of the nest in the form of creeks, ponds, or wet meadows was noted, and the elevation at each nest was measured with an altimeter. To describe patch-level habitat, all trees $\geq$8 cm dbh and $>$2 m in height were recorded by species and size class in an 11.3-m radius circular plot (0.04 ha) centered at the nest. Some vegetation variables were not recorded for nests monitored from 1989 to 1993, so sample sizes vary.

In addition to nest-site data, habitat data were collected for 35 random plots on each of the 18 study sites ($N = 630$) from 1996 to 1999. 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. Basal area of live trees was measured at the plot center, and the presence of water within 30 m of the plot center was noted. All trees were recorded by species and size class in an 11.3-m radius circular plot (0.04 ha) centered at the random point. In 1996 and 1998–1999, species, height, dbh, and foliage density of the tree closest to the plot center were recorded. In 1997, plots were divided into four quadrants, with variables recorded for the nearest tree in each quadrant, only one of which was used in analyses. Canopy cover was based on four spherical densiometer readings taken at the random tree at right angles to each other.

Statistical analysis. The characteristics of nest trees and randomly selected trees (height, dbh, foliage density, basal area, and percent canopy cover) were compared using general linear models (Proc Mixed, SAS Institute 2000). All nests were in live trees so only data from live trees were used. Because tree size varied with elevation, elevation was included as an independent variable, and study site was included as a random effect in the model. Data from random sites in lodgepole pine sites were excluded because few nests were found in that forest type. Differences in tree species and the presence of water within 30 m were tested with chi-square tests (SAS Institute 2000). Rayleigh's test was used to determine if nest orientation was nonrandom (Mardia 1972).

A successful nest was defined as a nest that survived to fledge at least one young. I used the logistic exposure method (Shaffer 2004) to examine whether daily nest survival rates (henceforth survival) were influenced by habitat characteristics. Prior to analysis, I examined nest site and habitat variables for nonlinearity using generalized additive models (GAM; R Development Core Team 2003). Transformations suggested by GAM to describe the functional forms of variables were obtained by trying quadratic and logarithmic functions. I evaluated candidate models using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) and used the effective sample size (Rotella et al. 2004) to calculate AIC_c. Akaike weights, which estimate the probability a specified model is the best of those considered, were used to address model selection uncertainty (Burnham and Anderson 2002). Analyses were conducted using Proc GENMOD (SAS Institute 2000).

To control for potentially confounding effects of time-specific factors, all candidate models included the most-supported time-specific model based on previous analysis (Purcell 2006) and following Grant et al. (2005). This model included a linear effect of nest date and quadratic effects of nest age. I also found that nest survival was strongly influenced by quadratic effects of elevation (Purcell 2006). Thus, the base model included these elevation and time-specific effects.

Candidate models were developed based on *a priori* hypotheses. I investigated three models that evaluated the relationship between nest survival and variables that described (1) nest tree species, (2) properties of the nest site, and (3) vegetation structure surrounding the nest site. Related to nest tree species, I predicted that more successful nests would be in deciduous trees (Gardali and Ballard 2000), incense cedars, and California black oaks (because these species were used more than expected in my study). I further predicted that successful nests would be higher and in larger trees (Gardali and Ballard 2000) with sparser foliage (Smith et al. 2005). Finally, I predicted that successful nests would be closer to water (Gardali and Ballard 2000), and would have less canopy cover and basal area (Gardali and Ballard 2000, Smith et al. 2005). For each of the three models, I compared the base model to the variables taken one at a time to determine the model that was best supported by the data.

To evaluate Model 1, I tested dummy variables for whether the nest tree was deciduous or coniferous, incense cedar versus all other species, and black oak versus all other species, and the base model. Nest height, tree height, foliage density, and the base model were examined to evaluate Model 2. Because two measures of tree size, tree height and dbh, were highly correlated ($r = 0.81$, $P < 0.0001$), only tree height was used. Variables examined for Model 3 included basal area of live trees, percent canopy cover, a dummy variable for the presence of water (creek, pond, or wet meadow) within 30 m, and the base model. The most inclusive models with $\Delta AIC_c < 2.0$ from each group along with the base and global models were examined in a combined model to examine the relative importance of each factor. The global model included all variables brought forward to the combined analysis. I assessed the fit of this global model with the Hosmer–Lemeshow decile of risks test (Hosmer and Lemeshow 2000).

Differences in orientation between successful and unsuccessful nests were tested with the q-sample Uniform Scores test (Mardia 1972). Values reported are means ± 1 SE, and $\alpha \leq 0.05$ is considered significant for frequentist approaches.

RESULTS

Nesting habitat. From 1995 to 2002, 83 nests were located and monitored, with 15 in ponderosa pine sites, 58 in mixed conifer, nine in true fir, and one in lodgepole pine. An additional 25 nests were located and monitored from 1989 to 1993 in one of the mixed conifer sites. Most nests were found in the nest building stage (54%), with 16% found during the laying stage, 24% during incubation, and 6% during the nestling period.

All nests were in live trees, including five coniferous species and four deciduous species. Although deciduous trees were used by Warbling Vireos more than expected based on availability ($\chi^2_1 = 62.6$, $P < 0.001$; Fig. 2), 69% of all nests were in conifers. Deciduous trees were found only in ponderosa pine and mixed conifer sites (Fig. 3A, B).

Most vireo nests in ponderosa pine sites (87%) were in deciduous trees, primarily California black oak (Fig. 3A). In mixed conifer sites, 65% of nests, more than expected based on availability ($\chi^2_1 = 19.7$, $P < 0.001$), were in incense cedar, with black oaks the second-most commonly used species (24% of nests; Fig. 3B). Except for sugar pine, other coniferous trees were seldom used. The most common tree species in true fir habitat were white fir and red fir, and white fir, sugar pine, and lodgepole pine were used for nesting (Fig. 3C). At the scale of nest patches, the number of hardwood trees surrounding nest sites and random sites did not differ ($P = 0.89$ for ponderosa pine and $P = 0.60$ for mixed conifer).

Mean nest height was 15.7 ± 0.7 m (range 3.4–41.5 m, $N = 108$), and trees used for

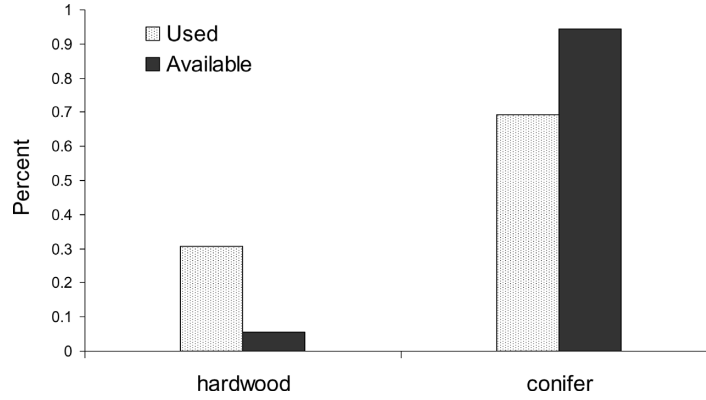

Fig. 2. Warbling Vireos nested in hardwood tree species more often than expected, but 69% of all nests ($N = 108$) were in conifers. Trees used for nesting were compared to random trees in the three forest types where vireos most commonly nested (ponderosa pine, mixed conifer, and true fir). Numbers over bars are numbers of trees of each type.

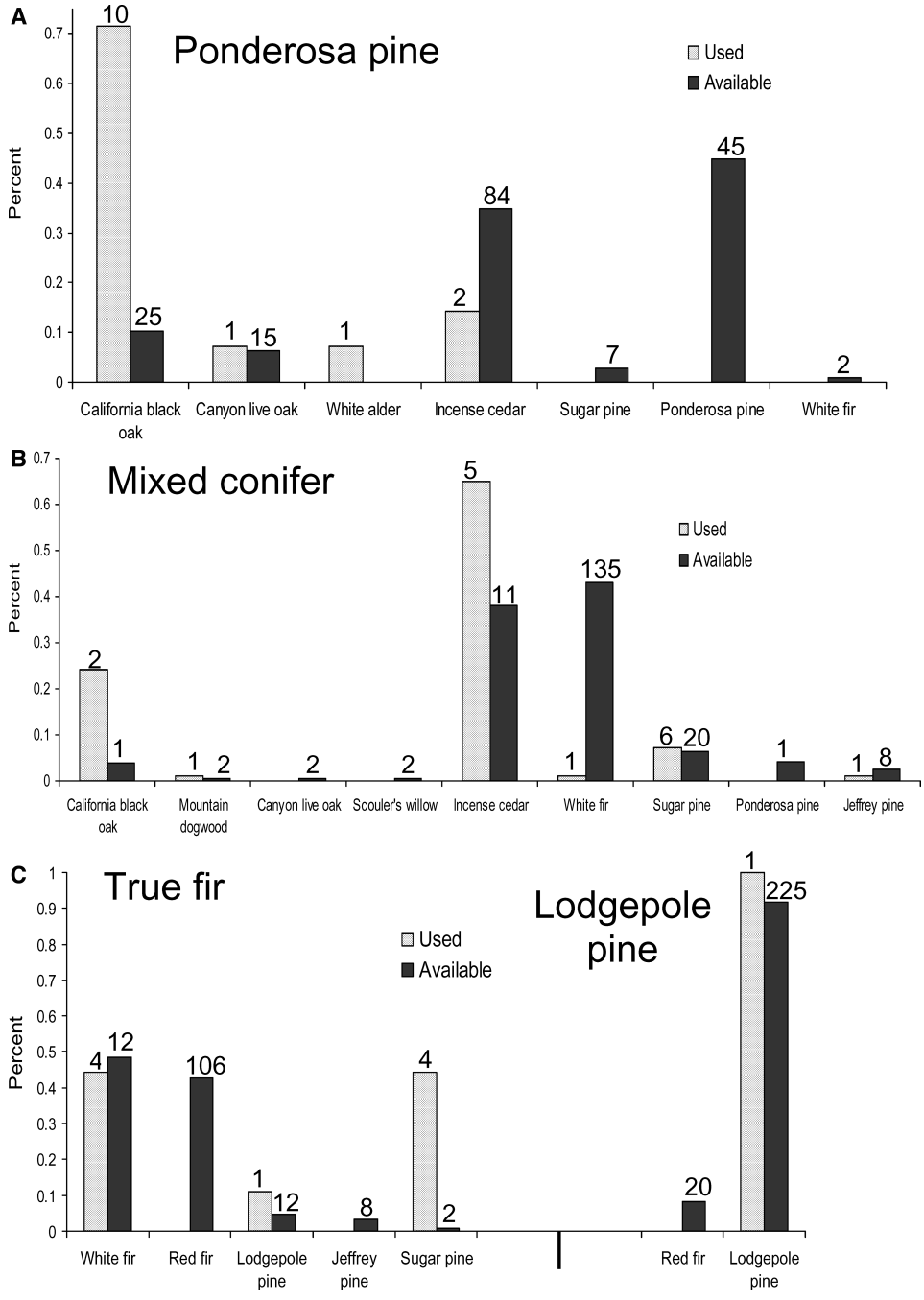

Fig. 3. Comparison of tree species used by nesting Warbling Vireos and available trees revealed that (A) hardwood tree species were used more than expected in ponderosa pine habitat (elevation 1024–1372 m), with California black oak used most often ($N = 15$ nests), (B) in mixed conifer habitat (elevation 1707–2012 m), 65% of nests ($N = 83$) were in incense cedar, and (C) all nests found in true fir (elevation 2170–2347 m; $N = 9$ nests) and lodgepole pine (elevation 2469–2774 m; $N = 1$ nest) habitat were in conifers. Numbers over bars are numbers of trees of each species.

Table 1. Results of general linear models for nest site variables at Warbling Vireo nest sites and random sites revealed that Warbling Vireo nest trees were taller, had greater diameter, and higher foliage density than random trees in the southern Sierra Nevada, California.[a]

	Nests means ± SE (*N*)	Random means ± SE (*N*)	*t*	*P*
Nest tree height (m)	25.2 ± 0.9 (107)	17.0 ± 0.6 (489)	6.1	<0.0001
Nest tree dbh (cm)	65.9 ± 2.6 (107)	36.9 ± 1.5 (489)	8.7	<0.0001
Foliage density[b]	3.14 ± 0.08 (104)	2.89 ± 0.04 (490)	2.8	0.005
Basal area (m^2/ha)	43.7 ± 1.8 (107)	43.3 ± 1.1 (490)	0.6	0.55
Percent canopy cover	84.6 ± 1.3 (89)	83.2 ± 0.8 (490)	1.4	0.16

[a]Elevation was included as an independent variable and study site as a random effect.
[b]Based on a scale of 0–5, with 0 for a snag (no live foliage) and 5 the densest.

nesting by Warbling Vireos were taller and had larger diameters than randomly selected trees (Table 1). In addition, foliage density of nest trees was higher than that of random trees, but basal area and canopy cover did not differ (Table 1). Nest orientation was random ($\bar{R}$= 0.2, $P = 0.08$). More than half of all nests were >30 m from water (53%, 57 of 108), but vireo nests were within 30 m of water more often than randomly selected sites ($\chi^2_1 = 22.0$, $P < 0.001$).

Nest survival. The relationship between nest survival and nest height was best explained by a quadratic function that included both linear and quadratic terms; GAM results suggested linear forms of the other nest site and habitat variables. Model selection results for nest tree species indicated that no model was clearly superior. The base model was the most-supported model. However, the model with black oak versus other species was the second-most supported model, the only other model with $\Delta AIC_c < 2.0$, and was therefore included in the combined model (Table 2). Nest tree height was the most-supported nest site model, and the base model was the only other model with $\Delta AIC_c < 2.0$. Basal area of live trees was the most-supported nest vegetation model, and the base model was again the only other model with $\Delta AIC_c < 2.0$ (Table 2). Results from the combined models indicated that both nest tree height and basal area were important in predicting Warbling Vireo nest survival (Table 2). Successful Warbling Vireo nests were in taller trees with higher basal area. The global model fit the data well ($\hat{C}$= 8.9, $P = 0.35$). Successful nests were more often located on the southwest side of the nest tree ($\bar{x}$= 221°) whereas unsuccessful nests were on the northeast side ($\bar{x}$= 41°), and this difference was significant (w = 9.9, $N = 102$, $P = 0.04$).

DISCUSSION

Nesting habitat requirements of Warbling Vireos in my study differed in several respects from those reported in other studies, particularly in the wide variety of conifer tree species used for nesting and use of upland conifer habitat for nesting. In contrast to other studies (James 1971, Barlow 1977, Easton and Martin 2002, Ward and Smith 2000, Ortega and Ortega 2003), Warbling Vireos in the southern Sierra Nevada were not restricted to deciduous vegetation and regularly occurred in upland coniferous forest lacking deciduous trees. Nests did not have more deciduous trees around them than random sites, and many nest sites had no deciduous trees around the nest. In contrast, Warbling Vireo presence and abundance showed a negative relationship with percent cover of conifers in the eastern Sierra Nevada (Richardson and Heath 2004).

Similar to previous studies, my results suggest that moist habitats are selected for nesting by Warbling Vireos. Nests were close to a source of water more often than random sites, but some nests were also at some distance from water (pers. obs.). As also noted by Grinnell and Storer (1924), this suggests that water is not necessary for nesting vireos. The presence of water near nests is probably more related to the resulting riparian vegetation than any direct attraction to water (Grinnell and Miller 1944).

Nest tree species. Although Warbling Vireos in my study used hardwood trees more than

Table 2. Factors affecting daily survival of Warbling Vireo nests in the southern Sierra Nevada, California, were evaluated by combining the most inclusive model, with $\Delta AIC_c < 2.0$ (in bold) from each group along with the base and global models ($N_{effective} = 1599$ exposure days).

Model variables[a]	$Log_e(L)$[b]	K[c]	ΔAIC_c	Akaike weight
Tree species models				
Base	–103.2	6	0.0	0.45
Black oak	–103.0	7	1.5	0.21
Cedar	–103.2	7	2.0	0.17
Deciduous	–103.2	7	2.0	0.17
Nest site models				
Nest tree height	–101.4	7	0.0	0.51
Base	–103.2	6	1.6	0.23
Nest height^{2}[d]	–101.4	8	2.0	0.18
Foliage density	–103.2	7	3.6	0.08
Nest vegetation models				
Basal area	–101.7	7	0.0	0.45
Base	–103.2	6	1.0	0.27
Water within 30 m	–102.8	7	2.3	0.14
Percent canopy cover	–102.9	7	2.5	0.13
Combined models				
Nest tree height	–101.4	7	0.0	0.34
Basal area	–101.7	7	0.6	0.26
Global	–100.1	9	1.5	0.16
Base	–103.2	6	1.6	0.16
Black oak	–102.9	7	3.2	0.07

[a]All models included linear effects of date, quadratic effects of nest age, and quadratic effects of elevation (base model). The three models tested the base model and variables taken one at a time that characterized nest tree species, the nest site, and vegetation surrounding the nest site. The most inclusive model with $\Delta AIC_c < 2.0$ from each group was included in the combined models.

[b]$Log_e(L)$ is the value of the maximized log-likelihood function.

[c]K is the number of parameters in the model.

[d]Nest height^2 is the quadratic form of nest height and includes the lower order term.

expected based on availability, 69% of all nests were in coniferous trees, which included five different conifer species. Conifers were used exclusively as nest substrates at the higher elevation sites, and a significant proportion of nests were in incense cedars in the mixed conifer forests where Warbling Vireos were most abundant and most productive (Purcell 2006). Although previous investigators have also found that Warbling Vireos were selective in the tree species used for nesting, most have also reported an almost exclusive use of deciduous trees (Walsberg 1981, MacKenzie et al. 1982, Gardali and Ballard 2000, Ortega and Ortega 2003, Richardson and Heath 2004). However, Walsberg (1981) reported one of 18 nests (6%) in a ponderosa pine in Arizona, and Smith et al. (2004) reported 30 of 70 (43%) nests in lodgepole pines in riparian habitat on the eastern slope of the Sierra Nevada. In the latter study, 43% of nests were in quaking aspens (*Populus tremuloides*) and the rest in cottonwoods and willows.

Incense cedars are relatively unusual among conifers in having scaly foliage consisting of minute, flat needles arranged in flat branchlets, and this has led to conjecture about the potential role of their unique foliage in habitat selection. Airola and Barrett (1985) found that incense cedar was avoided as a foraging substrate by Warbling Vireos breeding in mixed conifer forests in the Sierra Nevada. Regarding nest site selection, selection of any tree is likely related to the availability of an appropriate horizontal forked twig from which to hang their nests.

California black oak, a deciduous species, was a preferred nest substrate at lower elevations and has not been previously documented as a nesting substrate for Warbling Vireos. Black oaks are also a preferred foraging substrate in mixed conifer forests (Airola and Barrett 1985). Unlike

deciduous species used by Warbling Vireos in other studies, Black oaks are not associated with riparian habitat, and are typically found in fairly xeric upland sites with well-drained soils associated with mountain slopes and ridges (McDonald 1969, Warner 1980, Pavlik et al. 1995). The use of upland sites, particularly those occupied by California black oaks in the southern Sierra Nevada, demonstrates the nonrequisite nature of moist habitats to Warbling Vireos in the southern Sierra Nevada.

Fire exclusion during the past century has favored shade tolerant species such as incense cedar, resulting in increased abundance and density of this species (Parsons and DeBenedetti 1979, Warner 1980). Incense cedar also appears to be adapted to a wide variety of microclimates and conditions (Stark 1965). On the other hand, the more frequent fires that occurred prior to suppression activities would have favored shade-intolerant species such as California black oak (Warner 1980). Successful regeneration of black oaks requires openings in the understory; openings that were probably created primarily by fire in the past (Parsons and DeBenedetti 1979). Based on the nest tree species preferences of Warbling Vireos in the Sierra Nevada and postulated changes in tree species composition since presettlement times, incense cedars may have, historically, been less important and California black oaks more important to Warbling Vireos in the southern Sierra Nevada. Nevertheless, it seems unlikely that Warbling Vireos in the southern Sierra Nevada were ever associated with habitat dominated by deciduous tree species.

Nest site characteristics. Warbling Vireos in my study nested in trees taller than randomly selected trees, and nests in taller trees were also more successful. Other investigators have also reported an apparent preference for taller trees, both as nest sites and as nesting habitat (James 1971, Whitmore 1975, MacKenzie et al. 1982). Although the mean nest height in my study (15.7 m) was higher than reported by other investigators (Gardali and Ballard 2000), nest height is likely related to the height of trees used for nesting. Smith et al. (2004) found that nest heights differed among nest tree species, with higher nests in taller trees.

I found that Warbling Vireo nests located on the southwest side of trees were more successful. Similarly, Smith et al. (2005) found more successful nests on the west or "warmer" side of lodgepole pine trees. Although Walsberg (1981) found no selection for thermally favorable orientation of nests in trees by Warbling Vireos in Arizona, denser leaf cover over the western half of nests reduced exposure to solar radiation during the hot afternoon hours.

My results indicate that large trees are important for Warbling Vireos because they were both selected for and provided substrates for successful nests. However, contrary to my hypothesis that nests and successful nests would be located in areas with lower basal area, nests in habitats with greater basal area were more successful, and basal area of used and available sites did not differ. Because basal area reflects both tree density and size, and because canopy cover was not higher at nest sites compared to random sites, habitat with large trees and semi-open canopy cover appears to be more important than dense stands of small trees.

Recommendations. My results demonstrate the range and flexibility of nesting habits used by Warbling Vireos in the southern Sierra Nevada. Importantly, vireos using these novel nest sites and habitats were reproducing successfully, at least in mid-elevation forests (Purcell 2006). My results also suggest that Warbling Vireos in the Sierra Nevada would benefit from management for stands of large trees with dense foliage and a semi-open canopy, conditions generally believed to represent historic forest conditions. Management that retains large California black oaks and encourages recruitment, such as the use of prescribed fire (Garrison et al. 2002), would benefit Warbling Vireos breeding at lower elevations in the Sierra Nevada.

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