

## WARBLING VIREO NESTING ECOLOGY IN THE NORTHERN SIERRA NEVADA

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**ABSTRACT:** In California, for unknown reasons, the Warbling Vireo (*Vireo gilvus swainsonii*) has poor reproductive success, and its numbers have declined over the past 20 years. From June through August 1998 we monitored 70 nests of the Warbling Vireo in a previously unstudied population on the eastern slope of the northern Sierra Nevada. Nests were generally placed 7 m or higher in mature trees, situated at over 50% of the nest-plant's height, and most often in the periphery of the nest-plant's foliage. The two most common nest-plant species were the Quaking Aspen (*Populus tremuloides*,  $n = 30$ ) and Lodgepole Pine (*Pinus contorta*,  $n = 30$ ). Such heavy reliance on a conifer by the Warbling Vireo has not been reported previously. Nest success was not significantly associated with habitat or nest-site characteristics; thus successful sites did not differ dramatically from unsuccessful sites. Most egg dates were concentrated within a single week (2–9 July), and most of the successful nests were in the egg-incubation phase during the first two weeks of July. Eighteen nests fledged at least one Warbling Vireo; one nest fledged a Brown-headed Cowbird (*Molothrus ater*). Seventy-four percent of nesting attempts failed; most failed nests showed signs of avian rather than mammalian predation. We recommend that vireo conservation efforts in the northern Sierra Nevada focus on increasing the availability of suitable nest sites by promoting mature stands of aspens and pines offering well-concealed nest sites in the periphery of the foliage, limiting forest disturbance in July during the critical nesting period, and minimizing environmental modifications that favor avian nest predators such as Steller's Jay (*Cyanocitta stelleri*).

Several species of North American vireo have endured drastic population declines or regional extirpation in recent times (e.g., Bell's, *Vireo bellii*, Black-capped, *V. atricapillus*, and Gray, *V. vicinor*, Gardali et al. 2000). Despite considerable research attention focused on endangered vireos, the basic natural history and population trends of the much more widespread Warbling Vireo (*V. gilvus*) are not well known (Gardali and Ballard 2000, Ward and Smith 2000). Various lines of evidence suggest that Warbling Vireo (*V. g. swainsonii*) populations are declining in California (Gardali et al. 2000, Gardali and Jaramillo 2001), despite moderately positive population trends in North America as a whole (+1.2% per year,  $P < 0.05$ ; Sauer et al. 2001). Breeding Bird Surveys imply that California populations of the Warbling Vireo have declined annually by 1.0% ( $P < 0.04$ , Sauer et al. 2001). In addition, at Palomarin, Marin County, autumnal capture rates of the Warbling Vireo have decreased over the past two decades by 9% per year (Ballard et al. 2003). Furthermore, in the last century, the Warbling Vireo has been largely extirpated from the Sacramento Valley and San Diego County (Gaines 1974, Unitt 1984, Gardali and Ballard 2000).

Demographic studies suggest that low reproductive success rather than low adult survivorship is the most important contributor to the decline (Gardali et al. 2000, Gardali and Jaramillo 2001). Because the species' basic nesting ecology has been characterized for only a few populations in western North America (Gardali and Ballard 2000), the ultimate causes of this low productivity remain unknown.

For conservation plans for declining neotropical migrants such as the Warbling Vireo to be effective, the stage or stages in the annual cycle that limit population growth, as well as habitat features that directly influence reproduction and survival, must be identified (Martin 1992, Gardali et al. 2000). Toward that end, we analyzed in detail the breeding cycle and nest-site characteristics of a previously unstudied population of Warbling Vireos nesting in broadleaf and mixed coniferous forests on the eastern slope of the northern Sierra Nevada. Avian habitat relationships in the northern Sierra Nevada are poorly understood in comparison to those in the southern Sierra Nevada and Sierra foothills, for which there is extensive literature, e.g., Verner and Boss (1980) and numerous references therein. Thus identifying key environmental characteristics for vireos in this area will not only deepen our understanding of avian habitat associations in western North America but will also advance the development of land management appropriate to benefit the Warbling Vireo in California.

## METHODS

We studied Warbling Vireo breeding ecology from June through August of 1998 in three riparian areas on the eastern slope of the Sierra Nevada in northern California in the Tahoe National Forest: Sagehen Creek (7 km northwest of Hobart Mills in Nevada County at 39° 25.852' N, 120° 14.481' W, elevation 1937 m), Davies Creek (12 km north of Hobart Mills in Sierra County at 39° 30.699' N, 120° 9.632' W, elevation 1900 m), and Klondike Meadow along East Martis Creek (17 km southeast of Hobart Mills in Placer County at 39° 18.357' N, 120° 03.206' W, elevation 2120 m). Each study area consisted of Sierran montane riparian and meadow habitats with stands of willow (*Salix* sp.) and occasionally alder (*Alnus* sp.) bordered by conifers, primarily Lodgepole Pine (*Pinus contorta*), and broadleaf trees, primarily Quaking Aspen (*Populus tremuloides*) and Fremont Cottonwood (*P. fremontii*).

We located Warbling Vireo nests by following adult vireos (Martin and Geupel 1993). We monitored the progress of each nest at least once a week and no more than twice a week. To identify critical periods in the nesting cycle, we recorded dates on which pairs were observed building nests, laying eggs, incubating eggs, or brooding nestlings. For unsuccessful nesting attempts, we noted the stage at which failure occurred (i.e., abandonment while building or laying, egg incubation, or nestling period). Failed nesting attempts were those in which the adult pair, the nest, or all of its contents disappeared before fledging was possible. Whenever possible, we classified failed nests to the most likely type of predator as outlined by Morton et al. (1993). We identified the nest predator as "avian" if the nest contents

disappeared before fledging but the nest cup appeared undisturbed, and “mammalian” if the nest was knocked down or the nest cup lost its integrity. Clearly, there are limitations to this indirect method of identifying nest predators (Larivière 1999, Thompson and Burhans 2003).

We examined a suite of nest-site characteristics, many of which are likely to be affected by proposed management to restore late-seral forest structure and regenerate aspen stands throughout the Sierra Nevada (SNFPADSEIS 2003). For each nest, using protocols from Ralph et al. (1993), we determined the plant species containing the nest, height of the nest, height of nest plant, nest-plant diameter at breast height (dbh), nest orientation measured as the compass direction from the main stem to the nest, number of branches supporting the nest, average diameter of the branches supporting the nest, nest distance from central stem, nest distance from the periphery of the plant, nest concealment measured in each of the four cardinal directions from the nest (0–25% concealment was ranked “1,” 26–50% concealment was ranked “2,” 51–75% concealment was ranked “3,” and 76–100% concealment was ranked “4”), and canopy cover measured in each of the four cardinal directions from the nest (percent canopy cover was ranked in a fashion similar to nest concealment). We tabulated summary scores for both nest concealment and canopy cover by averaging the scores in each of the four cardinal directions. To enhance the reliability of all measures, early in the field season we trained the study’s participants until they achieved a high degree of repeatability.

To characterize general habitat associations for Warbling Vireos nesting in the northern Sierra Nevada, we investigated differences in nest-site characteristics among nest-plant species. Nest-site data were first tested for normality and then analyzed with a one-way analysis of variance (ANOVA, Sokal and Rohlf 1995). A Bonferroni correction was used to maintain an alpha level of 0.05 for the overall analysis (Lehner 1996). The variables “average diameter of the branches supporting the nest” and “nest distance from the periphery of the plant” were log-transformed for normality. The “number of branches supporting the nest” and the “nest canopy cover summary score” did not conform to a normal distribution even after transformation and were therefore analyzed with a Kruskal–Wallis one-way analysis of variance (Lehner 1996).

To highlight habitat characteristics critical to vireo productivity in the northern Sierra Nevada, we determined percent nest success by study site and nest-plant species. We then analyzed the likelihood of nest success using logistic regression. Independent variables included study site (Sagehen Creek, Davies Creek, and Klondike Meadow), nest-plant species, nest height, and within a nest-plant species the plant’s height and diameter. The dependent variable “nest success” (Kus 2002) was coded as “0” for pairs failing to fledge young or fledging a Brown-headed Cowbird (*Molothrus ater*), and “1” for pairs where we either observed fledging, observed adults feeding fledglings in the natal territory, or observed fledglings within the natal territory accompanied closely by adults. Significance was accepted at  $P < 0.05$ .

## RESULTS

We found Warbling Vireos nesting in Quaking Aspen, Lodgepole Pine, Fremont Cottonwood, and willow; the two most common nest plants were the aspen and pine (Table 1). Nest heights ranged from 1.2 m (in a willow) to 19.0 m (in a Lodgepole Pine), reflecting that the plants in which these nests were placed ranged in height from 1.8 m (a willow) to 28.0 m (a Lodgepole Pine). Among the four nest-plant species nest-site characteristics were very similar. Five of the nine habitat characteristics compared did not differ significantly (Tables 1–3). Most nests found (68%, 46 of 68) were in mature trees (10 to 17 m tall) and positioned in the periphery of the nest-plant's foliage (Tables 1 and 3); 51% (33 of 64) were placed at least three times as far from the main stem as they were from the periphery of the plant. Furthermore, the distance of the nest from the periphery was on average less than 1 m and invariant among the plant species (Table 3). In general, the nests were well hidden by foliage: 63% (41 of 65) had more than 50% concealment around the entire nest, and 74% (40 of 54) had more than 50% canopy cover. Most nests (81%, 50 of 62) were situated in a fork between two branches of relatively small diameter (0.20–2.50 cm); 19% of nests (12 of 62, five in Quaking Aspen and seven in Lodgepole Pine) were supported by three branches.

Four of the nest-site characteristics differed significantly by nest-plant species (Tables 1–3). For all but one of these nest-site characteristics, nests in willows (a shrub) varied the most from the general pattern. The “average diameter of branches supporting the nest” was typically small (< 2 cm), but for nests in willows it was especially small (Table 2). The general pattern for the variables “nest height” and “distance from the main stem to the nest” was that the taller the nest plant the higher the nest was placed in it and the farther it was from the main stem. Nests in willows also showed this pattern, but the distances were disproportionately small in comparison to those in other nest plants (Tables 1 and 3). The fourth differing nest-site characteristic was “nest height as a percentage of tree height.” In this case, the Lodgepole

**Table 1** Heights of Warbling Vireo Nests by Type of Nest Plant<sup>a</sup>

Nest Plant	Number of Nests	Nest Height (m)	Plant Height (m)	Nest Height (% of Tree Height)
Aspen	30	7.0 ± 3.3	10.9 ± 5.0	65.1 ± 17.0
Cottonwood	4	6.4 ± 4.0	10.6 ± 5.8	57.9 ± 12.4
Lodgepole Pine	30	8.2 ± 4.2	17.6 ± 5.6	46.6 ± 19.0
Willow	6	2.0 ± 0.6	2.7 ± 0.6	70.2 ± 9.8
All nests	70	7.0 ± 4.0 <sup>b</sup>	13.0 ± 5.0	57.2 ± 19.4 <sup>b</sup>

<sup>a</sup>Mean ± standard deviation.

<sup>b</sup> $P \leq 0.05$  for single-factor ANOVA examining differences in nest-site characteristics among tree and shrub species. (No statistical analysis was done on number of nests, and because of pronounced differences in growth form among plant species no analysis was performed on plant height).

**Table 2** Nest-Plant Diameters, Nest Orientations, and Numbers of Supporting Branches of Warbling Vireo Nests by Type of Nest Plant<sup>a</sup>

Nest Plant	Diameter (cm) <sup>b</sup>	Nest Orientation (°)	Number of Supporting Branches	Average Diameter of Branches Supporting Nest (cm)
Aspen	28.7 ± 15.6	163.0 ± 80.5	2.2 ± 0.4	1.0 ± 0.6
Cottonwood	38.0 ± 24.8	156.8 ± 128.5	2.0 ± 0	1.1 ± 0.5
Lodgepole Pine	49.3 ± 21.4	227.9 ± 104.6	2.3 ± 0.4	1.5 ± 0.6
Willow	—	244.0 ± 128.9	2.0 ± 0.0	0.3 ± 0.1
All nests	38.2 ± 21.6	197.3 ± 102.0	2.2 ± 0.4	1.1 ± 0.7 <sup>c</sup>

<sup>a</sup>Mean ± standard deviation.

<sup>b</sup>Of trunk at breast height (dbh).

<sup>c</sup> $P \leq 0.05$  for single-factor ANOVA or Kruskal-Wallis test examining differences in nest-site characteristics among tree and shrub species. (Because of pronounced differences in growth form among plant species no statistical analysis was performed on plant diameter).

Pine was the only nest-plant species in which nests were situated on average at less than 50% of the height of the nest plant (Table 1).

Nest success was low; 74% (52 of 70) of nesting attempts failed to produce fledglings. Of the nests that failed, 12% ( $n = 6$ ) were abandoned during building/laying, 44% ( $n = 23$ ) failed during incubation, 42% ( $n = 22$ ) failed during the nestling stage, and one (2%) fledged only a Brown-headed Cowbird. Ten of the failed nests were positioned low enough that we could see the contents of the entire nest. Of those ten, three were abandoned during incubation, six showed signs of avian predation, and one showed sign of mammalian predation. At an additional eleven nests we were able to see the heads of nestlings above the nest's rim: eight showed signs of avian predation and three showed signs of mammalian predation. Because the contents of these nests were not completely visible we cannot rule out the possibility that some were abandoned and not depredated. However, we

**Table 3** Position and Concealment of Warbling Vireo Nests by Type of Nest Plant<sup>a</sup>

Nest Plant	Distance from Main Stem to Nest (m)	Distance of Nest from Periphery (m)	Nest Concealment Summary Score	Nest Canopy Cover Summary Score
Aspen	1.5 ± 1.0	0.8 ± 0.6	3.31 ± 0.6	3.2 ± 0.9
Cottonwood	1.0 ± 0.8	0.8 ± 0.2	3.94 ± 0.1	3.92 ± 0.1
Lodgepole Pine	2.1 ± 0.8	0.6 ± 0.5	2.94 ± 0.7	3.21 ± 0.7
Willow	0.06 ± 0.03	1.1 ± 1.2	3.45 ± 0.6	NA <sup>b</sup>
All nests	1.6 ± 1.0 <sup>c</sup>	0.7 ± 0.6	3.2 ± 0.7	3.2 ± 0.8

<sup>a</sup>Mean ± standard deviation.

<sup>b</sup>NA, not applicable.

<sup>c</sup> $P \leq 0.05$  for single factor ANOVA or Kruskal-Wallis test examining differences in nest-site characteristics among tree and shrub species.

have no evidence of abandonment during brooding from those nests whose contents were visible. Combining these two groups of nests together ( $n = 21$ ) yields an estimate of 67% ( $n = 14$ ) failure due to avian predation, 19% ( $n = 4$ ) failure due to mammalian predation, and 14% ( $n = 3$ ) failure due to abandonment.

Successful Warbling Vireo nests (26%, 18 of 70) were not associated strongly with specific habitat characteristics. The likelihood of an attempt's being successful did not vary significantly by study site (log-likelihood of study-site model  $\chi^2 = 3.9$ ,  $P = 0.14$ ): 35% successful (13 of 37) at Sagehen Creek, 17% successful (4 of 24) at Davies Creek, and 11% successful (1 of 9) at Klondike Meadow. The likelihood of a successful nesting attempt was also not significantly affected by nest-plant species (log-likelihood of nest-plant species model  $\chi^2 = 3.0$ ,  $P = 0.40$ ): 27% (8 of 30) successful in Quaking Aspen, 30% (9 of 30) successful in Lodgepole Pine, 17% (1 of 6) successful in willow, and zero (of 4) successful in Fremont Cottonwood. Neither was the likelihood of a successful attempt significantly affected by nest height (log-likelihood of nest height model  $\chi^2 = 2.5$ ,  $P = 0.11$ ), nest-plant height (log-likelihood of nest-plant-height model  $\chi^2 = 3.2$ ,  $P = 0.08$ ), or nest-plant diameter (log-likelihood of nest-plant-diameter model  $\chi^2 = 1.0$ ,  $P = 0.31$ ). Inclusion of study site and nest-plant species (i.e., performing the logistic regression using both study site and nest-plant species as independent variables) did not improve the model (log-likelihood of study-site and nest-plant-species model  $\chi^2 = 6.9$ ,  $P = 0.23$ ), nor did including nest-plant height and nest-plant diameter (log-likelihood of nest-plant-height and nest-plant-diameter model  $\chi^2 = 1.7$ ,  $P = 0.43$ ).

The nest surveys allowed us to detail the Warbling Vireo's nesting cycle on the eastern slope of the northern Sierra Nevada. The peak period for incubation was the first two weeks in July; 46 of the nests we studied were discovered during egg incubation, and 56% ( $n = 26$ ) of those were found during the first two weeks in July. Sixteen of the successful nests were monitored during incubation, and of those 75% ( $n = 12$ ) were being incubated during the first two weeks in July. Fifty-three percent of egg dates (26 of 49 nests discovered with at least one egg) ranged from 2 to 9 July. The first Warbling Vireo nest was found 19 June in the egg-incubation stage at Davies Creek; the last was discovered on 10 August, also at Davies Creek. When discovered, the last nest contained one Warbling Vireo egg and one Brown-headed Cowbird nestling. Thus, the eggs for this last nesting attempt were probably laid near the end of July. One pair nesting in a willow at Sagehen Creek incubated two apparently infertile eggs for at least 25 days.

Four of the 70 nests (6%) were renesting attempts; we observed renesting only at Davies Creek. Only pairs whose first nesting effort failed during incubation and early in the breeding season (between 19 June and 24 June) attempted to renest. One female was observed dismantling the first unsuccessful nest and using those pieces to build a second nest. Another female built a nest composed of a great deal of white material, and after this nest failed she then built a second white nest that also failed. We did not observe any double brooding. Our study population was not color-banded, so it is possible that we failed to detect some renesting attempts and that some pairs could have dispersed and renested outside of the study area.

## DISCUSSION

On the eastern slope of the northern Sierra Nevada Warbling Vireos nested predominantly in Quaking Aspen and Lodgepole Pine; other plant species less commonly used were Fremont Cottonwood and willow. Despite differences in growth form between trees and shrubs, in all of the nest-plant species nest-site characteristics were very similar (Tables 1–3). Warbling Vireos generally nested 7 m or higher in mature trees, placing their nests at over 50% of the nest-plant's height and most often in the periphery of the nest-plant's foliage. This preference for nesting in the periphery of the tree is especially evident in nests in Lodgepole Pine being situated at less than 50% of the tree's height (Table 1). Because of the pyramidal shape of this conifer, the branches below the midpoint extend farther from the main stem and only nests on those branches may be positioned in the outermost periphery of the plant.

Although the characteristics of the nests that we studied conform to the general pattern reported for the species (Gardali and Ballard 2000), we did discover two differences. Warbling Vireos in the northern Sierra Nevada nest regularly in Lodgepole Pine ( $n = 30$ , 43%), in contrast to the preference for deciduous trees described in the literature (Gardali and Ballard 2000). Studies of the vireo's nest-site selection in southern Ontario, Arizona, coastal California, and the foothills of the Owens Valley of eastern California, reported only a single nest (0.6%,  $n = 162$ ) in a conifer (Ponderosa Pine, *P. ponderosa*; reviewed by Gardali and Ballard 2000). Also, in contrast to the general pattern described in the literature, 19% of the Warbling Vireo nests we found were supported by three branches rather than two.

The percent nest success we observed was low (26%) in comparison to other high-elevation populations (62% success in Arizona, Martin and Li 1992). In contrast to other western populations (Ward and Smith 2000), this poor success was apparently not the result of pressure from brood parasites. Of the 19 nests that fledged offspring only a single nest fledged a cowbird. Similarly, the analysis of nest success illustrated that successful Warbling Vireo nest sites do not differ dramatically from unsuccessful sites; the likelihood of a successful nesting attempt was not significantly affected by study site, nest-plant species, nest height, or within a nest-plant species by nest-plant height or diameter. This lack of differentiation may signify that less obvious habitat features play an important role in determining the Warbling Vireo's nest success. The nest site's microclimate (a subtle feature of nesting habitat) may be an important factor (Smith, Reynolds, and LeBuhn unpubl. data). The lack of differentiation also suggests that preserving and enhancing mature aspens and pines with well-concealed sites in the periphery of the foliage (i.e., those features of the habitat most often associated with vireo nests) might benefit vireo productivity simply by increasing the availability of suitable sites.

Egg dates on the eastern slope of the northern Sierra Nevada range from 19 June to the end of July. Previous estimates of Warbling Vireo egg dates for California range from 26 April through 25 July (Gardali and Ballard 2000). Altitudinal effects on local climatic conditions may explain the delayed initiation of egg laying in the northern Sierra Nevada. The majority

of egg dates in the northern Sierra Nevada fell within a single week of July (2 July through 9 July). This contrasts dramatically with other western populations, in which the majority of egg dates have been reported to span over two or three weeks (Gardali and Ballard 2000). Most (75%) of our successful nests were in the egg-incubation phase during the first two weeks in July; this was also the peak egg-incubation period for the population as a whole. On the basis of an incubation period of 12 or 13 days (Gardali and Ballard 2000), the peak nestling phase falls during the last two weeks of July. In terms of offspring mortality there is little difference in risk between incubation (44% failed) and the nestling stage (42% failed). Because reproductive success is thought to be the primary factor limiting the vireo's population growth in California (Gardali et al. 2000), minimizing activities that disturb nesting during the month of July should be a focal consideration in the development of management plans in the northern Sierra Nevada.

We observed no double brooding, which Tewksbury et al. (1998) considered common among Warbling Vireos nesting in Montana. In addition, unlike Warbling Vireos near Point Reyes (Gardali and Ballard 2000), very few pairs we studied attempted to renest after a failure. A highly synchronized pulse of egg laying combined with a lack of double brooding and renesting argues that the breeding season for Warbling Vireos at high elevation in California is shorter than at lower elevations, making the birds more sensitive to disturbance.

Far more failed nests apparently suffered predation by birds (67%) than by mammals (19%). Among the avian nest predators occurring in the study area, such as Clark's Nutcracker (*Nucifraga columbiana*), American Crow (*Corvus brachyrhynchos*), and Common Raven (*C. corax*), Steller's Jay (*Cyanocitta stelleri*) is by far the most numerous and widespread (Reynolds and Smith unpubl. data). Steller's Jays are known to exert tremendous nest-predation pressure on passerines and neotropical migrants in particular (Sieving and Willson 1999). We did not observe Steller's Jays preying on Warbling Vireo nests but we did observe vireos scolding jays near nests, a reaction to a nest predator (Gardali and Ballard 2000).

Throughout its range the Warbling Vireo prefers open parkland, forest edge, and forest openings (James 1976, Gardali and Ballard 2000, Ward and Smith 2000). Open and parklike coniferous and riparian habitats in the Sierra Nevada have declined significantly over the last 150 years as a result of fire suppression and the encroachment of smaller trees (SNEP 1996). In addition, photographic analysis has revealed that all Sierran riparian corridors have been interrupted by human factors like roads, railroads, and grazing (SNEP 1996). Jay populations increase dramatically near man-modified environments (Sieving and Willson 1999), and Steller's Jays have increased significantly in California during the same period in which Warbling Vireos have declined (Gardali et al. 2000). Human alteration of the landscape of California may have contributed to the decline in the Warbling Vireo by limiting suitable breeding habitat and increasing populations of nest predators.

Our findings suggest that mature stands of Quaking Aspen and Lodgepole Pine are important features of Warbling Vireo nesting habitat on the eastern slope of the northern Sierra Nevada. In addition, our data highlight the



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restricted and synchronous nature of the Warbling Vireo's breeding season at high elevations and thus the importance of reducing forest disturbance during July, the critical nesting period. Our results also argue that the vireo's low reproductive success in the northern Sierra Nevada is currently determined more by nest predation than by habitat or brood parasites. Thus management practices that promote avian nest predators should be minimized. Future studies should focus on the relationship between proposed habitat changes in the Sierra Nevada (SNFPADSEIS 2003) and the feedback on the population dynamics of nest predators and the reproductive success of Warbling Vireos.

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