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Warbling Vireo reproductive success and nest-site characteristics in the northern Sierra Nevada, California

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ABSTRACT. Over the past 20 yr Warbling Vireo (*Vireo gilvus*) populations have declined in California. We monitored Warbling Vireo nests in the high elevations of the northern Sierra Nevada in the Tahoe National Forest near Truckee, California. Nest survivorship was low (29.9% Mayfield estimate) compared to Warbling Vireo populations outside of California, but similar to levels reported for other California populations. Brown-headed Cowbird (*Molothrus ater*) parasitism in the study population was low (7%). Warbling Vireo nest fate was related to nest-site location; successful nests in lodgepole pine (*Pinus contorta*) were situated on the west or "warmer" side of the tree, in the outer periphery of the foliage, and in areas with slightly less canopy cover compared to unsuccessful nests. These features of the nest site may help reduce the threat of predation and combat cold stress. Our results argue that Warbling Vireos in the northern Sierra Nevada have low nest survivorship (similar to populations in other areas of the state), and that successful nests are often found on thin branches well removed from the main stem.

SINOPSIS. **Exito de anidamineto y características claves del lugar de anidamiento de *Vireo gilvus* en la parte norte de la Sierra Nevada, California**

En los ultimos 20 anos las poblaciones de *Vireo gilvus* se han reducido en numeros en California. Monitoreamos nidos del ave en las partes atlas de la Sierra Nevada, California. La éxito de nidos resultó bajo (29.9%, estimado Mayfield), al comparar los datos obtendios con lo informado para el ave en otras localidades de California. El parasitismo reproductivo por parte del tordo (*Molothrus ater*) resultó bajo (7%). El éxito, de los nidos estuvo relacionado a la localización de los mismos. Los nidos exitosos fueron construidos en *Pinus contorta*, localizados en la parte oeste (el área de temperatura más cálida), en la parte externa del follaje y en áreas de menos docel, comparado con nidos fracasados. Estas particularidades del lugar de construcción pudieran ayudar a combatir el frío y a reducir la depredación. Nuestros resultados indican que los nidos de la especie estudiada en la Sierra Nevada, tienen altas posibilidades de fracaso (similar a otras poblaciones del estado) y que los nidos exitosos usualmente se encuentran en ramas finas, ampliamente separadas del tronco del árbol.

Key words: Neotropical migrant, nest success, *Vireo gilvus*

Warbling Vireos (*Vireo gilvus*) have shown persistent population declines in California from 1966 to 2003 (−1.27%/yr, $P = 0.008$; Sauer et al. 2004). Breeding Bird Survey declines are corroborated by breeding season declines (site-attached individuals; Gardali et al. 2000) and indirectly by declines in migrants in coastal California (Gardali and Jaramillo 2001; Ballard et al. 2003). In addition, within recent times in California, Warbling Vireos have been extirpated from the Sacramento Valley and San Diego County (Unitt 1984; Gardali and Ballard 2000), and fall capture rates in coastal California have steadily declined (−9% per yr; Ballard et al. 2003). Demographic studies indicate that reproductive success, and not adult survivorship, is the most important contributor to Warbling Vireo population declines in California (Gardali et al. 2000; Gardali and Jaramillo 2001). Ward and Smith (2000) suggested that Warbling Vireos at low elevation in British Columbia may be especially hard hit by habitat loss and increasing incidence of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). In the southern Sierra Nevada of California, Purcell and Verner (1999) found the highest rate of brood parasitism in Warbling Vireo populations at the lowest elevation study site. If Ward and Smith's (2000) hypothesis applies in California, then declining populations at low elevation might be maintained by recruitment

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from more productive populations found in high elevation habitats.

The ecological factors responsible for the decline of Warbling Vireos in California are largely unknown. One suspected agent is rapid urban and agricultural expansion in low elevations, which is dramatically changing the ecosystems of the Great Central Valley and Coast Ranges, and increasing populations of brood parasites and nest predators, which are positively affected by habitat fragmentation (Rothstein et al. 1980; Purcell and Verner 1999; Sieving and Willson 1999). Smith et al. (2004) identified nest predation as the most likely cause of Warbling Vireo nest failure in the northern Sierra Nevada of California. Throughout California, estimates of brood parasitism in populations of Warbling Vireos (albeit based on small samples) range from 0–80% (Rothstein et al. 1980; Purcell and Verner 1999). Because the extensively forested high elevation areas of the Sierra Nevada have been subject to less overall conversion of habitat (Sierra Nevada Ecosystem Project 1996) and areas far from pack stations and livestock holding facilities have low cowbird abundances (Rothstein et al. 1980), they might be expected to harbor Warbling Vireo populations with higher reproductive success.

To understand better the condition of California populations of Warbling Vireos, we conducted a study of nesting success in the high elevations on the eastern slope of the northern Sierra Nevada. We targeted these populations because they had not been studied previously. We made a detailed analysis of nest-site attributes, with the goal of identifying habitat characteristics that are associated with successful nesting attempts. Should Warbling Vireo populations continue to decline in California these data will aid conservation efforts by identifying whether productive Warbling Vireo populations exist at high elevation and determining whether certain nest-site characteristics are key to vireo productivity.

METHODS

Warbling Vireos were studied in three riparian areas on the eastern slope of the Sierra Nevada in northern California in the Tahoe National Forest. One study site was along Sagehen Creek (7 km northwest of Hobart Mills in Nevada County; 39°25.852′N, 120°14.481′W, elevation 1937 m), a second site was located along Davies Creek (12 km north of Hobart Mills in Sierra County; 39°30.699′N, 120°09.632′W, elevation 1900 m), and a third site was Klondike Meadow located along East Martis Creek (17 km southeast of Hobart Mills in Placer County; 39°18.357′N, 120°03.206′W, elevation 2120 m). Each of these riparian areas consisted of high elevation meadow with relatively flat to rolling topography with stands of willow (*Salix* sp.) and occasionally alder (*Alnus* sp.) bordered by conifers (primarily lodgepole pine, *Pinus contorta*) and broadleaf trees such as quaking aspen (*Populus tremuloides*) and Fremont cottonwood (*P. fremontii*). The Sagehen Creek study site, as part of the University of California's special use area, is subject to less grazing and logging pressure and is the most protected of the three sites.

To generate estimates of nesting success, we located and monitored nests from June through August of 1998. Using Mayfield's (1975) method, we monitored progress of each nest at least once a week and no more than twice a week. Whenever possible, we made visual inspection of the nest contents, checking nests high in trees with mirrors mounted on telescoping aluminum poles. When this was not possible, we relied on behavioral observations (such as adults carrying food or fecal sacs, heads of nestlings visible above the nest rim, or adults feeding fledglings in the natal territory) and the condition of the nest to provide information on nesting status. Martin and Geupel (1993) report that adults may carry food up to 24 h or longer after predation of the nest. Thus, when only behavioral data were available, we returned to each nest at least once after we suspected failure to verify status. A nest was considered successful if it fledged at least one young, excluding cowbirds (Barber et al. 2001). Following Gardali et al. (2000), we generated Mayfield (1975) estimates of nest survivorship based on a 29-d laying, incubation, and nestling period. Following the recommendation of Manolis et al. (2000), nest exposure was terminated with the last observed active date for nests with uncertain fate and with the midpoint between the last observed active and the first observed inactive dates for nests of known fate. We used program CONTRAST (Hines and Sauer 1989; Sauer and Williams 1989) to compare using a χ^2 statistic daily nest survival estimates among study sites and among nest plant

species. We also compared Mayfield (1975) estimates of overall nest survivorship with 95% confidence limits (Nur et al. 1999) among study sites and nest plant species.

To identify nest-site attributes key to Warbling Vireo reproductive success, we compared the habitat characteristics between successful and unsuccessful nests. Because of dramatic differences in growth form among conifers, broadleaf trees, and shrubs, this analysis was done separately by nest plant species. We measured the following nest variables: nest height, nest plant height, nest height as a percentage of plant height, plant dbh, nest orientation measured as the compass direction from the main stem to the nest, average diameter of the branches supporting the nest, distance of nest from main stem, distance of nest from periphery, an estimate of nest concealment based upon a summary of the concealment scores in each of the four cardinal directions, and an estimate of nest canopy cover based upon a summary of the canopy cover in each of the four cardinal directions. The summary scores range from "1" indicating less than 25% to "4" indicating greater than 75% total nest concealment or canopy cover. For a detailed description of nest-site variables, see Ralph et al. (1993). For a review of nest-site characteristics for all nests studied, see Smith et al. (2004). Warbling Vireos parasitized by Brown-headed Cowbirds reared no young of their own; thus we considered all parasitized nests unsuccessful.

We used a stepwise discriminant function analysis (Williams 1983) to identify which habitat variables most reliably predicted nest success for each nest plant species. Each stepwise discriminant function analysis, for successful and unsuccessful nests by tree species, was based on the pooled covariance matrix and Wilks' lambda (Morrison 1976). Only those nests ($N = 43$) with no missing information and whose fate was certain (e.g., we either observed parents feeding fledglings, or the nest or all of its contents disappeared before fledging could have occurred) were used in this part of the analysis. We log-transformed counts that were not normally distributed. Covariance matrices were tested for homogeneity using Box's M criterion (Martin and Roper 1988). There was no evidence of heteroscedasticity for the within-group covariance matrices ($P > 0.05$). Values given for nest-site characteristics significantly discriminating between successful and unsuccessful nests represent means ± SD. Because there were so few nests found in cottonwood and willow, they were eliminated from analyses regarding nest-site characteristics, but they were included in the overall estimate of nesting success and comparisons of success among study sites.

RESULTS

We located 69 Warbling Vireo nests, distributed in lodgepole pine ($N = 30$), quaking aspen ($N = 29$), Fremont cottonwood ($N = 4$), and willow ($N = 6$). The Mayfield (1975) estimate of nest survivorship for all nests studied was 29.9% (Table 1). Despite significant differences in nest-site characteristics by nest plant type (Smith et al. 2004), estimates of Warbling Vireo daily nest survival and Mayfield estimates of nest survivorship did not vary (Table 1). Similarly, these estimates did not vary by study site (Table 1).

Ten of the nests in the study were positioned low enough such that we could see the contents of the entire nest. Of those, one (10%) was parasitized. For a separate group of 12 nests, we were able to see the heads of nestlings above the rim. Of those, one (8%) was parasitized. At another 19 nesting attempts, we were able to identify adult Warbling Vireos feeding fledglings in the natal territory; only one pair (5%) fed a single Brown-headed Cowbird fledgling. Combining these three groups of nests together yields an estimate of brood parasitism of 7% (3 of 41). Brown-headed Cowbird parasitism was evident only at the Davies Creek study site.

For nests in lodgepole pine with complete data ($N = 26$), three nest-site characteristics were significant in discriminating successful from unsuccessful nests (eigenvalue = 0.63, canonical correlation = 0.62, 88% of nests correctly classified). These variables are (in descending order of importance): nest orientation (Wilks' lambda = 0.86, $P = 0.05$, Partial $R = -0.51$), the log-transformed distance of the nest from the periphery (Wilks' lambda = 0.73, $P = 0.03$, Partial $R = 0.40$), and the nest canopy cover summary score (Wilks' lambda = 0.61, $P = 0.01$, Partial $R = 0.22$). Group centroids for the lodgepole nests were located along the canonical discriminant function as follows: group mean for unsuccessful was 0.51 and

Table 1. Warbling Vireo nesting success by nest plant type and study site.

	Number of nests[a]	Exposure days	Daily nest survival[b,c]	Nest survivorship[d]
Nest plant type				
Quaking aspen	29 (4)	459.5	0.965 ± 0.009	0.358 (0.215, 0.590)
Fremont cottonwood	4 (0)	62.5	0.936 ± 0.031	0.147 (0.021, 0.910)
Lodgepole pine	30 (0)	432.5	0.951 ± 0.010	0.236 (0.126, 0.435)
Willow	6 (1)	123.5	0.976 ± 0.014	0.490 (0.216, 1.086)
Study site				
Davies Creek	24 (1)	371	0.954 ± 0.011	0.257 (0.133, 0.486)
Klondike Meadow	8 (3)	97	0.959 ± 0.020	0.295 (0.087, 0.953)
Sagehen Creek	37 (1)	610	0.962 ± 0.008	0.328 (0.207, 0.516)
Total	69 (5)	1078	0.959 ± 0.006	0.299 (0.208, 0.426)

[a] Number in parenthesis represents the number of nests with an uncertain outcome.
[b] Daily nest survival ± SE.
[c] Daily nest survival does not vary by nest plant type ($\chi^2_3 = 3.0$, $P = 0.39$) or by study site ($\chi^2_2 = 0.35$, $P = 0.84$).
[d] Mayfield estimate with 95% confidence limits in parenthesis.

group mean for successful was −1.15. This indicates that the successful nests in lodgepole pine ($N = 8$) were on the west side of the tree (successful, 286.9° ± 57.4 vs. unsuccessful, 201.3° ± 112.7), closer to the outermost periphery of the tree's foliage (successful, 0.32 m ± 0.17 vs. unsuccessful, 0.65 m ± 0.58), and with slightly less canopy cover than unsuccessful nests (successful, 3.1 ± 0.59 vs. unsuccessful, 3.3 ± 0.77).

No variable significantly discriminated between successful and unsuccessful nests in quaking aspen ($N = 17$; eigenvalue = 0.26, canonical correlation = 0.45, 50% of nests correctly classified).

DISCUSSION

Regardless of nest plant type or study site, Warbling Vireo nest success in the northern Sierra Nevada was low (29.9%) in 1998 and contrasts dramatically with estimates from high-elevation populations in Arizona in which 62% of nests were successful (Martin and Li 1992). Nest survivorship at our sites in the Sierra Nevada (based upon a single season) was similar to that derived for high-elevation populations of Warbling Vireos in southwestern Colorado (22%; Ortega and Ortega 2003) and declining coastal California populations (21%; Gardali et al. 2000). Overall, Warbling Vireo nest survivorship in California is low and perhaps cause for concern, when compared to Mayfield estimates given for other open-cup nesters in forested landscapes (43%; Hanski et al. 1996) and for Neotropical migrants in general (42%; Martin 1992).

Warbling Vireo populations in the northern Sierra Nevada had a low rate of brood parasitism (7%), similar to rates reported for Warbling Vireos at high elevation sites in the southern Sierra Nevada (Verner and Ritter 1983; Purcell and Verner 1999). This low rate of parasitism is not due to a low incidence of Brown-headed Cowbirds. In fact, the Brown-headed Cowbird is one of the most commonly detected species in the study area (ranking 13 of 91 species; M. D. Reynolds and J. I. Smith, unpubl. data). The low rate of brood parasitism for Warbling Vireos in the Sierra Nevada is an order of magnitude lower than rates reported for other western populations (Tewksbury et al. 1998; Gardali and Ballard 2000; Sealy et al. 2000; Ortega and Ortega 2003), including those at lower elevation in the Sierra Nevada (43% parasitized, $N = 7$; K. Purcell, pers. comm.) and is most similar to rates reported for eastern populations in which adults are known to recognize and eject cowbird eggs (Sealy 1996). We never observed puncture-ejection behavior, but it has been observed in populations within the contact zone of the two subspecies (Sealy et al. 2000). One possible explanation for the surprisingly low rate of brood parasitism in our population is the abundance of alternate host

species. In particular, Yellow Warblers (*Dendroica petechia*; one of the most frequent cowbird hosts; Ehrlich et al. 1988) are one of the most commonly detected species in the study area; it ranked 10 of 91 species in number of detections and is almost four times as likely to be detected in the study area as is the Warbling Vireo (M. D. Reynolds and J. I. Smith, unpubl. data). Another possible explanation for the low rate of parasitism is the climatic effects of La Niña in 1998. This event resulted in severe drought, which can negatively impact passerine productivity (DeSante and Geupel 1987) and perhaps the abundance and timing of the arrival of brood parasites in the study area. We consider this unlikely, however, in that Brown-headed Cowbirds were observed throughout the study area during the breeding season in 1998, and data from our long-term constant-effort banding station show that the Warbling Vireo breeding cycle in 1998 was not unusual compared to other breeding seasons (M. D. Reynolds and J. I. Smith, unpubl. data). Furthermore, over the past eight yr (including La Niña) researchers at similar elevations and habitats in the southern Sierra Nevada found no parasitism of Warbling Vireo nests (K. Purcell, pers. comm.). Although brood parasitism negatively impacts some populations of Warbling Vireos in California (Rothstein et al. 1980), it was not a significant factor accounting for low reproductive success in the high elevations of the northern Sierra Nevada. Smith et al. (2004) argued that increasing populations of nest predators pose the greatest threat to Warbling Vireo productivity in the northern Sierra Nevada.

Warbling Vireo nests are typically placed much closer to the periphery of the plant's foliage than to the main stem (Smith et al. 2004). The results of this study indicate that placement in the periphery is linked to success, perhaps because it limits the access of larger nest predators such as the Douglas' squirrel (*Tamiasciurus douglasii*; Morton et al. 1993), as the size of the branches supporting the nest can be very small (average diameter is 1 cm; Smith et al. 2004). Larger trees, be they conifer or aspen, generally have more expansive foliage than smaller trees. Thus, forest management plans promoting mature forest stands may benefit Warbling Vireo reproductive success by enhancing the availability of suitable nest sites found on thin branches well removed from the main stem.

Warbling Vireo nest success may be influenced by the microclimatic conditions surrounding the nest. Specifically, nest orientation (i.e., the side of the tree in which the nest was placed) was the single most important discriminator between successful and unsuccessful Warbling Vireo nests. In the Northern Hemisphere the angle of the sun relative to the earth is such that east-facing objects tend to receive direct sunlight only in the morning and thus have cooler mean temperatures compared to their western counterparts (Krohne 1998). There was no successful nest placed on the east side or the "cold side" of a lodgepole pine. In addition, successful nests in lodgepole pine had slightly less canopy cover than unsuccessful nests. While Walsberg (1981) did not examine an association with nest fate, he did report that Warbling Vireos ameliorate the nest environment in the Arizona desert by selecting sites that maximize the time during the day that the nest is shaded. We did not observe any nest failure attributable to cold stress alone (e.g., abandoned eggs or dead nestlings). However, in the high elevations of the northern Sierra Nevada, local temperatures are often well below the Warbling Vireo thermal neutral zone (the lower limit of this zone is approximately 25°C; Walsberg 1981). Average minimum–maximum temperature range in the study area during the peak of the breeding season is 5.3–27.7°C (Western Regional Climate Center 2003). Therefore, nests placed on the west side of a tree with slightly less canopy cover may successfully combat cold stress in the Sierra Nevada by increasing the exposure of the nest to direct sunlight during the heat of the day. This in turn may promote nest success.

There was no variable that discriminated significantly between successful and unsuccessful nests in aspen; the small sample size may have contributed to this lack of discrimination. Roden and Pearcy (1993a,b) report that most members of the genus *Populus* (including quaking aspen and Fremont cottonwood) exhibit leaf fluttering, which increases light penetration into the lower canopy and produces a more spatially uniform light and thus perhaps a more uniform temperature regime. Poplar trees may not present as much microclimatic variation between east and west sides as trees in which the

leaves do not flutter (e.g., lodgepole pine and willow). In this study nests were equally common on the east side ($N = 15$) and west side ($N = 15$) of poplars whereas nests in non-poplar trees showed a distinct westerly bias (23 of 34 nests were on the west side of the tree): mean nest orientation in non-poplars (225.35° ± 108.85 SD) was significantly different from mean nest orientation in poplars (161.07° ± 86.48 SD, $F_{1,62} = 14.03$, $P < 0.001$, Rayleigh Test; Brown and Downhower 1988). Thus, the more uniform microclimatic environment due to leaf fluttering may explain why nest orientation in quaking aspen was not a significant predictor of success, as compared to nests in lodgepole pine.

Based upon one of the largest samples of Warbling Vireo nests ever studied, we determined that populations in the high elevations of the northern Sierra Nevada have low nesting success (29.9%) despite uncommonly low rates of brood parasitism (7%). Therefore, contrary to Ward and Smith's (2000) prediction, Warbling Vireo populations at high elevation in the northern Sierra Nevada of California have levels of nest survivorship similar to populations at low elevation. Management for forests with larger tree size classes and greater canopy area might enhance Warbling Vireo nest success in the northern Sierra Nevada by increasing the availability of advantageous nest sites. Conservation strategies, including habitat management, that are designed to yield even modest improvements in nest success would probably slow or even reverse the widespread population declines of Warbling Vireos in California.

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