ABUNDANCE AND PRODUCTIVITY OF WARBLING VIREOS ACROSS AN ELEVATIONAL GRADIENT IN THE SIERRA NEVADA

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Abstract. Recent studies have shown that Warbling Vireos (*Vireo gilvus*) are declining in California and that these trends are due to low reproductive success. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) has been implicated in the low productivity. I explored two hypotheses related to population dynamics of Warbling Vireos along an elevational gradient: (1) potential source populations exist at high elevations where cowbirds are rare, and (2) potential source populations occur in the center of the elevational distribution with less productive populations at upper and lower elevations. From 1985 through 2002 I studied the abundance and productivity of Warbling Vireos over an elevational gradient in the southern Sierra Nevada. Warbling Vireos were most abundant in mid elevation mixed conifer sites, less abundant in lower elevation ponderosa pine sites and upper elevation true fir sites, and rare in upper elevation lodgepole pine sites. Likewise, daily survival rates of nests were highest at mid elevations (~1800 m) and gradually decreased at both higher and lower elevations. Compared to other populations studied in California, nest success in mixed conifer habitat was high (60%, $n = 58$). Although rates of brood parasitism were high enough to be of concern in low-elevation ponderosa pine forests, cowbird parasitism was not observed in mid- to upper-elevation forests. Warbling Vireos were most productive where they were most abundant. The hypothesis that potential source populations exist at upper elevations did not appear to hold at the upper bounds of the elevational distribution. The results of this study provide support for the hypothesis that potential source populations occur in the center of the elevational distribution, with less productive populations at both lower and higher elevations.

Key words: Abundance, brood parasitism, elevational gradient, nest success, productivity, Vireo gilvus, *Warbling Vireo.*

Abundancia y Productividad de *Vireo gilvus* en un Gradiente Altitudinal en la Sierra Nevada

Resumen. Estudios recientes han demostrado que las poblaciones de *Vireo gilvus* de California están declinando, y que estas tendencias se deben a un bajo éxito reproductivo. El parasitismo de cría por parte de *Molothrus ater* se ha considerado como una causa de la baja productividad. En este estudio, exploré dos hipótesis relacionadas con la dinámica poblacional de *V. gilvus* a lo largo de un gradiente altitudinal: (1) en las elevaciones altas, donde *M. ater* es raro, existen poblaciones que sirven potencialmente como fuentes; y (2) las poblaciones que sirven potencialmente como fuentes se encuentran en el centro de la distribución altitudinal y las poblaciones menos productivas a elevaciones mayores y menores. Estudié la abundancia y productividad de *V. gilvus* en un gradiente altitudinal en la parte sur de la Sierra Nevada entre 1985 y 2002. Esta especie fue más abundante a elevaciones medias en bosques mixtos de coníferas, menos abundante a elevaciones menores en bosques de *Pinus ponderosa* y a elevaciones mayores en sitios dominados por árboles del género *Abies*, y rara en sitios a elevaciones altas dominadas por *Pinus contorta*. Igualmente, las tasas diarias de supervivencia de los nidos fueron máximas a elevaciones medias (~1800 m) y disminuyeron gradualmente hacia elevaciones mayores y menores. En comparación con otras poblaciones estudiadas en California, el éxito reproductivo en ambientes mixtos de coníferas fue alto (60%, $n = 58$). Aunque las tasas de parasitismo de nidos por parte de *M. ater* fueron lo suficientemente altas como para ser motivo de preocupación en los bosques de pino ponderosa a elevaciones bajas, no se observó parasitismo en bosques ubicados a elevaciones medias y altas. La productividad de *V. gilvus* fue máxima en las localidades donde la especie fue más abundante. La hipótesis de que podrían existir potenciales poblaciones fuente a elevaciones mayores no pareció ser correcta en el límite superior de la distribución altitudinal. Los resultados de este estudio apoyan la hipótesis de que las poblaciones con potencial de servir como fuentes se

encuentran en el centro de la distribución altitudinal, y las poblaciones menos productivas a elevaciones mayores y menores.

INTRODUCTION

The Warbling Vireo (*Vireo gilvus*) is a Neotropical migrant with a large breeding distribution in North America and populations that appear to be stable or increasing in most areas. Survey-wide Breeding Bird Survey (BBS) trends for all of North America and for all three BBS regions (East, Central, and West) show increasing trends, although numbers in some states are declining (Michigan, West Virginia, and California; Sauer et al. 2005). In California, BBS data from 1966 to 2004 show a significant declining trend for Warbling Vireos of 1.32% ± 0.04% SE per year ($P < 0.01$, $n = 123$ routes; Sauer et al. 2005). Larger declines based on standardized mist net captures have been found in coastal California sites. Based on 19 years of capture-mark-recapture data, Gardali et al. (2000) found declines of 9.24% ± 0.02% SE ($R^2 = 0.52$, $P < 0.001$) per year for locally breeding vireos in coastal California and 9.88% ± 0.02% SE ($R^2 = 0.70$, $P < 0.001$) per year for all adults, indicating potential declines over a larger area. Using 21 years of capture data from the same site, Ballard et al. (2003) found a decline of 9.4% ± 2.2% SE (Adj. $R^2 = 0.43$, $P < 0.01$) per year for migratory birds captured in the fall. At another coastal site, Gardali and Jaramillo (2001) found a decline in fall migrants of 12.20% ± 0.05% ($R^2 = 0.39$, $P = 0.02$) per year based on 12 years of capture data.

Previous work has indicated that declining trends observed in California are due to low reproductive success (Gardali et al. 2000, Gardali and Jaramillo 2001). Although many nests are lost to predators (Tewksbury et al. 1998, Gardali et al. 2000), an important factor in low productivity throughout much of the range of Warbling Vireos is brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Previous studies have shown Warbling Vireos to be heavily parasitized (Rothstein et al. 1980, Tewksbury et al. 1998, Ward and Smith 2000, Banks and Martin 2001, Ortega and Ortega 2003).

Results of several studies in western North America have suggested that reproductive success of the populations studied was insufficient to maintain population size without immigration. In western Montana, neither forested nor fragmented agricultural landscapes appeared to provide source habitat for Warbling Vireos due to the dual effects of nest predation and brood parasitism (Tewksbury et al. 1998). High levels of brood parasitism in southwest Colorado likely resulted in a sink population (Ortega and Ortega 2003). Ward and Smith (2000) found that the observed levels of brood parasitism at low elevations in the Okanagan Valley of British Columbia likely resulted in sink populations maintained by emigration from source populations. They suggested that source populations may exist at high elevations and in extensive forested areas where few cowbirds exist and emphasized the need for a metapopulation analysis comparing populations at high and low elevations to ascertain whether sufficient dispersal among populations exists to prevent extinction at lower elevations.

Although the species is widespread, little information is available on the breeding biology of Warbling Vireos, probably because their nests tend to be high and difficult to see into (Gardali et al. 2000, Ortega and Ortega 2003). In this study, I examine abundance, nest success, and the impact of brood parasitism on Warbling Vireos breeding in coniferous forests over an elevation gradient in California. I explore two hypotheses related to population dynamics of Warbling Vireos along an elevational gradient: (1) potential source populations of Warbling Vireos exist at the upper elevation limits of their distribution in areas of low Brown-headed Cowbird abundance (based on Ward and Smith 2000), and (2) potential source populations occur in the center of their elevational distribution and sink populations occur at the upper and lower extremes of their elevational distribution. I combine results on abundance and productivity with results from population growth models to examine whether forest types found along the elevational gradient have the potential to maintain stable populations.

METHODS

STUDY AREAS

Eighteen study sites in four forest types along an elevational gradient were selected in the

Sierra National Forest in the southern Sierra Nevada, California. Sites at the lowest elevations (1024–1372 m) were in ponderosa pine (*Pinus ponderosa*) forests codominated by incense cedar (*Calocedrus decurrens*), and included several hardwood species, most notably California black oak (*Quercus kelloggii*) and canyon live oak (*Q. chrysolepsis*). Mixed-conifer stands (elevation 1707–2012 m) included a mixture of primarily white fir (*Abies concolor*), incense cedar, sugar pine (*P. lambertiana*), ponderosa pine, and California black oak. True fir stands (elevation 2170–2347 m) included both white fir and red fir (*A. magnifica*). At the highest elevations (2469–2774 m) were lodgepole pine (*P. contorta*) stands. Study sites were replicated four times in each forest type except for mixed conifer where there were six sites. Of the six sites in the mixed conifer forest type, four were sampled per year on a rotating schedule, such that each site was sampled an equal number of years during the period of the study. Each site consisted of at least 60 ha of mature forest with relatively high canopy cover, although natural heterogeneity resulted in all sites having some open, rocky, or brushy areas and small meadows or streams. All sites were protected from major disturbance for the duration of the study. Portions of the ponderosa pine and mixed conifer sites and two of the true fir sites had been logged in the past using selective tree harvest techniques. A 40 ha gridded plot was established in each of the 60 ha sites to facilitate censusing and mapping and relocation of nests.

FIELDWORK

From 1995 through 2002, field crews counted birds on eight (1995) or 16 (1996–2002) of the 18 study sites each year, using a timed transect method. Transects were 1000 m long and observers walked at a rate of 50 m per 3 min. Observers recorded all birds seen or heard within 50 m of the transect line and those detected at unlimited distance but still within the study site. Only detections within 50 m are analyzed here and I assumed that detection probabilities were similar within this distance across forest types for the purpose of describing broad patterns of abundance. Efforts were taken to control for observer variability—likely the greatest source of error in bird surveys (Sauer et al. 1994). Observers were carefully

selected to be proficient at bird identification and, to help minimize observer variability, all observers participated in a two-week training period at the beginning of each field season to sharpen their identification skills and to familiarize them with the details of the methods used. Additional training was provided as observers moved into higher forest types and encountered new species. Each observer's hearing was tested annually. Three (six years) or four (two years) observers counted each transect six times each year during the peak singing period for that forest type. All observers visited each site an equal number of times each year to help control for observer variability. A total of seven observers counted birds over the eight years of the study, so that most observers were repeat observers for several years of the study. Surveys were completed between 17 April and 16 May in ponderosa pine habitat, 22 May to 15 June in mixed conifer, 5 June to 6 July in true fir, and 21 June to 25 July in lodgepole pine. 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 07:00 PDT in all forest types except ponderosa pine, where counting began at 07:30 PDT to accommodate shorter day lengths earlier in the season. All transects were completed within 1.5 hr.

Field assistants searched for nests of all species, including Warbling Vireos, on the study sites used for bird surveys each year. Nests were monitored every 3–4 days. Where possible, Warbling Vireo nests were checked with a mirror on a pole or a small video camera mounted on an extendable fiberglass pole. When nests were too high to reach from the ground, field crews climbed to nests using a variety of climbing techniques. During early nesting stages and when nests were in locations where we could not monitor them using other methods, we observed nests from the ground. Elevation at each nest was measured with a digital altimeter. We spent approximately 3224 hours searching for nests in ponderosa pine, 2316 hours in mixed conifer, 1361 hours in true fir, and 1303 hours in lodgepole pine sites. While effort was lower at higher elevation sites, the number of nests of all species found per hour was higher at higher elevations due to the compressed breeding season (0.33, 0.57,

0.70, and 0.67 nests per hour in ponderosa pine, mixed conifer, true fir, and lodgepole pine sites, respectively).

Nest age was determined by extrapolation from identified events such as the beginning of incubation, hatching, or fledging. 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 determination of nest age; these nests were excluded from all analyses that included age as an explanatory variable.

Based on average values from nests with complete information for a particular period, the incubation period of Warbling Vireos averaged 12.3 ± 0.1 SE days ($n = 32$) and the nestling period averaged 15.8 ± 0.2 SE days ($n = 20$). Average clutch size (3.6 ± 0.1 SE, $n = 44$) was used to determine the duration of the laying phase, subtracting one day for the beginning of incubation and assuming one egg was laid per day. Thus, the length of a successful nesting attempt was 30.6 days.

STATISTICAL ANALYSIS

The index of abundance for each forest type was calculated as the total number of detections from all six visits per transect averaged over the eight years of the study. Standard errors were based on the mean count over the eight years.

Nest success. To be considered a nest, a nest cup had to contain at least one egg or nestling during the period the nest was under observation. 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 nest survival was influenced by elevation and habitat characteristics. I used the effective sample size (Rotella et al. 2004) to calculate Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002), which was used to rank candidate models. Akaike weights, which estimate the probability that a specified model is the best of those considered, were used to address model selection uncertainty (Burnham and Anderson 2002). Analyses were done using Proc GENMOD in SAS version 9.1 (SAS Institute 2000). Model fit was assessed with the Hosmer-Lemeshow decile of risks test (Hosmer and Lemeshow 2000).

Candidate models of nest survival were developed based on *a priori* hypotheses. I first evaluated time-specific effects of nest age, date,

and year. Following Grant et al. (2005), I considered models that included linear, quadratic, and cubic effects of age, linear and quadratic effects of date, and a categorical effect of year. A cubic effect of age is plausible if survival differs among the egg-laying, incubation, and nestling stages. Quadratic effects of date are plausible if nest survival is higher midseason. Quadratic and cubic models included all lower order terms. The 24 models evaluated included a constant daily survival model (null model) and all combinations of age, date, and year effects. I included the most supported time-specific model in subsequent analyses.

Based on the two hypotheses related to effects of elevation on population dynamics, I predicted that either daily survival rates would increase linearly with increasing elevation, or daily survival rates would be highest in the center of the elevational distribution and lower at both lower and higher elevations, following a quadratic distribution. I tested three models that compared linear and quadratic effects of elevation and the best time-specific model only.

I did not examine the effects of Brown-headed Cowbird brood parasitism in nest survival models because we were able to verify the contents of only 72% of nests and this subsample was biased toward nests located lower in trees.

Population models. I used simple population growth models to calculate annual productivity and to predict survival rates needed to maintain stable population sizes. I calculated season-long estimates of fecundity in each forest type. The annual production of fledglings per female was calculated using the equations of Ricklefs and Bloom (1977) as adapted by Lloyd et al. (2005). Model parameters included: (1) daily nest mortality rate, (2) nest success, (3) average number of young fledged per successful nest, (4) the interval between a failed nesting attempt and initiation of a new nest (r_f), (5) the interval between successful fledging and the initiation of a new nest (r_s), and (6) the duration of the laying season. Daily nest mortality rates and nest success were calculated for each forest type based on a logistic exposure model that included only forest type. The duration of the laying season was estimated using observed nest initiation dates for each forest type and then calculating the number of equally good days for

nest initiation during the nesting season following Ricklefs (1966). The number of equally good nest initiation days (EGD) is given by

$$EGD = 7 \exp\left(-\sum_{i=1}^{52} p_i \ln(p_i)\right),$$

where p_i is the proportion of nests initiated in week i (pooled across years). This formula accounts for the fact that breeding is not equally intense throughout the period in which nests are initiated. The interval between termination of one nest and initiation (whether following failure or successful fledging) of the following nest is not known for most species. I estimated these intervals based on the observed duration of nest building from this study ($\bar{x} = 8.4$ days, $n = 5$). I assumed two additional days for renesting following a successful attempt, resulting in $r_f = 8.4$ and $r_s = 10.4$ days. Although these intervals are longer than those reported in the literature (Ricklefs 1969, Lloyd et al. 2005), nest construction time in this study appears to be longer than published lengths for Warbling Vireos from other studies (Howes-Jones 1985, Banks and Martin 2001). Two of the five nests used in this estimate were likely second attempts, which are often completed in less time than first attempts. While the sample size is small, the observed time spent building a nest based on nests found early in the nest construction period (but not the entire period) was only slightly shorter (7.2 days, $n = 20$). In addition, the difference between the two rates r_f and r_s (two days) falls between those reported by Ricklefs (1969; 0.4 days) for temperate passerine birds and by Lloyd et al. (2005; 4 days) for Red-eyed Vireos (*Vireo olivaceous*).

Following Ricklefs and Bloom (1977), the rate of nest initiation per day (I) was calculated by the equation

$$I = \frac{m}{p_f + m(p_s r_s + p_f r_f)},$$

where m is the daily nest mortality rate, p_f is the nest failure rate, p_s is the nest success rate, r_f is the delay before a new clutch is initiated after nest failure, and r_s is the delay before a new clutch is initiated after successful fledging. The rate at which young are fledged (F) is calculated as
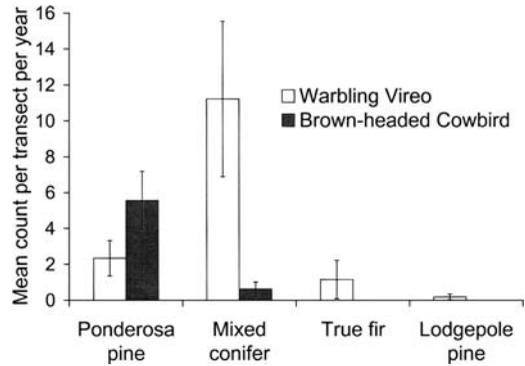
$$F = fl * p_s * I,$$

FIGURE 1. Abundance (total detections within 50 m of the transect averaged over the eight years of the study) of Warbling Vireos and Brown-headed Cowbirds in four forest types over an elevational gradient in the southern Sierra Nevada. Error bars represent 95% confidence intervals.

where fl = the number fledged per successful attempt. The annual production of fledglings (the number of fledglings produced per pair) in each forest type (P) is

$$P = F * EGD,$$

where EGD is the duration of the breeding season as calculated above.

I used a simple, two-stage population model to predict the minimum adult survival rates needed to achieve $\lambda = 1$, or a stable population, for each forest type. Annual productivity per pair (P) was divided by two to get the number of female fledglings produced per female (assuming a 50:50 sex ratio for fledglings). Minimum adult and juvenile survival were calculated by iteratively solving the equation

$$\lambda = P_A + P_J * \beta,$$

where λ is set equal to 1, P_A is adult survival, P_J is juvenile survival, and β is the number of female fledglings produced per female. I assumed juvenile survival was 50% of adult survival (Greenberg 1980, Temple and Cary 1988, Thompson 1993, Gardali et al. 2003). Values reported are means ± SE.

RESULTS

ABUNDANCE AND PRODUCTIVITY

Although Warbling Vireos occurred in all four forest types along the elevational gradient, abundance varied greatly (Fig. 1). Warbling
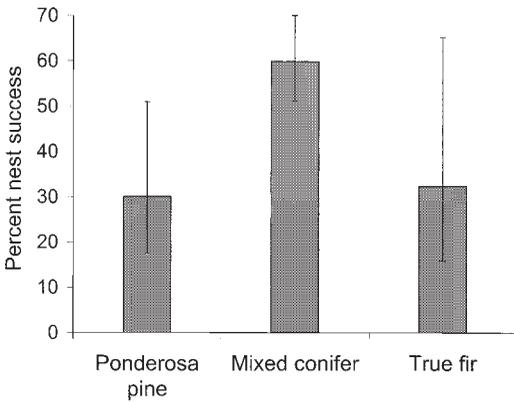
FIGURE 2. Nest success of Warbling Vireos breeding in three forest types across an elevational gradient in the southern Sierra Nevada, 1985–2002, based on logistic exposure estimates. Error bars represent 95% confidence intervals. Sample sizes are n = 15, 58, and 9 nests for ponderosa pine, mixed conifer, and true fir, respectively.

TABLE 1. Selection results for models explaining variation in nest survival as a function of time-specific effects of nest age, date, and year. Twenty-four candidate models were considered that included linear effects of age (Age), date (Date), and year (Year), quadratic effects of age (Age^2) and date ($Date^2$), cubic effects of age (Age^3), and a null model. Quadratic and cubic models included all lower order terms. $Log_e(\mathcal{L})$ is the value of the maximized log-likelihood function, K is the number of parameters in the model, AIC_c is Akaike's information criterion corrected for small samples and ΔAIC_c is the scaled value of AIC_c, and w_i is the Akaike weight. Only models with $\Delta AIC_c \leq 2.0$ are shown. Effective sample size was 1599 exposure days.

Model	$Log_e(\mathcal{L})$	K	ΔAIC_c[a]	w_i
Age^2 + Date	−106.2	4	0.0	0.16
Null	−109.5	1	0.6	0.11
Date	−108.7	2	0.9	0.10
Age + Date	−107.7	3	1.0	0.09
Age^2	−107.8	3	1.1	0.09
Age^3 + Date	−106.0	5	1.5	0.07
Age^2 + $Date^2$	−106.2	5	2.0	0.06

[a] The lowest AIC_c value was 220.4.

Vireos were rare at high elevations and were most abundant in mid-elevation mixed conifer forests.

We located and monitored 83 nests from 1995 through 2002: 15 in ponderosa pine sites, 58 in mixed conifer, 9 in true fir, and one in lodgepole pine. Nest success was highest in mixed conifer habitat and lower in ponderosa pine and true fir habitat (Fig. 2). Sample sizes for the ponderosa pine and true fir forest types were small, which resulted in larger confidence intervals. Daily survival rates were 0.962 ± 0.009 for ponderosa pine, 0.983 ± 0.003 for mixed conifer, and 0.964 ± 0.011 for true fir, which, extrapolated to overall nest success, yielded estimates of 30%, 60%, and 32% for ponderosa pine, mixed conifer, and true fir forest types, respectively.

Model selection results for time-specific effects on nest survival revealed little support for a single best model (Table 1) and model-averaged parameter estimates all had large standard errors. The global time-specific model fit the data according to the Hosmer-Lemeshow decile of risks test ($\hat{C}$ = 12.0, P = 0.15). The best model describing time-specific effects on nest survival included a quadratic effect of nest age and a linear effect of date. Results from this model suggested that nest survival was lowest six days after hatching and increased with date. The null model was the second most supported model. The best model was used in subsequent analyses, but results based on the null model were also examined.

Model selection results for hypotheses related to elevation indicated that quadratic effects of elevation best explained variation in daily survival rates (Table 2), and the model with quadratic effects of elevation fit the data well ($\hat{C}$ = 9.0, P = 0.34). Model rankings remained the same when analyses were conducted without time-specific effects and including data from nests for which I could not assign nest age. Daily survival rate of vireo nests was highest at an elevation of approximately 1800 m and gradually decreased at both higher and lower elevations (Fig. 3).

The distribution of nest initiation dates was clearly bimodal (Fig. 4), both within and across forest types, and long enough to accommodate two nesting attempts in ponderosa pine and mixed conifer habitats, suggesting the potential for double brooding at low and mid elevations.

BROOD PARASITISM

Brown-headed Cowbirds were most abundant at lower elevation sites in ponderosa pine forest and decreased sharply with increasing elevation (Fig. 1). Cowbirds were not detected in true fir

TABLE 2.   Summary of model selection results for the most supported models of daily nest survival of Warbling Vireo nests in the southern Sierra Nevada, California. $\text{Log}_e(\mathcal{L})$ is the value of the maximized log-likelihood function, K is the number of parameters in the model, AIC_c is Akaike's information criterion corrected for small samples and ΔAIC_c is the scaled value of AIC_c, and w_i is the Akaike weight. All models include the most supported time-specific model $\text{Age}^2 + \text{Date}$ (Table 1). Three elevation models were tested that included a linear effect of elevation (Elevation), a quadratic effect of elevation (Elevation^2), and the best time-specific model only. The effective sample size is 1599 survival days.

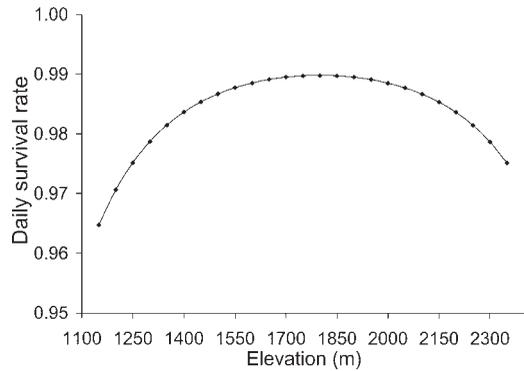| Model	$\text{Log}_e(\mathcal{L})$	K	ΔAIC_c[a]	w_i
Elevation^2	−103.2	6	0.0	0.58
Time-specific only	−106.2	4	2.0	0.21
Elevation	−105.3	5	2.1	0.20

[a] The lowest AIC_c value was 218.4.

FIGURE 3.   Daily survival rates of Warbling Vireo nests in the southern Sierra Nevada, 1985–2002, along an elevational gradient. Estimates are based on the best model where $\log(S/1 - S) = -5.52 - 0.22$ nest age $+ 0.01$ nest age$^2 + 0.01$ date $+ 0.01$ elevation $- 3.0 \times 10^{-6}$ elevation^2.

and lodgepole pine forest. Only four Warbling Vireo nests were parasitized by cowbirds and all of these were in lower-elevation ponderosa pine sites. The overall parasitism rate for nests whose contents we were able to observe was low (7%, $n = 60$), but in ponderosa pine sites 50% (4 of 8) of nests we could see into were parasitized. None of the four parasitized nests fledged any vireo young; two nests fledged one cowbird, one fledged two cowbirds, and one was depredated.

POPULATION MODELS

The lengths of the breeding season, as measured by the number of equally good nest initiation days, were 42.8, 46.4, and 31.2 days for ponderosa pine, mixed conifer, and true fir forest types, respectively. Annual productivity (number of fledglings produced per pair) was highest in mixed conifer (2.2 fledglings produced per pair), lower in ponderosa pine (1.3 fledglings per pair), and lowest in true fir (1.0 fledglings per pair). The two-stage population models predicted that adult survival rates for Warbling Vireos would need to be greater than 0.75 to achieve $\lambda = 1$ in ponderosa pine, greater than 0.64 in mixed conifer forests, and greater than 0.80 in true fir forests.

DISCUSSION

This study provides insight into the population dynamics of Warbling Vireos in the southern Sierra Nevada and the ecological factors influencing them, including the importance of differing local conditions that can affect populations breeding in fairly close proximity.

ABUNDANCE AND PRODUCTIVITY

Warbling Vireo productivity was highest in the mixed conifer habitats where they were most abundant. Populations breeding at lower and higher elevations had low reproductive success and low abundance. Nest success of Warbling Vireos in mixed conifer habitat (60%) was high compared to other studies. Reported estimates of nest success from California include 10% in eastern California (Gardali and Ballard 2000), 21% in coastal California (Gardali et al. 2000), and 30% on the eastern slope of the northern Sierra Nevada (Smith et al. 2005). Outside California, reported estimates range from 29% to 62% (Easton and Martin 1998, Tewksbury et al. 1998, Gardali and Ballard 2000, Ortega and Ortega 2003), with only one study reporting slightly higher values than ours for mixed conifer forest (Martin and Li 1992). The high nest success and productivity, lack of brood parasitism, longer breeding season, and possibility of multiple nesting attempts suggest a self-sustaining population in mixed conifer habitat.

These results are reassuring in light of studies that have shown inverse relationships between abundance and productivity in other species (Purcell and Verner 1998, Pidgeon et al. 2003, Remeš 2003) and especially so for a species whose population trends are a concern. A
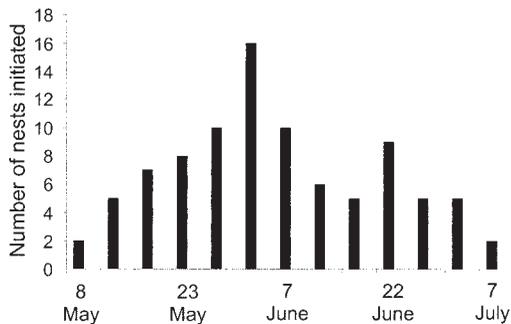
FIGURE 4. The distribution of Warbling Vireo nest initiation dates across all forest types in the southern Sierra Nevada, 1985–2002, showing the bimodal distribution.

review of the relationship between density and reproduction found a positive correlation for 70% of songbird studies and 64% of studies in forest or shrub habitat (Bock and Jones 2004). Nevertheless, a negative relationship was found in more than 30% of these studies and adaptive habitat selection cannot be assumed.

Habitat used by Warbling Vireos in this study differed from that typically used throughout their range and in studies with low reproductive success. Warbling Vireos in the southern Sierra Nevada were not tied to deciduous tree species for nesting and nested in five conifer species. In mixed conifer forest, most nests were found in incense cedar (KLP, unpubl. data).

ELEVATIONAL GRADIENT HYPOTHESES

The hypothesis that potential source populations exist at upper elevations did not appear to hold at the upper-elevation bounds of the Warbling Vireo distribution, where brood parasitism cannot be implicated. Warbling Vireos were nearly absent from lodgepole pine forest and had low productivity at high elevations. The shorter breeding season at upper elevations is a likely factor, but low nest success suggests that physiological or community-level mechanisms could also play a role.

The results of this study provide support for the hypothesis that potential source populations occur in the center of the elevational distribution, with less productive populations at both lower and higher elevations. The distribution of a species is strongly influenced by its ecological niche, the habitat and conditions where populations are maintained without

immigration. Studying the demographic responses of a species at its distributional limits will lead to a better understanding of the ecological niche of that species and help predict responses to environmental change (Holt and Keitt 2005). Species are limited by both abiotic factors and biotic interactions. At high elevations species are generally believed to be limited by cold temperatures, whereas at low elevations interspecific interactions among the more abundant and diverse species are believed to be limiting (MacArthur 1972). This study provides support for abiotic limitations at high elevations (primarily evident in the shorter breeding season) and biotic limitations at low elevations (primarily brood parasitism but also nest predation).

BROOD PARASITISM

I found cowbird parasitism of Warbling Vireos only in the lowest elevation forest type. Brood parasitism was not a significant factor affecting Warbling Vireo productivity in mid and upper elevation forests. At 1900–2100 m elevation in the northern Sierra Nevada (intermediate to the mixed conifer and true fir sites studied here), the rate of brood parasitism was only 7% (three of 41 nests; Smith et al. 2005). In contrast, Ortega and Ortega (2003) found high parasitism rates and low vireo productivity at a high elevation site (2316 m) in southwest Colorado. They suggested that Warbling Vireos are present and cowbirds less abundant at yet higher elevations in Colorado and that Ward and Smith's (2000) hypothesis may hold at those higher elevations if nest success improves as a result of lower parasitism pressure.

Cowbirds do appear to play a significant role in Warbling Vireo nest failure in the ponderosa pine forests studied here. Cowbirds were more abundant at lower elevations, however cowbird occurrence is not limited by elevation if supplemental food sources are present (Purcell and Verner 1999). Previous work in the Sierra Nevada has suggested that Warbling Vireo numbers may be depressed by brood parasitism in the vicinity of stables, pack stations, campgrounds, grazed meadows, and human habitation (Rothstein et al. 1980, Verner and Rothstein 1988).

Brown-headed Cowbirds were largely absent from the Sierra Nevada until about 1940 (Grinnell and Miller 1944). Host responses to

TABLE 3. Published adult survival probabilities for Warbling Vireos in the western United States.

Location	Survival ± SE	Number of years	Number of sites[a]	Source
Northwest region[b]	0.57 ± 0.05	5	63	DeSante et al. (1998)
Northwest region[b]	0.47 ± 0.03	7	67	DeSante and O'Grady (2000)
North coastal California	0.50 ± 0.05	19	1	Gardali et al. (2000)
Southwest region[b]	0.83 ± 0.15	5	2	DeSante et al. (1998)
Southwest region[b]	0.55 ± 0.06	7	67	DeSante and O'Grady (2000)

[a] All sites followed Monitoring Avian Productivity and Survivorship (MAPS) protocol, with 10 mist nets (12 m length, 30 mm mesh) run for six hours per day, one day per 10-day period, for 6–10 consecutive periods, except for Gardali et al. (2000) who used 20 nets (30 mm or 36 mm mesh) at 14 locations, run for 6 hr, operated 6–7 days per week from May through September.
[b] The northwest region includes most of northern California and the Sierra Nevada. The southwest region includes southern California and the Central Valley.

them are probably still evolving (Verner and Rothstein 1988, Peer and Sealy 2004), as demonstrated by the fact that the eastern subspecies of Warbling Vireo (*V. g. gilvus*) is an ejecter of cowbird eggs while the western subspecies (*V. g. swainsonii*) appears to be an accepter (Sealy 1996). The eastern subspecies, which is larger than the western subspecies both in mass and bill size (Gardali and Ballard 2000), is the smallest host species known to puncture and eject cowbird eggs (Sealy 1996, Sealy et al. 2000). The western subspecies may be just below the minimum size for an egg ejecter (Sealy 1996).

POPULATION MODELS

I did not collect the data needed to estimate site-specific survival, but values reported in the literature can provide a helpful comparison. Reported adult survival probabilities for Warbling Vireos range from 0.47 to 0.83 in the western United States (Table 3). Of the published estimates, only one value was higher than our estimates of 0.64 to 0.80 needed to maintain stable population sizes in our study sites. However, our estimate of survival needed for a stable population in mixed conifer fell within the confidence intervals of the three highest estimates, suggesting that survival and reproductive success may be adequate to maintain viable populations of Warbling Vireos in mixed conifer habitat.

These population models are admittedly simple and depend on the veracity of model assumptions and the precision of model parameters. Productivity models have been found to be sensitive to renesting intervals (Powell et al.

1999), variables that are unknown for most species and were probably imprecisely estimated here. Using more conservative values of 8.2 days for successful and 7.8 days for failed attempts (Ricklefs 1969) did not change the adult survival values needed to maintain a stable population. Even assuming an 18-day renesting interval following a successful attempt (as found for Wood Thrushes; Lang 1998) increased the adult survival rates needed for a stable population only 1% and 3% for true fir and mixed conifer, respectively.

The duration of the laying season is sensitive to sample size and the number of nests with extreme initiation dates and is likely a source of error in these simple population models. Based on a sample size of 52 nests, the calculated laying season in mixed conifer was longer than in the lower elevation ponderosa pine sites ($n = 14$), whereas in actuality the breeding season is assuredly longer in the latter. Small sample sizes will negatively bias laying season length and underestimate annual productivity. Lloyd et al. (2005) used samples with at least 100 nest initiation dates to attempt to minimize this problem (P. Lloyd, University of Montana, pers. comm.).

Despite potential problems with the population models, our results suggest that Warbling Vireo populations in lower and upper elevation forests in the southern Sierra Nevada are not self-sustaining. The shorter breeding season in true fir forest and the low nest success and annual productivity (<1 female fledged per adult female) in both true fir and ponderosa pine habitats are important factors contributing to this conclusion.

Warbling Vireo population trends vary and appear to be increasing in some areas and decreasing in others (Gardali and Ballard 2000). California populations, in particular, appear to have declined, underscoring the potential for factors acting on a small scale to affect vireo populations. While BBS data from 1966 to 2004 for California indicate a significant declining trend, BBS results from the Sierra Nevada show a much smaller and nonsignificant decline ($-0.24\% \pm 0.20\%$ per year, $P = 0.82$, $n = 28$ routes; Sauer et al. 2005) and provide further support that healthy populations of Warbling Vireos exist in the Sierra Nevada.

Studies such as this that explore local elevational and environmental gradients can help predict the responses of species to anthropogenic-induced changes such as global warming, land-use changes, and exotic species invasions (Parmesan et al. 2005). Results of this study suggest that activities and development that provide conditions beneficial to Brown-headed Cowbirds, especially at mid elevations, could be detrimental to Warbling Vireos in the Sierra Nevada.

ACKNOWLEDGMENTS

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