

DEMOGRAPHY OF A DECLINING POPULATION OF WARBLING VIREOS IN COASTAL CALIFORNIA¹

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Abstract. We investigated population trends, adult survival, and productivity indices of a breeding population of Warbling Vireos (*Vireo gilvus*) in north coastal California using capture-recapture data from 19 years of standardized mist-netting conducted at Point Reyes National Seashore. We found significant long-term declines in abundance of both breeding and migratory Warbling Vireos. In addition, we found a significant long-term decline of hatching-year birds captured during the breeding season. The number of new adults in a given year, defined as those birds not previously banded and assumed to be an index of adult recruitment, was significantly correlated with the capture rate of hatching-year birds in the previous year, suggesting a link between reproductive success and adult abundance and recruitment. Our analysis of capture-recapture data provided an estimate of 50.4% for adult annual survival, similar to estimates for other species in stable populations. We could detect no temporal trend in survival. Nest survivorship from areas near our netting site was relatively low. We suggest that the decline of breeding and migratory populations of Warbling Vireos observed in coastal California may be the result of low productivity on the breeding grounds.

Key words: annual survival, constant-effort mist-netting, population trend, productivity, *Vireo gilvus*, Warbling Vireo.

INTRODUCTION

Many of the vireos (Vireonidae) that breed in North America have experienced at least some level of population decline or localized extirpation in recent times. One species that breeds in the south-central United States, the Black-capped Vireo (*Vireo atricapillus*), was designated as a Federally endangered species in 1987 (Grzybowski 1995). In California, two vireo species, Gray (*V. vicinior*) and Bell's (*V. bellii*), have had substantial population decreases over the past 100 years (DeSante and George 1994). The western Warbling Vireo (*V. gilvus swainsonii*), however, has received little attention. Declines in North American landbird populations, in general, have become the focus of research and monitoring to identify the demographic mechanisms responsible, including changes in reproductive success, over-winter survival, survival and recruitment of young into the breeding population, and immigration or emigration (Nur and Geupel 1993).

Despite intense research and monitoring, understanding the mechanisms of declines in Neotropical migratory birds remains elusive because measuring population parameters is difficult, and

multiple mechanisms are probably operating. Many studies have hypothesized that tropical deforestation has reduced over-winter survival for adult and hatching-year birds (Askins et al. 1990, Rappole and McDonald 1994). Several recent studies suggest that events at migratory stopover areas may also have significant consequences (Moore et al. 1995, Yong et al. 1998), and at least one study examined the role that juvenile survival plays (Anders et al. 1997). Still other evidence, mostly from studies conducted in middle North America, suggests that poor reproductive success on the breeding grounds is responsible for population declines (Askins et al. 1990).

It is an oversimplification to attribute population declines to any one period in the annual cycle of Neotropical migrants. A review of current information indicates that populations may be limited by events occurring at various periods in the annual cycle, and conclusions are probably dependent upon a particular species' life history characteristics (Sherry and Holmes 1993). Moreover, a recent study has even suggested that events on the wintering grounds could be influencing individual fitness on the breeding grounds (Marra et al. 1998).

Understanding where in the annual cycle a species is *primarily* limited is essential for developing conservation strategies for declining

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species. Several studies have shown that population size was responsive to changes in productivity (Sherry and Holmes 1992, Roth and Johnson 1993, Chase et al. 1997). Long-term studies like these can help determine which demographic parameter has the most influence on the population dynamics of a species.

Using 19 years (1979–1997) of standardized mist-net data, we examined three demographic parameters for Warbling Vireos captured at the Palomarin Field Station. We began by investigating long-term trends in abundance (using capture rates) of summer and fall captures. Next, we estimated productivity (as indexed by mist-net capture rates) and adult survival in order to gain insight into the mechanisms that might explain trends in abundance. Productivity was also directly estimated from 1997 to 1999 by locating and monitoring nests. We address two questions: (1) are capture rates declining?, and if so, (2) are changes in productivity responsible for the decline?

METHODS

STUDY AREA

Constant-effort mist-netting was conducted at the Palomarin Field Station of the Point Reyes Bird Observatory (PRBO) from 1979 through 1997, as part of ongoing research and monitoring efforts. The study area is located at the southern end of the Point Reyes National Seashore, Marin County, coastal California (37°56'N, 122°45'W). We used an array of 20 12-m nylon mist nets established at 14 permanent locations. All nets were within 200 m of each other. Fourteen of the nets were located at eight sites along the edge of a riparian woodland in a mixed evergreen forest. Six of these eight forest nets were double nets stacked one over the other. The remaining six nets were located in coastal scrub adjacent to the forest. All nets located in the forest area were 30-mm mesh, whereas all nets in the coastal scrub sites were 36-mm mesh. Predominant woodland plant species were coast live oak (*Quercus agrifolia*), California bay (*Umbellularia californica*), Douglas-fir (*Pseudotsuga menziesii*), California buckeye (*Aesculus californica*), and red alder (*Alnus rubra*). The coastal scrub plant community was dominated by coyote brush (*Baccharis pilularis*), California sagebrush (*Artemisia californica*), bush monkeyflower (*Mimulus auranti-*

tiacus), and poison oak (*Toxicodendron diversilobum*). For a more detailed description of the study site and flora, see DeSante and Geupel (1987). For a map of the study site refer to Johnson and Geupel (1996).

A total of 41 Warbling Vireo nests were located at four riparian drainages, all located within 20 km of our mist-netting station. Nests were located in the Point Reyes National Seashore at Muddy Hollow (38°02'N, 122°52'W), Olema Creek (38°03'N, 122°48'W), and Laguna Creek (38°02'N, 122°52'W) in 1997, and in the Golden Gate National Recreation Area at Lagunitas Creek (38°02'N, 122°45'W) and Redwood Creek (37°51'N, 122°34'W) from 1997 to 1999. Vegetation at all drainages was similar. Dominant trees were red alder and willow (*Salix* spp.) with some coast live oak, California buckeye, and California Bay.

NETTING PROTOCOL

Nets were opened 15 min after local sunrise and left open for 6 hr (weather permitting), thus accumulating 120 net hr per full day of netting. The nets were opened and closed in a standardized order. Nets were operated 6 to 7 days per week from May through September 1979 to 1997. In all of our analyses, we used the number of individual birds captured per 1,000 net-hours to standardize capture rate by netting effort. However, net-hours did not differ greatly between years (breeding season mean = 13,983, range 11,466–15,998; fall mean = 6,613, range 5,508–7,177). Captured Warbling Vireos were banded and released at the on-site field station. Two age classes were distinguished by the degree of skull pneumatization: hatching-year birds (those in their first calendar year) and after hatching-year birds (adults in their second or later calendar years; Pyle et al. 1987). A few captures (0.5%) could not be aged and were excluded from all analyses.

NEST MONITORING

We located and monitored nests using standardized procedures described by Martin and Geupel (1993). Nest-finding began in mid-April and lasted until breeding activity declined in late July. Nest fate was determined by checking nest status every 1 to 4 days. Of the 41 nests monitored, only 2 were low enough for us to see nest contents. Nests were considered to have failed when they were torn apart, fledged only a

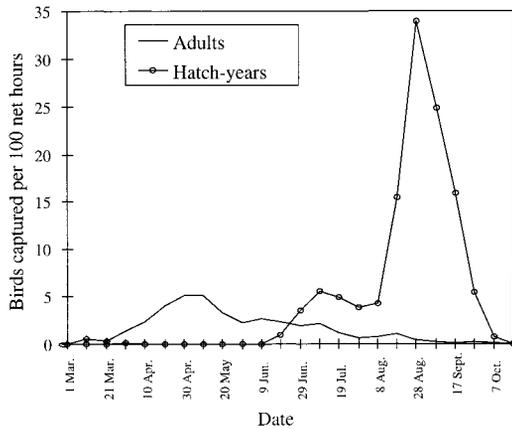


FIGURE 1. Mean number of adult and hatching-year Warbling Vireos captured per 100 net hours during 10-day periods from 1 March to 17 October, 1979–1997.

Brown-headed Cowbird (*Molothrus ater*), or adults no longer attended them before the expected fledge date. A nest was considered successful if it fledged at least one Warbling Vireo young.

STUDY SPECIES

The Warbling Vireo is a Neotropical migrant with a wide breeding range in North America and a comparably small wintering range in Mexico (AOU 1983). Summer residents begin arriving at Palomarin in mid March and begin nesting by late April. Migrants breeding farther north pass through in peak numbers during late April and early May, synchronous with the arrival of the species on Southeast Farallon Island (mean \pm SD = 10 May \pm 16 days), 32 km offshore of Palomarin where all Warbling Vireos are migrants (Pyle and Henderson 1991). Adults leave the area in July and early August (Fig. 1), and at this time there is an increase of hatching-year birds, probably representing dispersal of locally produced young (Ralph 1971). Fall migration, which primarily consists of hatching-year birds, peaks in late August (Fig. 1).

At Palomarin, Warbling Vireos breed exclusively in the narrow riparian woodland described above and show a predilection for this habitat type throughout Marin County (Shuford 1993). However, they also commonly breed in pure riparian forests as well as Douglas fir, Bishop pine (*Pinus muricata*), and coast redwood (*Sequoia sempervirens*) if they possess a hardwood component. Warbling Vireos occupy a wide variety

of habitat types in winter from dry wash habitats to pine forests (Gardali and Ballard, in press).

CLASSIFICATION OF CAPTURES

To estimate adult abundance of summer residents, it was necessary to eliminate transients (those birds that pass through Palomarin in spring during their northerly migration but do not stay to breed) from resident breeders (Pradel et al. 1997). Vireos typically begin arriving in mid March and capture rates increase to a peak in late April (Fig. 1). We believe that the earliest arrivals are local breeders (Ralph 1971), so 1 March was chosen as the beginning of the "breeding season." We used a within-season recapture criterion similar to that employed in other studies (Peach et al. 1991, Nur and Geupel 1993, Chase et al. 1997) to select territorial individuals, henceforth called "local breeders." We chose a recapture period of 7 or more days based on stopover duration (\pm SD) of known migrants at Palomarin (fall captures) of 3.4 ± 2.6 days. Similarly, Morris et al. (1996) reported a mean stopover period for migrating Warbling Vireos in the fall of 3.1 ± 2.5 days. Other studies have found that most Neotropical migrants do not stay in one area for more than 7 days while migrating (Moore and Kerlinger 1987) and one reported no differences in stopover duration between spring and fall seasons (Yong et al. 1998). The latest date an adult was recaptured within a season was 7 August, so we used that date as the end of the breeding season. This date is weeks before capture rates reach a second peak in late August and September during the fall migration. Individuals caught in more than one breeding season also were considered local breeders, because between-year recaptures of nonbreeding migrants at Palomarin and other netting sites are extremely rare (PRBO, unpubl. data). This criterion follows Pradel et al. (1997). We defined "new" adults as those birds which were previously unbanded, and assume they provide an index of new recruits to the study population (following Roth and Johnson 1993, Johnson and Geupel 1996).

We used the number of individual hatching-year birds captured per 1,000 net-hours and the ratio of hatching-year birds to adults during summer as two indices of local productivity, and assumed that young birds captured in the fall were produced over a larger area than sampled during the breeding season. Other studies have

used mist-net data to assess productivity in the same manner (DeSante and Geupel 1987, Chase et al. 1997). Both indices may be directly proportional to the number of young produced from territories around nets, or they may measure annual variation in productivity at a larger spatial scale (Nur and Geupel 1993).

STATISTICAL ANALYSES

We examined trends in Warbling Vireos separately for summer (1 March–7 August) and fall (18 August–17 November). Our sample consisted of 1,729 individuals (661 in summer and 1,068 in fall). We used linear regression to examine trends in both groups. All statistical analyses were carried out using the program STATA (STATA Corp. 1997). Capture totals were log-transformed in order to improve the normality of the residuals (Zar 1996). Linear regression also was used to describe the relationship between productivity and adult captures the following year. We examined whether residuals from linear regression analyses demonstrated autocorrelation (Cochrane and Watson 1949), using two procedures (*corc* and *hilu*) available in STATA. In no analysis reported here was there significant autocorrelation (all $P > 0.1$). We examined whether trends were non-linear by testing for a significant quadratic coefficient for year in the presence of a linear term. In no case was there a significant quadratic coefficient for year.

We used capture/recapture data of adults to estimate annual survival and recapture probabilities using the program SURGE 4.3 (Lebreton et al. 1992, Cooch et al. 1996). Capture/recapture analyses were conducted only on presumed non-transient individuals. Local breeders were included in the SURGE analysis from the point of their second capture. Sixty-five adults met the "local-breeder" criterion. Recapture probability was assumed constant, which we feel is reasonable given that the configuration of nets and effort in running mist nets was similar across years; in any case, there were too few data to allow examination of year to year variation in recapture probability. With respect to survival, we estimated survival probability assuming a constant survival value for the period 1979 to 1997. Using SURGE 4.3, we also fit a linear trend in survival over this time period (as described in Cooch et al. 1996) and tested for sig-

nificance of the linear trend using the Likelihood Ratio test (Lebreton et al. 1992).

Nest survival was estimated using the Mayfield method (Mayfield 1975) as modified by Johnson (1979) using a 29 day laying, incubation, and nestling period (Gardali and Ballard, in press). Nests from all sites and years were lumped for this analysis.

Significance was assumed at the $P < 0.05$ level. Values presented are mean \pm SE.

RESULTS

SEASONALITY OF CAPTURES

Capture rates of Warbling Vireos were characterized by three seasonal peaks (Fig. 1). Most adults were captured for the first time each year in late April or early May. Young birds peaked once in early June (probably locally produced young), and again in the fall. Fall capture rates of young birds were by far the highest, and presumably represented a nonbreeding population of Warbling Vireos. Very few adult Warbling Vireos were captured in the fall (23 of 1,091 total fall captures; 2.1%).

CAPTURE RATES AND DEMOGRAPHY

The capture rates of four different demographic groups declined steadily from 1979 to 1997: local breeders ($\beta = -0.097 \pm 0.021$, $P < 0.001$; Fig. 2a), total adults ($\beta = -0.104 \pm 0.016$, $P < 0.001$; Fig. 2b), young captured in breeding season ($\beta = -0.091 \pm 0.035$, $P = 0.02$; Fig. 2c), and young caught as fall migrants ($\beta = -0.103 \pm 0.030$, $P = 0.003$; Fig. 2d). The ratio of young to adult birds in the breeding season as well as young to local breeders showed no significant trend over the years of study ($\beta = 0.032$, $P = 0.46$ and $\beta = 0.025$, $P = 0.56$, respectively). Only 2 of 202 hatching-year Warbling Vireos (1%) captured in the breeding season were recaptured as adults in a subsequent year.

Capture rates for young birds in the breeding season were lowest in 1986 and were followed by low capture rates of total adults and breeders the following year (Fig. 2a–c).

Abundance of three demographic groups (total adults, local breeders, and "new" adults) in a given year was positively correlated with the total young captured during the breeding season of the previous year (all $P < 0.01$, all $F > 7.50$; Table 1, Fig. 3). The strength of the relationship depended on the demographic group. Total adults showed the strongest coefficient of deter-

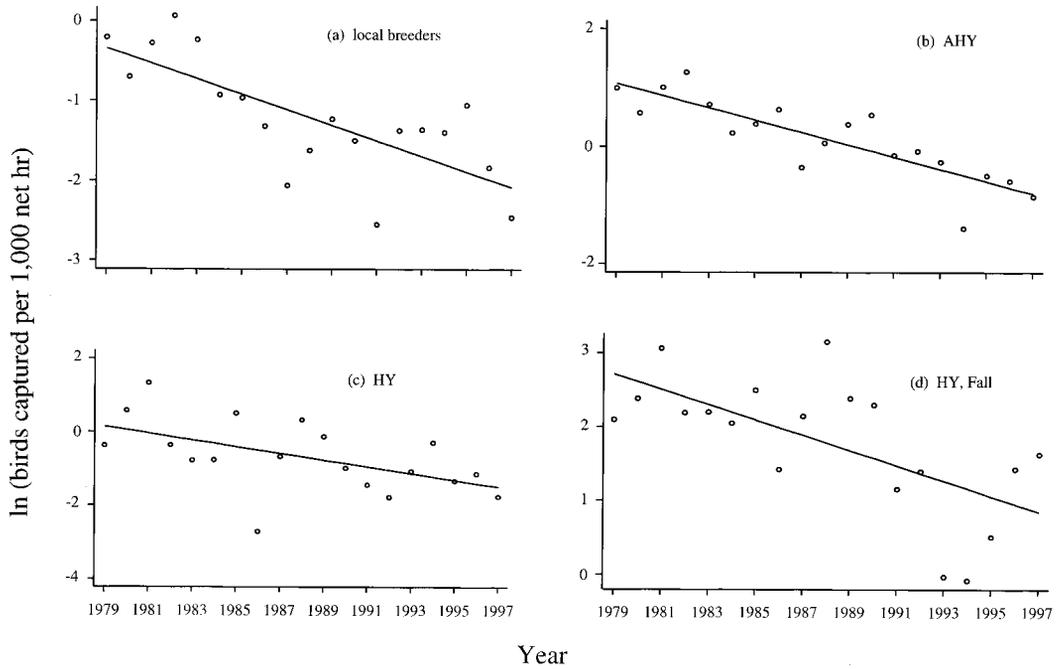


FIGURE 2. Trends for four demographic groups of Warbling Vireos, 1979–1997. Each circle represents datum for one year with least-square line of best fit. (a) local breeders ($P < 0.001$, $r^2 = 0.52$), (b) total adults (AHY) captured in breeding season ($P < 0.001$, $r^2 = 0.70$), (c) total hatch-year (HY) birds captured in breeding season ($P = 0.02$, $r^2 = 0.24$), and (d) hatch-year birds captured in fall, ($P = 0.003$, $r^2 = 0.37$).

mination in relation to young captured in the previous year ($r^2 = 0.46$), whereas “new” adults showed the weakest ($r^2 = 0.28$). There was no significant relationship between the ratio of young to adult captures and any of the demographic groups of adults the following year (all $P > 0.1$).

Nest monitoring yielded a Mayfield estimate of nest survival of 0.21 ± 0.1 .

RECAPTURE AND ADULT SURVIVAL PROBABILITIES

For individuals that met our criterion as a presumed local breeder ($n = 65$ individuals), recapture probability, the probability that a bird will

be recaptured given that it is alive, was 0.674 ± 0.089 . Survival probability, the probability an adult will survive from one year to the next, whether or not it was recaptured, was 0.504 ± 0.052 . There was no significant linear trend for survival to increase or decrease (Likelihood Ratio statistic = 0.01, $df = 1$, $P > 0.9$). The esti-

TABLE 1. Regression statistics for the relationship between total adult, breeding adult, and “new” adult abundances in year $t + 1$ and productivity in year t (per 1,000 net hours, 1979–1997).

Index	Slope	SE (β)	r^2	P
Total adults	0.50	0.12	0.46	0.001
Breeders	0.48	0.14	0.38	0.004
“New” adults	0.48	0.17	0.28	0.01

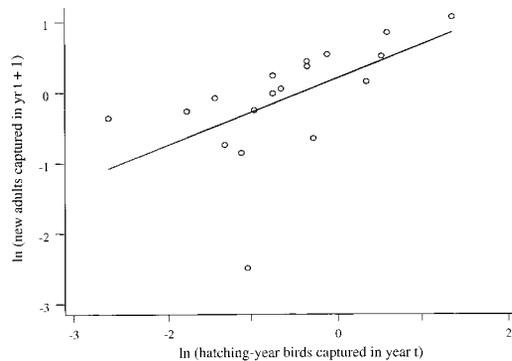


FIGURE 3. Capture rate of “new” adult Warbling Vireos in year $t + 1$ as a function of capture rates of hatching-year birds in year t , 1979–1997 ($P < 0.01$, $r^2 = 0.27$).

mate of the trend was very weak and positive ($0.072 \pm 1.22\%$ per year trend). The 95% confidence interval around the trend was broad, ranging from -2.32% to $+2.46\%$.

DISCUSSION

The abundance of Warbling Vireos breeding near Palomarin declined steadily during the 19 years of our study (Fig. 2a–d). Our summer capture numbers indicate local declines, whereas fall migrant captures, which are almost entirely young birds produced elsewhere (Fig. 1), indicate potential declines over a larger area. Capture rates from mist nets have been shown to give reliable information on trends in densities (Silkey et al. 1999). Large-scale declines in California have already been reported by the Breeding Bird Survey (BBS) for the same period, 1979–1996 (Trend = $-1.96 \pm 0.84\%$ per year, $P = 0.02$, $n = 87$ routes; Sauer et al. 1997).

Population fluctuations detected at localities have been correlated with fluctuations in larger areas in several other studies (see Chase et al. 1997 for review). Total fall captures at nearby Southeast Farallon Island demonstrated no trend from 1968–1992 (Pyle et al. 1994). The Farallon captures were of both adults and young birds, in contrast with mostly young at Palomarin. The Farallon study did report a significant negative trend in the ratio of young to adult birds ($P < 0.01$), supporting our contention that there has been a decline in Warbling Vireo productivity over a large geographical area.

Abundance of three demographic groups of adults was positively related to hatching-year captures (an index of productivity) in the previous year (Table 1), thereby linking changes in productivity with changes in adult abundance and recruitment. Other studies that have examined the relationship between productivity and adult capture rates in subsequent years have reported similar results. Nolan (1978) noted that the percentage of adult Prairie Warblers (*Dendroica discolor*) in summer was positively correlated with productivity the previous year. Swainson's Thrushes (*Catharus ustulatus*) and Wilson's Warblers (*Wilsonia pusilla*) at Palomarin also showed a positive relationship between productivity and adult captures the following year (Johnson and Geupel 1996, Chase et al. 1997).

Sherry and Holmes (1992) also found a positive relationship between productivity and adult

abundance, and because American Redstarts (*Setophaga ruticilla*) exhibit delayed plumage maturation, they were able to document the recruitment of second-year birds into the breeding population. Warbling Vireos do not exhibit delayed plumage maturation, so we used the capture rates of “new” adults as our index of first-year recruits (sensu Roth and Johnson 1993, Johnson and Geupel 1996, Chase et al. 1997). Although our index of “new” adults was positively correlated with productivity, it was our weakest relationship (Table 1). However, there was one statistically anomalous year, 1994 (Fig. 3), and if that year was omitted, then the relationship was the strongest among all analyses ($r^2 = 0.50$). Nevertheless, we had no biologically compelling reason to remove that year (1994). These results suggest that productivity may be influencing the overall population by influencing recruitment; i.e., years when more young are produced are followed by years with apparently more recruitment.

Productivity as indexed by the ratio of hatching-year to after hatching-year birds in our study showed no correlation with any index of adults the following year. This is contrary to the results produced by using capture rates of hatching-year birds as our index of productivity. This contradiction may best be explained by differences in the catchment area of adults and young rather than concluding that productivity is not related to adult abundance. In other words, the number of adults caught may not be a sensitive index of breeding density in the area that is producing the young birds. Indeed, in a mist-net validation study, total captures of hatching-year Song Sparrows (*Melospiza melodia*) at Palomarin were better correlated with two different *direct* measures of productivity (total number of fledglings produced and number of fledglings per pair) than was the ratio of young to adults (Nur et al., in press).

Poor reproductive success is indicated not only by low capture rates of hatching-year individuals but also by our low estimate of nest survivorship for Warbling Vireos breeding nearby. Our nest survivorship estimate of 21% is low compared to 61.6% ($n = 41$ nests) in Arizona (Martin and Li 1992) and 52% ($n = 66$ nests) in Montana (BBIRD, unpubl. data). Moreover, BBS data for Arizona and Montana do not show significant population trends (Sauer et al. 1997).

Ascertaining the cause of nest failure was dif-

ficult, partly because nests were too high to check contents. For example, we do not know what percentage of nests were parasitized but we do know Warbling Vireo nests were parasitized at our study sites (observations of vireos feeding cowbirds). The two nests that were low enough for us to observe their contents were not parasitized. Regardless of whether or not a nest was parasitized, most nests were depredated. Likely nest predators at our study sites were Steller's Jays (*Cyanocitta stelleri*) and Western Scrub-Jays (*Aphelocoma californica*).

Our estimate of adult survival for breeding Warbling Vireos (0.504) is slightly lower than an estimate reported for northwestern North America (0.56; DeSante et al. 1998) and within the range of estimates reported for Red-eyed Vireo (*V. olivaceus*; 0.50–0.59) (Martin and Li 1992). In addition, our estimate is nearly identical to the estimate reported for Wilson's Warblers at Palomarin (0.503), a breeding population that is not declining (Chase et al. 1997). Still, the annual survival estimate of 50% for breeding Warbling Vireos may be low because we could not distinguish permanent dispersal from mortality. We believe that applying a criterion for identifying local breeders for use in our adult survival model provides more accurate estimates of survival. To include transients in the capture/recapture analyses would violate the assumption of homogeneity of recapture probabilities (Lebreton et al. 1992). Other studies also have excluded transient adults, thus improving the accuracy of survival estimates (Peach 1993, Chase et al. 1997, Pradel et al. 1997).

We found no evidence of a trend in survival over the 20-year period, 1976–1995. What trend there was appeared weakly positive. Although this finding is consistent with our inference that the observed decline in Warbling Vireo abundance is due to low reproductive success rather than to poor overwinter survival of adults, our power to detect any trend in survival was weak. The very manifestation of a population decline (hence fewer adults caught later in the study period) has made it more difficult to detect a trend in survival.

Warbling Vireos, like many Neotropical migrants, can be found in a wide variety of habitat types during migration (Hutto 1985) as well as on their wintering grounds (Gardali and Ballard, in press). Such flexibility may lessen the effects of habitat loss in migratory and wintering hab-

itats. Although the western Warbling Vireos' breeding habitat requirements are not restricted to any one habitat type, they do require large trees most often with a deciduous or hardwood component (Gardali and Ballard, in press). Thus, breeding season habitat use is more restricted relative to other times of the year. Sherry and Holmes (1995) hypothesized that species may be most limited when habitat use in one season is more restricted than habitat use at other times of the year. Factors on the breeding grounds that influence reproductive success, such as predator densities and nest parasitism, may have the strongest influence on the population. For example, the dual effects of nest depredation and parasitism in the Bitterroot Valley of western Montana appear to be limiting Warbling Vireo populations in agricultural landscapes (Tewksbury et al. 1998).

Reproductive success in migratory birds may also be influenced by date of arrival to the breeding grounds (Marra et al. 1998). Earlier arriving individuals may acquire the highest quality breeding territories and have additional time to replace lost clutches. Warbling Vireos have been arriving later to Palomarin over the course of our study (PRBO, unpubl. data) and as a result could be suffering reduced productivity. Factors that determine arrival date are poorly understood but one recent study suggested that the quality of wintering habitat was responsible for the variation in arrival schedules for the American Redstart (Marra et al. 1998).

We had no way of measuring juvenile survival and thus have no way to assess its importance in the population decline of Warbling Vireos. One study that estimated post-fledging juvenile survival of a Neotropical migrant concluded that the main factor affecting the source/sink status for a population of Wood Thrush (*Hylocichla mustelina*) was reproductive success (Anders et al. 1997).

Analyses of mist-net data may provide valuable insight into assessing which stage of a species' life history has the greatest influence on population dynamics (Nur et al., in press). Mist nets, however, cannot provide specific information on the factors affecting demographic processes. For example, western Warbling Vireos are well known hosts of the Brown-headed Cowbird (reviewed in Sealy 1996) and as such their nesting success could be negatively impacted in areas where parasitism is common.

Parasitized Warbling Vireos usually rear only cowbirds (Sealy 1996). In fact, the precipitous decline of Black-capped and Bell's Vireos have both partly been attributed to parasitism (Goldwasser et al. 1980, Grzybowski 1995).

Steller's Jays, Western Scrub-Jays, and Brown-headed Cowbirds were present at Palomar over the course of our study. Unfortunately, these species are not sampled well by mist nets and capture rates were too low to detect trends in abundance. We examined California BBS data (1979–1996) for two known nest predators, Steller's Jay and Western Scrub-Jay, and the Brown-headed Cowbird. Steller's Jays were increasing by 1.29% ($P = 0.006$, $n = 100$ routes) and Western Scrub-Jays were increasing by 1.05% ($P = 0.007$, $n = 139$ routes) annually, whereas the Brown-headed Cowbird was slightly decreasing, although not significantly (Sauer et al. 1997).

In conclusion, our results point to a relationship between reproductive success and a decline in abundance of Warbling Vireos in California over the past two decades. Those factors responsible for reduced reproductive success in the Warbling Vireo may be highly variable in space and time (e.g., nest predator densities, variation in spring arrival dates), and were not assessed in our study. Studies designed to examine the relationships and interactions among the factors that may limit the reproductive success of the western Warbling Vireo are needed.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Washington, DC.

- ANDERS, A. D., D. C. DEARBORN, J. FAABORG, AND F. R. THOMPSON III. 1997. Juvenile survival in a population of Neotropical migrant birds. *Conserv. Biol.* 11:698–707.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. *Current Ornithol.* 7:1–57.
- CHASE, M. K., N. NUR, AND G. R. GEUPEL. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. *Auk* 114:354–366.
- COCHRANE, D., AND G. S. WATSON. 1949. Application of least-squares regression to relationships containing autocorrelated error terms. *J. Am. Stat. Assoc.* 44:32–61.
- COOCH, E., R. PRADEL, AND N. NUR. 1996. A practical guide to capture/recapture analysis using SURGE. Centre d'Ecologie Fonctionnelle et Evolutive CNRS, Montpellier, France.
- DESANTE, D. F., AND T. L. GEORGE. 1994. Population trends in the landbirds of western North America. *Stud. Avian Biol.* 15:173–190.
- DESANTE, D. F., AND G. R. GEUPEL. 1987. Landbird productivity in central coastal California: the relationship to annual rainfall, and a reproductive failure in 1986. *Condor* 89:636–953.
- DESANTE, D. F., D. R. O'GRADY, K. M. BURTON, P. VELEZ, D. FROEHLICH, E. E. FEUSS, H. SMITH, AND E. D. RUHLEN. 1998. The monitoring avian productivity and survivorship (MAPS) program sixth and seventh annual report (1995 and 1996). *Bird Populations* 4:69–122.
- GARDALI, T., AND G. BALLARD. In press. Warbling Vireo (*Vireo gilvus*). In A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia, PA.
- GOLDWASSER, S., D. GAINES, AND S. WILBUR. 1980. The Least Bell's Vireo in California: a de facto endangered race. *Am. Birds* 34:742–745.
- GRZYBOWSKI, J. A. 1995. Black-capped Vireo (*Vireo atricapillus*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 181. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, DC.
- HUTTO, R. L. 1985. Seasonal changes in habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120–132.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651–661.
- JOHNSON, M. D., AND G. R. GEUPEL. 1996. The importance of productivity to the dynamics of a Swainson's Thrush population. *Condor* 98:133–141.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. D. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62:67–118.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest moni-

- toring plots: methods for locating nests and monitoring success. *J. Field Ornithol.* 64:507–519.
- MARTIN, T. E., AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579–592.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456–466.
- MOORE, F. R., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulidae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.
- MOORE, F. R., S. A. GAUTHREAUX JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: important link in conservation, p. 121–144. *In* T. E. Martin and D. M. Finch [EDS.], *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues*. Oxford Univ. Press, New York.
- MORRIS, S. R., D. W. HOLMES, AND M. E. RICHMOND. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor* 98:395–409.
- NOLAN, V., JR. 1978. Ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26.
- NUR, N., AND G. R. GEUPEL. 1993. Evaluation of mist-netting, nest-searching, and other methods for monitoring demographic processes in landbird populations, p. 237–244. *In* D. M. Finch and P. W. Stangel [EDS.], *Status and management of Neotropical migratory birds*. U.S. Dept. Agric., For. Serv., Rocky Mt. Range Exp. Sta., Gen. Tech. Rep. RM-229, Fort Collins, CO.
- NUR, N., G. R. GEUPEL, AND G. BALLARD. *In press*. The use of constant-effort mist-netting to monitor demographic processes in passerine birds: annual variation in survival, productivity, and floaters. *In* D. Pashley and R. Bonney [EDS.], *Strategies for bird conservation: the partners in flight planning process*. Proc. 2nd Int. Conference on Status and Management of Neotropical Migratory Birds. Cornell Lab for Ornithology, Ithaca, NY.
- PEACH, W. 1993. Combining mark-recapture data sets for small passerines, p. 107–122. *In* J.-D. Lebreton and P. M. North [EDS.], *Marked individuals in the study of bird populations*. Birkhauser, Basel, Switzerland.
- PEACH, W., S. BAILLIE, AND L. G. UNDERHILL. 1991. Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to West African rainfall. *Ibis* 133:300–305.
- PRADEL, R., J. E. HINES, J.-D. LEBRETON, AND J. D. NICHOLS. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72.
- PYLE, P., AND R. P. HENDERSON. 1991. The birds of Southeast Farallon Island: occurrence and season distribution of migratory species. *West. Birds* 22: 41–84.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.
- PYLE, P., N. NUR, AND D. F. DESANTE. 1994. Trends in nocturnal migrant landbird populations at Southeast Farallon Island, California, 1968–1992. *Stud. Avian Biol.* 15:58–74.
- RALPH, C. J. 1971. An age differential of migrants in coastal California. *Condor* 73:243–246.
- RAPPOLE, J. H., AND M. V. McDONALD. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652–660.
- ROTH, R. R., AND R. K. JOHNSON. 1993. Long-term dynamics of a Wood Thrush population in a forest fragment. *Auk* 110:37–48.
- SAUER, J. R., J. E. HINES, G. GOUGH, I. THOMAS, AND B. G. PETERJOHN. 1997. The North American Breeding Bird Survey Results and Analysis. Version 96.4. Patuxent Wildl. Res. Center, Laurel, MD.
- SEALY, S. G. 1996. Evolution of host defenses against brood parasitism: implications of puncture-ejection by a small passerine. *Auk* 113:346–355.
- SHERRY, T. W., AND R. T. HOLMES. 1992. Population fluctuations in a long-distance Neotropical migrant: demographic evidence for the importance of breeding season events in the American Redstart, p. 431–442. *In* J. M. Hagen III and D. W. Johnson [EDS.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Inst. Press, Washington, DC.
- SHERRY, T. W., AND R. T. HOLMES. 1993. Are populations of Neotropical migrant birds limited in summer or winter? Implications for management, p. 47–57. *In* D. M. Finch and P. W. Stangel [EDS.], *Status and management of Neotropical migratory birds*. U.S. Dept. Agric., For. Serv., Rocky Mt. For. and Range. Exp. Sta., Gen. Tech. Rep. RM-229, Fort Collins, CO.
- SHERRY, T. W., AND R. T. HOLMES. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? p. 85–120. *In* T. Martin and D. Finch [EDS.], *Ecology and management of Neotropical migratory birds: synthesis and review of the critical issues*. Oxford Univ. Press, New York.
- SHUFORD, W. D. 1993. The Marin County Breeding Bird Atlas: a distributional and natural history of coastal California birds. California Avifauna Series 1. Bushtit Books, Bolinas, CA.
- SILKEY, M., N. NUR, AND G. R. GEUPEL. 1999. The use of mist-net capture rates to monitor annual variation in abundance: a validation study. *Condor* 101: 288–298.
- STATA CORP. 1997. STATA, Release 5.0. Stata Corp., College Station, TX.
- TEWKSBURY, J. J., S. J. HEIL, AND T. E. MARTIN. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890–2903.
- YONG, W., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *Auk* 115:829–842.
- ZAR, J. H. 1996. *Biostatistical analysis*. 3rd ed. Prentice Hall, Englewood Cliffs, NJ.