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Poor reproductive success of Gray Vireos in a declining California population

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ABSTRACT. Since the 1940s, populations of Gray Vireos (*Vireo vicinior*) in California have collapsed, presumably because of parasitism by Brown-headed Cowbirds (*Molothrus ater*). In 2012 and 2013, we studied the vireo's nesting ecology to assess factors affecting two of California's largest remaining populations in the chaparral of San Diego County. Nest success was extremely low, with a model-averaged probability of nest survival of only 0.08 ($N = 95$). More nest failures were due to predation (83%) than to cowbird parasitism (13%). Video-recording at 30 nests revealed that California Scrub-Jays (*Aphelocoma californica*) were the most common nest predator (67%). Of eight variables tested, height of shrubs surrounding the nest had the strongest negative influence on nest survival, but was more strongly correlated with cowbird parasitism than with jay predation. Despite frequent renesting, seasonal productivity was well below the level required to sustain a population, especially in northern San Diego County where we found no Gray Vireos at six of seven sites where they had been present from 1997 to 2001 and where cowbird parasitism was more frequent. The vireo's continuing range collapse contrasts with recent climate-change models predicting a range expansion, highlighting the importance of demographic studies. Low nest success is likely contributing to population declines in California, and the additive effect of cowbird parasitism suppresses productivity. Conservation of Gray Vireos in California will likely require development of alternative approaches to cowbird and scrub-jay control appropriate to sites widely scattered in rugged chaparral.

RESUMEN. **Bajo éxito reproductivo de *Vireo vicinior* en una población de California en declive**

Desde la década de 1940, las poblaciones de *Vireo vicinior* en California se han desplomado, presuntamente por el parasitismo por *Molothrus ater*. En 2012 y 2013, estudiamos la ecología de anidación de *Vireo vicinior*, con el objetivo de determinar los factores que afectan las dos poblaciones más grandes de California en el chaparral del condado de San Diego. El éxito reproductivo fue extremadamente bajo, con una probabilidad promedio de supervivencia del nido de solo 0.08 ($N = 95$). La mayor cantidad fracasos de nidos fue producto de depredación (83%) y no de parasitismo por *Molothrus ater* (13%). Grabaciones de 30 nidos revelaron que el depredador más común fue *Aphelocoma californica* (67%). De las ocho variables evaluadas, la altura de los arbustos alrededor del nido tuvo la influencia negativa más fuerte sobre la supervivencia del nido, sin embargo, estuvo más fuertemente correlacionada con el parasitismo por parte de *Molothrus ater* que por la depredación por parte de *Aphelocoma californica*. A pesar de los intentos frecuentes de re-anidación, la productividad estacional fue considerablemente menor al nivel requerido para sostener una población, especialmente en el norte del condado de San Diego, donde no encontramos *Vireo vicinior* en seis de las siete localidades donde había sido reportado entre 1997 y 2001, y donde el parasitismo por *Molothrus ater* fue más frecuente. La reducción actual de la distribución de *Vireo vicinior* difiere con los modelos recientes de cambio climático que predicen una expansión de la distribución, resaltando la importancia de estudios demográficos. Es probable que el éxito reproductivo bajo contribuya a la disminución en las poblaciones de California, y el efecto aditivo del parasitismo de *Molothrus ater* suprima la productividad. La conservación de *Vireo vicinior* en California requerirá del desarrollo de métodos alternativos para el control de *Molothrus ater* y *Aphelocoma californica* que sean apropiados para localidades muy dispersas en chaparral escabroso.

Key words: brood parasitism, chaparral, conservation, nest success, scrub-jay, video monitoring

Gray Vireos (*Vireo vicinior*) are one of the least-studied birds in North America (Barlow et al. 1999) and populations are inadequately

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monitored by existing programs, e.g., data from Breeding Bird Surveys are insufficient for trend analysis (https://www.pwrc.usgs.gov/bbs). However, because of their limited range, local extirpations, and presumed susceptibility to parasitism by Brown-headed Cowbirds (*Molothrus ater*), Gray Vireos have been identified as a species of conservation concern since 1978 (Remsen 1978, U.S. Fish and Wildlife Service 2008).

In most of their breeding range, Gray Vireos occur in pinyon-juniper woodlands, but they are found in arid chaparral in California's Transverse and Peninsular ranges (Unitt 1984). These areas tend to be remote and largely protected in national forests. Although habitat availability does not appear to be a limiting factor, Gray Vireos occur patchily at low densities in California (1.2–1.6 birds per 40 ha; Johnson et al. 1948, Weathers 1983) and elsewhere (Corman 2005, DeLong and Williams 2006, Schlossberg 2006, Wickersham and Wickersham 2008).

Populations in California once represented a substantial proportion of the known range of Gray Vireos, but they appear to have declined precipitously, probably by 75–95% (Supplemental Fig. S1; Remsen 1978, Unitt 2008, Hargrove and Unitt 2014). California's largest known population, estimated at 960 birds in the San Jacinto Mountains by Grinnell and Swarth (1913), is now nearly extirpated even though the habitat appears intact (Hargrove and Unitt 2014). Recent records in California are few and scattered except in two regions of San Diego County that appeared, as of 2002, to have the two largest populations, with numbers estimated in the low hundreds (Unitt 2004).

Cowbird parasitism has been suggested as the reason for the decline of the Gray Vireo population in California (Remsen 1978), but empirical support is limited (Hanna 1944, Friedmann 1963), and the prevalence of cowbird parasitism in the arid chaparral used by Gray Vireos is unknown. Other factors such as nest predation could also be contributing to the decline, perhaps interactively with cowbirds, as reported for other species (e.g., Stumpf et al. 2011).

Although reasons for the decline of California populations of Gray Vireos are unclear, their current status calls for monitoring and identification of current threats. Thus, our objectives were to document the nesting ecology and status of Gray Vireos in California, determine if cowbirds are a primary cause of nest failure, and identify other factors influencing nest success and seasonal productivity.

METHODS

To evaluate the current status of Gray Vireos in California, we targeted two areas of the Cleveland National Forest in San Diego County with most of California's remaining population as of 2001 (Unitt 2004): one north of Warner Springs (North County; 33°20′N, 116°38′W) and one 50 km south in the southern Laguna Mountains (South County; 32°47′N, 116°28′W) (Supplemental Fig. S1). Based on field work conducted from 1997 to 2001 (Unitt 2004), we identified seven sites most likely to be occupied in the North County study area and 12 in South County, representing at least 50% of the recorded sites and most of the known population in the county. We surveyed these 19 sites to determine current occupancy and to identify plots for monitoring. At sites where Gray Vireos were apparently absent, we resurveyed the site and other intervening habitat at least twice during May and early June 2012 and 2013 to confirm absence. In South County where we had estimated territory density by spot-mapping in two areas of ~250 ha each in 2002, we repeated that effort in 2012 for comparison (Hargrove and Unitt 2014).

To document nesting ecology and nest outcomes, we defined plots for intensive monitoring based on the area we could cover effectively in 4–5 h and the presence of Gray Vireos. One occupied site in the South County study area was too difficult to access so could not be included in our study. Lack of trails, rugged terrain, and thick vegetation limited plot size to 20–50 ha. At elevations from 1000 to 1500 m, plots were heterogeneous in shrub structure and composition, but dominated by chamise (*Adenostoma fasciculatum*; Fig. 1). To ensure a minimum sample of 30 territories monitored per year and 10 nests video-monitored per year, we surveyed 13 study plots in 2012 and nine of the same plots in 2013. Considerable searching in 2012 of the seven sites occupied in North County from 1997 to 2001 revealed Gray Vireos at only one, restricting us in that region to two adjacent study plots surveyed in both 2012 and 2013. The remaining plots

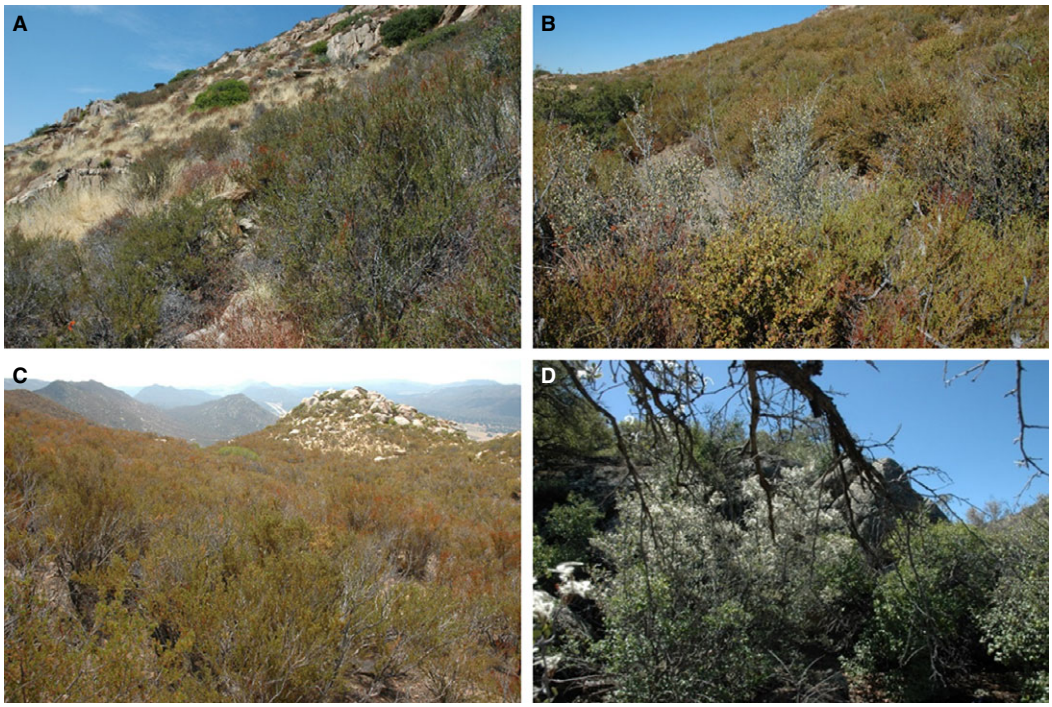


Fig. 1. Most Gray Vireo nesting habitat in southern California is dominated by chamise (*Adenostoma fasciculatum*), with shrub cover ranging from relatively open (A) to dense (B) and shrubs varying in height and composition from relatively short and uniform (C) to tall and heterogeneous (D). A Gray Vireo nest site is at the center of each photo (taken 3 m from nests).

were in South County (11 plots in 2012, and 7 in 2013).

At all plots, we mapped territories and monitored nests from first arrival of Gray Vireos (late March) to after the last active nest (late August). We searched each territory 2–3 times per week for evidence of nesting and fledging. We found most nests by observing pairs either carrying nest material or frequently returning to the same shrub. No adults were banded, but we were able to delineate territory boundaries because males sang nearly continuously during the day (including while on nests) and neighboring males often sang simultaneously. Boundaries of defended territories (mean area = 11 ha, range = 5–18 ha) changed little within and between years.

We typically checked nests every 2–5 days (mean = 2.9 days, range = 1–8 days). Confirming the date the first egg of a clutch was laid or, in some nests, whether eggs were ever laid was not always possible because birds sat tightly on nests beginning even before eggs were laid. Thus, instead of flushing birds from nests, we more often observed from a distance and checked nest contents when adults left nests. We were able to estimate the date of laying of first eggs to within 3 days for 93% of nests (mean = 1.2 days, range = 0–6 days). We excluded from analysis nests that were incomplete or nests where, because of a lack of subsequent incubation, we suspected no eggs were laid. We also recorded clutch sizes (after clutches were completed), final nest outcomes, and number of fledglings. For any nests with young near fledging age and without a video-recorder, we made additional visits as needed to confirm fledging and count fledglings.

After nests failed or young fledged, we returned between July and October (when shrubs are dormant) to measure variables associated with nest placement and surrounding vegetation. We identified nest substrates (shrub species) and measured nest height

above ground and shrub height and width. Within a radius of 3 m of each nest, we estimated shrub cover of the ground (viewed from above) visually (± 5%) and measured heights of all individual shrubs. We measured concealment by standing 3 m from nests and estimating the proportion of each nest obstructed from view (± 5%) at each of four cardinal directions, and then averaged the four estimates. Some nests (6%) were destroyed or missing, reducing the sample size for some nest-level variables, and we did not obtain concealment data for 17% (16 of 95) of nests because mostly intact nests were necessary for accurate estimates. For any missing data, we substituted the means from all other nests.

To quantify surrounding habitat, we also made similar nest-level measurements (substrate, shrub height and width, shrub cover within 3 m, and shrub height within 3 m) at random points stratified by study plot. In each study plot with at least three Gray Vireo territories, we established three random points by generating random coordinates within the plot's perimeter and excluding any points within 25 m of a Gray Vireo nest or another random point. At these points, we selected the nearest shrub within the range of heights at which Gray Vireos nest.

To analyze shrub composition at nests and surrounding habitat, we applied detrended correspondence analysis (DCA; McCune and Mefford 2006) based on 15 plant species or groups of species (with uncommon species pooled as miscellaneous). For abundance of each of these 15, we used the cover estimated within a 3-m radius at each nest as well as at random points. Based on the unconstrained ordination (Table 1), the first axis (DCA axis 1) represented a gradient of composition from chamise to oak (*Quercus* spp.), and the second from redshank (*Adenostoma sparsifolium*) to manzanita (*Arctostaphylos* spp.; lowest to highest species scores). Scores for each point (sample scores) are the weighted mean abundances (thus quantifying composition).

To evaluate any effects of year on nest success and seasonal productivity, we compared the weather in the 2 years of our study and against a 50-year average (1963 to 2013). We obtained monthly precipitation totals and monthly mean minimum and maximum temperature at 2.5-min resolution from the PRISM Climate Group (Oregon State University, http://prism.oregonstate.edu). We averaged the data for three points (points were from elevation 1300 m in North County and elevations 1200 m and 1400 m in South County).

Video cameras. We monitored 30 nests (20 in 2012, 10 in 2013) in eight plots with video cameras for a total of ~8000 h, deploying cameras as soon as nest building appeared complete and usually after incubation was confirmed. Cameras recorded continuously, but we checked nests with cameras on the same schedule as those without to confirm nest contents and narrow the intervals of video needing review. In addition to recording predation and parasitism, videos also improved the accuracy of our estimates of the duration of incubation and nestling periods. We tested for any influence of cameras on nest outcomes by comparing daily survival of nests with and without cameras, and evaluated their efficacy at documenting nest outcomes.

We designed our camera systems to be inconspicuous, easy to install quickly, and able to record continuously between exchanges of batteries and memory cards every 3–4 days. The components consisted of a miniature (2.3 × 0.8 cm) camera with 940-nm infrared illumination (PC2291R, Supercircuits, Inc., Austin, Texas), a 1.8-m camera cable enclosed in protective roofing tape, an additional 9-m video cable extension enclosed in a protective metal conduit, an H.264 miniature digital video recorder (MDVR14-4, Supercircuits, Inc.), a 32-GB memory card, a 6.4-cm portable monitor (LCD3-2, Supercircuits, Inc.), a rechargeable 12-volt battery, and a plastic toolbox to enclose the digital video recorder and battery. Cameras were inserted into 5-cm plastic protective funnels with their necks wrapped in duct tape to be clipped more easily to a shrub, and entire assemblages were spray-painted dull green and brown for camouflage. During set-up, cameras were affixed to a stem of either the nest shrub or an adjacent shrub ~0.5–1.0 m from nests (by clips and duct tape that were also camouflaged), and a toolbox containing the digital video recorder and battery was placed in a shaded spot at least 7 m from nests. Adult vireos usually stayed on nests during camera set-up, but returned within 5 min if flushed. Camera set-up

Table 1. Results of detrended correspondence analysis of plant species composition based on 15 plant species or groups within a 3-m radius centered on each point ($N = 109$), where points represent each Gray Vireo nest location and random points stratified by study plot in San Diego County, California, 2012–2013. Total variance in the data was 3.67.

		DCA Axis 1	DCA Axis 2
Plant category			
Chamise	*Adenostoma fasciculatum*	0	160
Salvia	*Salvia* and *Trichostema* spp. (mostly *S. apiana* and *T. lanatum*)	43	126
Ceanothus	*Ceanothus* spp. (mostly *C. greggii*)	49	160
Yerba santa	*Eriodictyon crassifolium* and *trichocalyx*	71	49
Dead	Dead shrub, unidentified	78	83
Deerweed	*Acmispon glaber*	113	60
Yucca	Yuccas (mostly *Hesperoyucca whipplei*, also *Yucca schidigera*)	125	161
Manzanita	*Arctostaphylos* spp.	133	381
Miscellaneous	Other spp.	135	283
Buckwheat	*Eriogonum fasciculatum*	139	166
Sugar bush	*Rhus ovata*	175	299
Mountain-mahogany	*Cercocarpus betuloides*	181	310
Redshank	*Adenostoma sparsifolium*	210	−23
Prunus	*Prunus* spp. (mostly *P. ilicifolia*)	254	280
Oak	*Quercus* spp. (mostly *Q. berberidifolia*)	301	76
Eigenvalue		0.62	0.40
Length of gradient		2.79	3.43

typically took 10–15 min, but occasionally up to 60 min. Continuous (24-h) recordings were stored as 0.5-h files and transferred to DVD for long-term storage.

Nest survival. We estimated the probabilities that nests survived 1 day (daily nest survival) and that nests survived from first egg to fledging (overall nest survival) by number of exposure days (Mayfield 1975). To explore the relative influence of variables on nest survival, we used program MARK, version 5.1 (White and Burnham 1999, Rotella et al. 2004), to rank a set of models containing all possible additive combinations of eight variables ($2^k = 256$) by maximum likelihood (Burnham and Anderson 2002). For each variable, we summed the Akaike weights (w) across all models containing that variable for a balanced measure of the variables' relative importance (Burnham and Anderson 2002, Arnold 2010, Symonds and Moussalli 2011, Doherty et al. 2012). All models were ranked by ΔAIC_c, and we retained for model-averaging the set of models whose value of AIC_c was no more than 2.00 units greater than that of the top model (Burnham and Anderson 2002, Arnold 2010). We estimated daily nest survival, overall nest survival, and values of individual variables by model-averaging of the reduced set. For each variable, we report the conditional model-averaged estimate (β) based on the set containing that variable and the unconditional standard error that accounts for error in parameter estimation as well as error due to uncertainty in model selection (Burnham and Anderson 2002, Symonds and Moussalli 2011).

The eight tested variables were year (2012 = 0 or 2013 = 1), lay date (date of first egg standardized to 1 for the earliest date observed, 20 April), study area (South = 0 or North = 1), nest shrub (chamise = 0 or other = 1), nest height, nest concealment, and height and cover of shrubs within a radius of 3 m of nests. We discarded nest-shrub height as a variable because it was correlated with the height of both the nest and surrounding shrubs. Of the remaining eight variables, correlations between any two were weak ($|r| < 0.50$). We treated each nest as independent because territories were large and heterogeneous, encompassing multiple aspects, habitat variables were limited to independent

nest-level measurements rather than landscape variables, distances between nests in neighboring territories were sometimes shorter than distances between successive nests in the same territory, scrub-jays and cowbirds were present in every territory, and birds were not banded.

We used descriptive statistics to characterize other nest-level measurements. For aspect and nest orientation, we calculated mean angle, angular deviation, and performed a Rayleigh test for non-uniform distribution (Zar 1999). For analysis of variation (ANOVA) and all other routine statistical analyses, we used R version 3.1.1 (R Core Team 2014) and considered $P < 0.05$ to be significant. We estimated seasonal productivity as a range by summing the minimum and maximum numbers of fledglings possible per study area and dividing by the total number of territories. Minimum was defined as the number of fledglings observed and maximum as the number of nestlings observed during the final nest check. Values are provided as means ± 1 SD.

RESULTS

Territory and nest monitoring. Two singing Gray Vireos were observed on the first survey date in both 2012 (25 March) and 2013 (24 March). Most, however, arrived during the first two weeks of April. In both years, there was a delay between arrival and nesting (Fig. 2). We monitored 40 territories in 2012 and 31 of those same approximate territories in 2013. Mean date of egg laying in 2013 was 16 days earlier than in 2012 ($F_{1,91} = 19.0$, $P < 0.001$), but there was no effect of study area ($F_{1,91} = 2.1$, $P = 0.15$) and no interaction between year and study area ($F_{1,91} = 0.3$, $P = 0.57$). Egg laying also ended earlier in 2013 (Fig. 2). The latest fledging of nestlings was on 1 August 2012 and 12 July 2013. We visited territories less regularly in September, but our latest vireo detections were on 12 September 2012 and 10 September 2013.

Incomplete nests excluded, we discovered 55 nests in 2012 and 40 in 2013 (overall mean = 1.3 nests per territory). Of the 95 nests, most (79%) were found prior to egg laying, and the rest within eight days of egg laying. After nests failed, pairs began constructing new nests in as little as one day. Many nests likely failed before we could locate them, but we observed at least six nesting attempts in a single season in one territory, each failing. Incomplete nests excluded, the mean number of days between a nest failure and egg laying in a new nest was 9.2 ($N = 36$; range = 3–38 days). Mean clutch size was 3.3 ± 0.8 eggs (3.4 in 2012, $N = 25$; and 3.2 in 2013, $N = 18$; range = 1–4, mode = 4). For one nest with only one egg, we confirmed partial predation; the single young eventually fledged. Based on the 10 best-monitored nests (Supplemental Fig. S2), the typical incubation period (laying to hatching of the first egg) was 16 days (range = 15–17 days), and the typical nestling period (from hatching to fledging of the first nestling) was 14 days (range = 12–16 days). For the two periods combined, the total nest period was at least 28 days but typically was 29–31 days (Supplemental Fig. S2). We documented one case of successful double-brooding, with the first brood fledging on 6 June and the second on 12 July 2013; a fledgling from the first nest begged from the adult female as she incubated eggs in the second nest, and remained in the territory after young from the second nest fledged.

All nests ($N = 95$) were in shrubs, including chamise (73%), desert ceanothus (*Ceanothus greggii*; 11%), mountain mahogany (*Cercocarpus betuloides*; 11%), scrub oak (*Quercus* spp.; 3%), redshank (1%), hollyleaf redberry (*Rhamnus ilicifolia*; 1%), and manzanita (1%). Mean height of nest shrubs was 1.8 ± 0.4 m ($N = 89$, range = 0.6–2.0 m), mean nest height was 1.2 ± 0.3 m ($N = 85$, range = 0.6–2.0 m), mean height of shrubs within 3 m of nests was 1.5 ± 0.5 m ($N = 87$, range = 0.8–5.2 m), mean cover of shrubs within 3 m was 71 ± 15% ($N = 88$, range = 25–95%), and mean nest concealment was 80 ± 15% ($N = 79$, range = 31–100%). Most nests were located on south-facing slopes (mean = 175 ± 60°; $z = 16.3$, $P < 0.001$, $N = 81$), and 66 of 78 nests were displaced from the center of shrubs, tending toward the southward or downslope side of shrubs (mean = 180 ± 56°; $z = 18.1$, $P < 0.001$, $N = 66$).

Nest outcomes. At least one young fledged from 17 of 95 nests (Table 2). Of 78 failed nests, at least 10 (13%) were parasitized by Brown-headed Cowbirds, including two consecutive nests in one territory. All

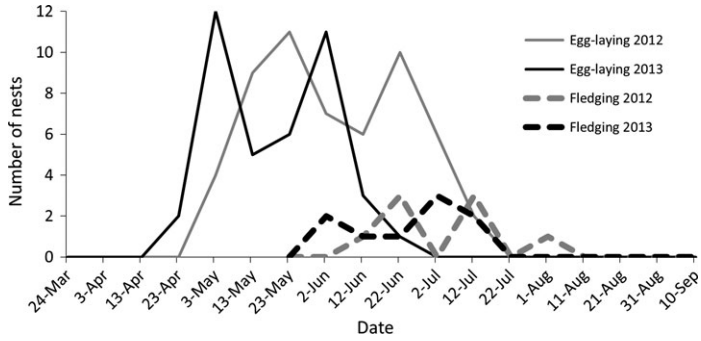


Fig. 2. Chronology of Gray Vireo nesting, showing distribution of nests by date of egg laying (solid lines) and fledging (dashed lines) in 2012 (gray) and 2013 (black).

Table 2. Gray Vireo nest outcomes in San Diego County, California, 2012–2013. A nest was considered successful if at least one nestling fledged. The category of predated nests includes both those where predation was confirmed (by video) and those where it was suspected (without video).

	2012		2013		Total	
Nest outcome	*N*	Percentage	*N*	Percentage	*N*	Percentage
Fledged young	8	14.5	9	22.5	17	17.9
Parasitized by cowbirds	7	12.7	3	7.5	10	10.5
Predated	39	70.9	26	65.0	65	68.4
Other failure or unknown	1	1.8	2	5.0	3	3.2
Total	55		40		95	

parasitized nests were abandoned, with adults renesting in six cases. Most nests (83%) failed because of confirmed or probable predation, including 50 during egg laying or incubation, eight near hatching (eggs or nestlings uncertain), and seven during the nestling stage. Two failed nests had the eggs punctured, possibly by cowbirds, but we categorized these as predated. Two nests failed likely because of wind (video evidence described below), and one nest was abandoned after probable loss of the female (only the male was observed on successive visits). An additional 15 nests where we observed no eggs were apparently abandoned and were excluded from our analyses.

Of 30 nests video-recorded, young fledged from seven, three were parasitized by cowbirds, two failed because of high winds (apparently abandoned and eggs later found cracked), three were probably predated (event not recorded or unclear), and 15 were predated. Of these 15 nests, California Scrub-Jays (*Aphelocoma californica*) removed eggs from 10 nests (67%), a gray fox (*Urocyon cinereoargenteus*) preyed on nestlings at one nest (Supplemental Video S1), a bobcat (*Lynx rufus*) took an incubating female at one nest, a Bewick's Wren (*Thryomanes bewickii*) removed eggs at one nest, and unidentified predators preyed on eggs at one nest and nestlings at another. California Scrub-Jays were the most frequent predator (goodness of fit test, $\chi^2_3 = 16.3$, $P = 0.001$; Supplemental Video S2). The three parasitized nests were abandoned after prolonged interactions with cowbirds (e.g., Supplemental Video S3).

Young fledged from only two of 18 nests in North County (e.g., Supplemental Video S4) and from 15 of 77 nests in South County. This difference appeared to be driven primarily by a significant difference in the rate of cowbird parasitism, 28% in North County and 6% in South County (Fisher's exact test, $P = 0.02$). The ordination showed an association of surrounding shrub composition with nest outcome, but independent of

study area. Compared to random points and unsuccessful nests, successful nests tended to be more strongly clustered near chamise and ceanothus (Fig. 3). The difference between average scores on DCA axis 1 (gradient of chamise to oak) of successful nests (score 22) and unsuccessful nests (score 43) appeared unrelated to any differences between study areas (North County score 37 vs. South County score 40), but scores of nests that failed because of scrub-jays (23) and cowbirds (69) differed.

More nests were successful in 2013 than in 2012 because of lower parasitism and predation rates (Table 2). Both years were slightly warmer and drier than the 50-year average, but 2013 was drier than 2012 (precipitation in 2013 was 46% below average). Nests were initiated earlier in 2013 (Fig. 2), the drier year.

Evaluation of nest video-cameras. Our camera design minimized influence on predators and allowed rapid set up with minimal disturbance. With the interval between discovery of nests and later set up of the camera excluded, daily nest survival was 0.93 (95% CI: 0.89–0.95) for nests with cameras and 0.91 (95% CI: 0.88–0.93) for nests without. With the possible exception of one case where a scrub-jay flew to a nest 1.5 h after camera set-up, we found no relationship either between camera set-up and time to predation or between nest checks and time to predation.

Nest-survival modeling. Based on summed model weights from all possible combinations of variables (256 models), surrounding shrub height, nest height, study area, and surrounding shrub cover were more important in predicting daily nest survival

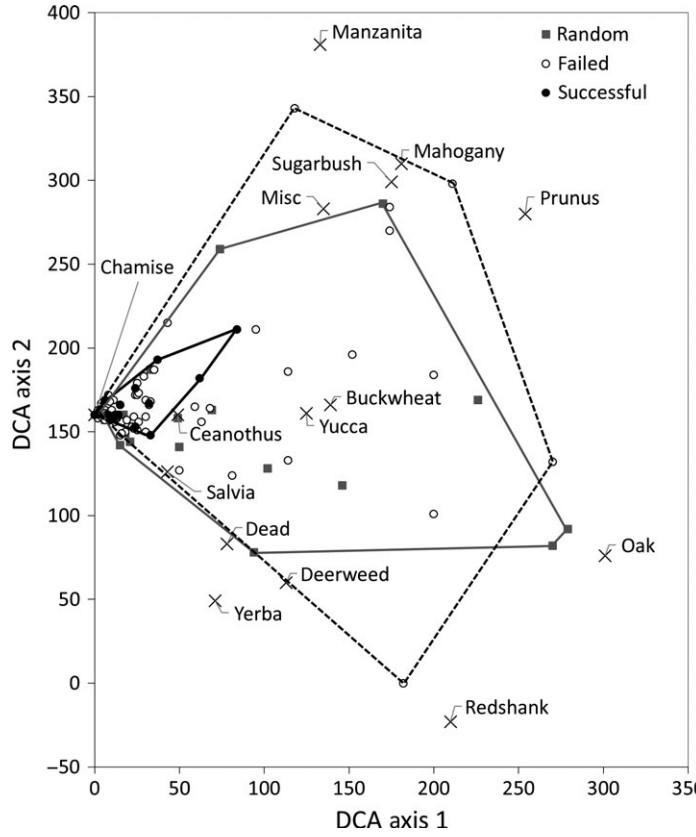


Fig. 3. Positions of Gray Vireo nests (successful, solid black circles; unsuccessful, open black circles) and random points (gray squares) relative to plant species within an unconstrained ordination of plant species composition by detrended correspondence analysis (DCA). DCA axis 1 represents a gradient from chamise to oak; axis 2 represents a gradient from redshank to manzanita.

than year, lay date, species of nest shrub, and nest concealment (Table 3). Eleven models were within 2.00 ΔAIC_c units of the top model ($AIC_c = 419.41$). Based on this top set, the model-averaged estimate was 0.91 (95% CI: 0.89–0.93) for daily nest survival and 0.08 (95% CI: 0.04–0.13) for overall nest survival. Each variable appeared in the top set at least twice, and model-averaged estimates for each variable corroborated the ranking based on summed weights from all models (Table 3). Interestingly, although taller surrounding shrubs had a negative effect on nest survival, greater nest height had a positive effect (Table 3). We also compared the mean height of shrubs around random points and all nests, as well as among three outcomes. Although surrounding shrubs tended to be shorter around nests (1.5 ± 0.5 m) than around random points (2.3 ± 2.9 m; two-sample *t*-test, $t_{106} = 2.4$, $P = 0.02$), we found no difference in this variable between successful nests (1.5 ± 0.3 m) and nests that failed because of either scrub-jay predation (1.4 ± 0.2 m) or cowbird parasitism (2.0 ± 1.2 m; $F_{2,34} = 2.4$, $P = 0.10$).

Productivity. Although mean clutch size was 3.4 (both years pooled), the mean number of fledglings produced per successful nest was only either 1.8 (based on minimum number of fledglings confirmed) or 2.5 (based on nestlings counted on the last nest check). Thus, summing all fledglings across a 2-year total of 71 territories monitored, we estimated that seasonal productivity was between 0.45 and 0.63 fledglings per territory (0.25–0.33 in North County, and 0.49–0.69 in South County).

Population status in San Diego County (1997–2001 vs. 2012–2013). Resurveys of 19 sites with records of Gray Vireos during field work for the San Diego County Bird Atlas (1997–2001; Unitt 2004) revealed Gray Vireos persisting at 11 of 12 sites in South County, but at only one of seven sites in North County. Additional surveys of intervening habitat in North County revealed no additional records. Resurveys of the two 250-ha sites in South County where we mapped Gray Vireo territories in 2002 (Hargrove and Unitt 2014) revealed a decline from 14 to six territories around the Pacific Crest Trail at Kitchen Creek Road and a decline from 10 territories to one at south Bear Valley Road (one singing male that did not persist).

DISCUSSION

Current status and nesting ecology in California. Model-averaged nest success (8%) and apparent nest success (18%) of Gray Vireos in the arid chaparral of California were lower than reported elsewhere within their range. The apparent success of Gray Vireo nests in pinyon-juniper woodland in Colorado (observed by Hutchings and Leukering in Barlow et al. 1999) was 33%, and Mayfield-adjusted estimates in pinyon-juniper habitats in New Mexico ranged from 20 to 43% (L. Wickersham and C. Nishida, pers. comm.). Possible reasons for differences in nest success across the range of Gray Vireos are unclear, but low nesting success is likely contributing to population declines in California. Nest success was especially low in our

Table 3. Relative importance (*w*, sum of model weights) and effect (β, model-averaged coefficient) of eight variables in predicting survival of Gray Vireo nests in San Diego County, California, 2012–2013.

Variable	w[a]	β[b]	SE[b]	95% LCI[b]	95% UCI[b]
Surrounding shrub height	0.91	−1.25	0.47	−2.18	−0.32
Nest height	0.84	1.45	0.62	0.23	2.66
Study area	0.71	−0.64	0.32	−1.26	−0.01
Surrounding shrub cover	0.51	1.29	0.86	−0.40	2.97
Year	0.37	0.25	0.26	−0.25	0.76
Lay date	0.34	−0.01	0.01	−0.02	0.01
Nest shrub	0.31	−0.23	0.28	−0.79	0.32
Concealment	0.29	0.66	0.97	−1.24	2.57

[a]Based on full set of 256 models.
[b]Average based on top 11 models.

North County study area where more extirpations have occurred during the past 10–12 years.

Despite frequent renesting, seasonal productivity during the two years of our study was below that needed to sustain populations in our two study areas. Survival of both fledgling and adult Gray Vireos is unknown, but DeSante et al. (2015) estimated yearly survival probability of adults of other vireo species of the western United States at 0.52–0.62 and first-year survival is likely lower. Even at the highest estimated seasonal productivity of Gray Vireos in our South County study area and the highest estimated survival, the population growth rate was still <1 (seasonal productivity per individual of 0.69/2 = 0.35 plus survival probability of 0.62). Seasonal productivity may typically be better because both years of our study were relatively dry, but nest survival was slightly greater in the drier year and modal clutch size was four in both years. Thus, our results suggest that any substantial increase in seasonal productivity of Gray Vireos would require a reduction in rates of nest predation or parasitism.

Projections that the range of Gray Vireos should increase with a warming climate (Van Riper et al. 2014, National Audubon Society 2015) run counter to declines in California, although more research is needed concerning differences in demographic trends rangewide. Monitoring efforts have increased in some areas (Walker and Doster 2009), but trends are unclear and populations appear to be highly patchy and discontinuous throughout the range. For example, Gray Vireos were observed in only 17% of atlas blocks in Arizona from 1993 to 2000 (Corman 2005), only 94 birds were detected at 282 points on the Colorado Plateau of Arizona and Utah in 2001 (Schlossberg 2006), and the estimated total population at 49 known sites in New Mexico ranged from 549 to 827 birds in 2005 (DeLong and Williams 2006).

Nest failure due to California Scrub-Jays and Brown-headed Cowbirds. All 10 nests parasitized by cowbirds in our study were abandoned, but most nests failed due to predation, primarily by California Scrub-Jays. Renesting was frequent because Gray Vireo nests were more likely to fail at an early stage; in all 10 cases of scrub-jay predation confirmed by video-recording, scrub-jays took eggs rather than nestlings. The range of scrub-jays overlaps the entire range of Gray Vireos, but their densities may be higher in coastal southern California than in other states, as suggested by the Breeding Bird Survey summer distribution map for 2007–2013 (10–30 birds per route in coastal southern California vs. 0.05–10 in other states; https://www.pwrc.usgs.gov/bbs).

Although not the primary cause of nest failure, cowbird parasitism tends to depress seasonal productivity. As reported for other species, cowbirds could also contribute to nest predation, either directly by destroying eggs or nestlings (e.g., Arcese et al. 1996, Hoover and Robinson 2007, Conkling et al. 2012) or indirectly by attracting predators (e.g., Stumpf et al. 2011). Brown-headed Cowbirds began spreading into California about 1910 (Willett 1933, Laymon 1987), leading to parallel declines in other bird species susceptible to parasitism (Unitt 2008). Parasitism rates of Gray Vireos elsewhere have been reported as low to moderate, with frequent abandonment (Barlow et al. 1999).

Nest placement and surrounding habitat. Aspects of nest-site selection associated with greater success of the Gray Vireo nests we studied were use of vegetation with a greater proportion of chamise and shorter surrounding shrubs. Such nest sites could help deter both scrub-jays and cowbirds by reducing the number of nearby perches from which a nest is more likely to be visible (Sharp and Kus 2006). In other parts of the range, nest-site selection has not been studied, but Schlossberg (2006) found that Gray Vireo territories were associated with less pinyon and more juniper mixed with other shrubs, especially sagebrush (*Artemisia tridentata*). However, in pinyon-juniper in New Mexico, Johnson et al. (2014, 2015) found that Gray Vireos apparently selected nest sites where trees were taller and denser than in nearby habitat. In our study areas, successful nests were more strongly affiliated with a greater proportion of chamise, suggesting a possible preference for more uniform cover of chamise or a mixture of chamise and ceanothus that tend to form large patches homogeneous in height and cover (Fig. 1C). Tall surrounding perches may be an important negative factor

in an otherwise homogeneous cover of chaparral, just as in more open habitat, where for many species the probability of parasitism decreases as distance to the nearest tree increases (e.g., Burhans et al. 2010). Preference for chamise over oak could also reduce rates of predation by scrub-jays that are typically associated with oaks in California (Carmen 2004). However, we found little difference in any nest-site variable between nests predated by scrub-jays and successful nests.

Gray Vireo conservation. Gray Vireos have been studied very little so our understanding of factors important in their conservation is limited. Nevertheless, we consider three topics as being high priorities for identifying effective management options, including (1) factors that influence rates of nest predation by scrub-jays, (2) alternative methods of cowbird control, and (3) the fire ecology of Gray Vireos.

In California, scrub-jays are strongly associated with oaks because cached acorns are an important component of their diet throughout winter until at least May (Carmen 2004). Scrub-jays can reduce the nest success of other passerines substantially, but Preston and Rotenberry (2006) found that providing the scrub-jays with supplemental food reduced their rates of nest predation. Thus, predation by scrub-jays could be reduced in years with increased abundance of acorns (Koenig et al. 2009). In addition, jays benefit from rural development, recreation, and campgrounds that supplement their food and water (Marzluff and Neatherlin 2006) and so are possibly increasing in the Gray Vireo's habitat of arid chaparral with few oaks. Where scrub-jays may be benefiting from human activity, nest predation rates might be reduced by aversive conditioning, i.e., exposing scrub-jays to decoy eggs spiked with an emetic and placed in vireo nests collected the previous year, a method used successfully with jays elsewhere (Gabriel and Golightly 2014). Any monitoring of Gray Vireo populations should also include monitoring of scrub-jay populations to determine the degree of annual variation and factors influencing the rate at which scrub-jays predate vireo nests.

In combination with nest predation by scrub-jays, the additive effect of parasitism may be critical, especially in our North County study area where the Gray Vireo population is declining more rapidly and parasitism was more common (28%), than in South County (6%). To improve the productivity of susceptible host species, cowbird control has been recommended if local parasitism rates exceed 20–30% for two or more years (Rothstein et al. 2003, Rothstein and Peer 2005). However, given the remoteness and ruggedness of Gray Vireo habitat, the low population density, and the limited number of cowbirds that may be traveling long distances from foraging grounds, we do not expect cowbird trapping (effective for the recovery of the Least Bell's Vireo, *Vireo bellii pusillus*; Kus 1999, 2002) to be cost-effective for Gray Vireos. Instead, mist-netting or shooting cowbirds lured with broadcast of recorded calls (Siegle and Ahlers 2004, Summers et al. 2006) merits testing.

Most areas where we studied Gray Vireos had burned within the last 40 years, but none had burned within the last 10 years. This suggests that an intermediate fire-return interval (10–40 years) may be ideal for the species. However, in the 21st century, the frequency and size of fires in this region have increased, and summers are predicted to be increasingly hot, dry, and more prone to fire (Hayhoe et al. 2004, Cayan et al. 2008, Lenihan et al. 2008, Loarie et al. 2008). Gray Vireos are rarely observed away from sites of known breeding or wintering, suggesting that high site fidelity (Barlow et al. 1999) may conflict with their need to shift to alternate sites as the habitat burns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Fig. S1. Historic and current distribution of Gray Vireos in California.

Fig. S2. Typical chronology of a successful Gray Vireo nest.

Video S1. Gray Vireo nest predated by a gray fox, San Diego County, 2013.

Video S2. Gray Vireo nest predated by California Scrub-Jay, San Diego County, 2013.

Video S3. Gray Vireo nest parasitized by Brown-headed Cowbird, San Diego County, 2012.

Video S4. Successful Gray Vireo nest, San Diego County, 2012.