



A MULTISCALE ANALYSIS OF NEST PREDATION ON LEAST BELL'S VIREOS (*VIREO BELLII PUSILLUS*)

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ABSTRACT.—We examined variables influencing nest predation on the endangered Least Bell's Vireo (*Vireo bellii pusillus*) at three spatial scales to determine what nest-site, habitat, or landscape characteristics affect the likelihood of nest predation and to determine the spatial distribution of predation risk and the variables influencing it. We used MARK to calculate daily survival rates of Least Bell's Vireo nests and applied an information-theoretic approach to evaluate support for logistic regression models of the effect of habitat variables on predation risk. Analysis of data for 195 nests collected during 1999 and 2000 at the San Luis Rey River and Pilgrim Creek in southern California revealed no effect of fine-scale factors, including nest height, supporting plant species, and three measures of nest concealment, on the likelihood of predation. At the intermediate scale, distances to the riparian-habitat edge and to internal gaps in the canopy were unrelated to nest survival. Surrounding land-use type was a poor predictor of predation risk, with the exception of proximity to golf course–park habitat and wetland. Nests within 400 m of golf course–park were only 20% as likely to avoid predation as nests >400 m from this habitat, and nests near wetland were more than twice as likely to survive as nests distant from wetland. Spatially, predation appeared to be random throughout the site, with localized clustering evident in the vicinity of golf course–park and wetland. Our results suggest that the landscape may be the most appropriate scale at which to manage nest predation in this system. *Received 26 February 2006, accepted 9 May 2007.*

Key words: edge, golf courses, landscape characteristics, Least Bell's Vireo, nest concealment, nest predation, *Vireo bellii pusillus*, wetlands.

Un Análisis a Varias Escalas de la Depredación de Nidos de *Vireo bellii pusillus*

RESUMEN.—Examinamos las variables que influyen la depredación de nidos del taxón en peligro de extinción *Vireo bellii pusillus* a tres escalas espaciales diferentes. Determinamos las características del sitio de anidación, del hábitat o del paisaje que afectan la probabilidad de depredación de los nidos, la distribución espacial del riesgo de depredación y las variables que lo influyen. Utilizamos el programa MARK para calcular las tasas de supervivencia diaria de los nidos de *V. b. pusillus* y aplicamos un enfoque de teoría de la información para evaluar diferentes modelos de regresión logística sobre el efecto de variables de hábitat sobre el riesgo de depredación. Los análisis de datos correspondientes a 195 nidos recolectados entre 1999 y 2000 en las inmediaciones del río San Luis Rey y Pilgrim Creek, sur de California, no revelaron un efecto sobre la probabilidad de depredación de los factores a la escala más fina, incluyendo la altura del nido, la especie de la planta que soporta al nido y tres mediciones del escondimiento de nido. A la escala intermedia, las distancias hacia el borde con las áreas ribereñas y hacia claros internos en el dosel no se relacionaron con la supervivencia de los nidos. El tipo de uso de suelo en el paisaje circundante no predijo el riesgo de depredación con excepción de la proximidad a parques, campos de golf y humedales. Los nidos que se encontraban a una distancia menor de 400 m de parques o campos de golf, tuvieron una probabilidad de evitar la depredación un 20% menor que la de los nidos que se encontraban a más de 400 m de este hábitat. Los nidos que se encontraban cerca de humedales tuvieron el doble de probabilidad de sobrevivir que los nidos más alejados de los humedales. Espacialmente, la depredación pareció ocurrir de manera azarosa en el sitio de estudio, con agrupaciones localizadas en las cercanías de los parques y campos de golf y humedales. Nuestros resultados sugieren que la escala del paisaje sería la más apropiada para manejar la depredación de nidos en este sistema.

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CONSERVATION OF ENDANGERED avian species relies on population growth to increase the chances of recovery. Nest predation is the strongest determinant of nest success in small birds (Ricklefs 1969; Best and Stauffer 1980; Martin 1992, 1993), which makes it one of the principal factors limiting population growth. Human alterations of natural landscapes, for example through habitat fragmentation and urban encroachment, can influence the process of nest predation. Understanding the factors associated with predation risk and how these factors differ under various land uses and habitat configurations (Kristan and Scott 2006, Lawler and Edwards 2006) is, thus, central to the management and recovery of endangered birds.

Habitat fragmentation and alteration can affect nest predation at a variety of scales. At the fine scale, measured within meters of a nest, placement and concealment influence a nest's visibility to predators (Martin and Roper 1988, Martin 1992) and, consequently, the likelihood that it will be depredated. At an intermediate scale (tens of meters), vegetation structure and the extent of gaps and edges can influence predator diversity and density (Soulé et al. 1988, Rogers and Caro 1998, Crooks and Soulé 1999), movement (Bider 1968, Yahner 1988), and behavior (Harrison 1997). At a broad, or landscape, scale (hundreds of meters), urbanization, agriculture, grazing, and other land uses encroach on native habitat and can affect both predator community composition and rates of nest predation (Wilcove 1985, Danielson et al. 1997, Stephens et al. 2003). Because the predators in a given area can include a wide array of birds, mammals, and snakes using a variety of search modes and hunting techniques, factors influencing overall nest predation are not easily identified or predicted.

An explicit understanding of scale (Levin and Pacala 1997) is important for understanding nest predation. As with all ecological systems, observed patterns or lack thereof depend on the scale at which the system is studied (Levin 1988, Wiens 1989). Often, processes such as nest predation, which appear to be random at one scale, are more predictable at another; therefore, examining nest predation at multiple scales can aid in detecting patterns and the factors responsible for them (Wiens et al. 1986).

We examined nest predation on the endangered Least Bell's Vireo (*Vireo bellii pusillus*; hereafter "vireo") and analyzed variables predicted to affect the likelihood of nest predation at three spatial scales. Vireos nest low in the understory of riparian vegetation, a habitat of special concern because it supports a high diversity of birds, including many sensitive species and Neotropical migrants. Because much of the vireo's current range lies within highly urbanized or otherwise human-altered landscapes in southern California, we sought to identify the effect of these habitat alterations on nest predation and the scale at which they operate. We examined variables individually and in combination to evaluate support for candidate models describing predation on vireo nests at three scales, and considered the spatial distribution of predation risk and explanatory variables for more insight into the causes of nest predation.

METHODS

We studied vireos in San Diego County, California, along a 16-km stretch of the San Luis Rey River and a 2-km stretch of one of its tributaries, Pilgrim Creek. We selected this area because it supports

a relatively large vireo population (~150 pairs during our study), is spatially heterogeneous, and encompasses all the adjacent land-use types typically associated with vireo habitat in coastal southern California. Habitat at the site consists of a linear corridor of riparian vegetation, ranging in width from 50 to 500 m, dominated by willows (*Salix* spp.). Early- to mid-successional vegetation is interspersed with open areas of deposited debris and sand washes caused by flooding, creating a natural pattern of patchiness. Anthropogenic disturbances such as roads, trails, and stands of exotic grasslands increase fragmentation within the riparian system. A mosaic of urban, rural, and agricultural lands, as well as native and disturbed upland habitat, surrounds the riparian corridor.

The vireo is a federally endangered migratory songbird that breeds exclusively in willow riparian woodlands in southern California and northern Baja California, Mexico. Nests are placed in the dense understory, suspended from forked branches within 1 m of the ground. Predation is the major cause of nest failure; on average (\pm SD), $37 \pm 7\%$ of nests are depredated annually (Kus 2002). Vireos may attempt as many as six nests in a season (Kus 2002), particularly if earlier nests are lost to predation. Confirmed nest predators include Western Scrub-Jays (*Aphelocoma californica*), Virginia Opossums (*Didelphis virginiana*), Gopher Snakes (*Pituophis melanoleucus*), Argentine Ants (*Linepithema humile*; Peterson et al. 2004), and Alligator Lizards (*Elgaria multicarinata*; D. Evans unpubl. data); other predators likely include corvids as well as and other snakes and small mammals.

Vireo territories were located and monitored throughout the breeding season (April–July) in 1999 and 2000 as part of a larger long-term demographic study (Kus 1999, 2002; Kus and Whitfield 2005; Sharp and Kus 2006). Each vireo territory was visited every five to seven days to locate nests and assess their status (Kus 1999). Nests were classified as successful if, at the expected time of fledging, the nest was intact and evidence indicated that at least one nestling had fledged. Such evidence included feather dust in the nest, fecal droppings below the nest, and detection of fledglings within the territory. Unsuccessful nests included nests that were depredated, were abandoned with eggs, or failed as a result of some other cause, such as inviable eggs or death of nestlings. Depredation was inferred from strong indicators such as the disappearance of all eggs or nestlings from active, monitored nests before their expected date of fledging or nests torn from their supporting branches (Peterson et al. 2004). Only successful and depredated nests were included in the analysis.

Fine-scale factors.—Data characterizing the environment immediately surrounding nests were collected at the end of the breeding season, before any major changes in vegetation structure, to prevent disturbance of nesting vireos. Nest height, the species of plant supporting the nest, and two measures of nest concealment were recorded. "Nest height" was defined as the distance from the ground to the top of the nest cup. For nests that were torn down, nest height was recorded only when we could determine where the nest had been located by observing remnants of the nest on the supporting branch. We recorded the species of plant supporting each nest and grouped them for analysis as Arroyo Willow (*S. lasiolepis*), Mule Fat (*Baccharis salicifolia*), Sandbar Willow (*S. exigua*), and "other" to create adequate sample sizes. Nest concealment was quantified by recording whether vegetation cover

was present (= "hit") or absent at ¼-m intervals along 1-m transects arrayed laterally from the nest in the four cardinal directions as well as vertically above and below the nest. Hits per transect were averaged over the six transects to produce a nest-concealment index ranging from 0 (no concealment) to 4 (highly concealed).

To determine the importance of gaps within the riparian habitat to predation risk, a second measure of nest concealment quantifying percent cover within a 15-m radius of each nest was recorded. We chose 15 m to correspond to the ability of nest predators to navigate through the vegetation and observe adult vireos and their nests. To associate gaps with both ground and aerial predators, we visually assessed two components of vegetation: vegetation below 2 m (percent understory) and vegetation between 2 m and the top of the canopy (percent canopy). We used a five-point scale to describe cover: category 1, <20%; 2, 21–40%; 3, 41–60%; 4, 61–80%; and 5, 81–100%. Cover classes were established on the basis of our experience with quantifying structural variability in vireo habitat and among nest sites (Kus 1998, Kus and Beck 2003). Percent understory was rarely <40% (categories 1–2); therefore, data from these categories were combined with data from category 3, forming three categories for analysis of this variable.

Intermediate-scale factors.—We considered distance to habitat edge an intermediate-scale variable likely to affect nest predation, given demonstration of "edge effects" in the literature (Wilcove 1985, Paton 1994, Donovan et al. 1997, Heske et al. 1999, Lahti 2001). Two types of edge were examined: (1) "habitat edge," or the outermost edge of the riparian habitat at the wetland–upland transition, or the boundary between riparian habitat and an anthropogenic feature within the flood plain such as a paved road, housing development, or golf course, and (2) "acting edge," created

by internal gaps within the riparian zone. Only gaps at least three times as wide as the height of adjacent trees were considered to form acting edge (Paton 1994). The distances from each vireo nest to the closest habitat edge and acting edge were measured, either in the field or from aerial photographs of the study area in ARCVIEW (ESRI, Redlands, California; see below).

Broad-scale factors.—We examined the nature and extent of land uses adjacent to the riparian corridor to identify broad-scale features affecting nest predation. Vireo nests were mapped onto aerial photographs of the study area using ARCVIEW. Thirteen land uses (Table 1) surrounding the study area were identified and recorded in ARCINFO (ESRI) as polygons. A circle with a 400-m radius was centered on each nest, and the number of pixels in each land-use category was calculated and converted to percent cover of each land-use type. We chose a 400-m radius as large enough to ensure that measurements for interior nests in wider riparian areas incorporated some type of adjacent land use while minimizing overlap among circles centered on nests in adjacent territories.

Statistical analyses.—We used MARK (White and Burnham 1999) to model the effects of fine-, intermediate-, and broad-scale habitat variables on daily survival rate (DSR) of vireo nests (Dinsmore et al. 2002). Nest survival was calculated across a 30-day cycle length (4 days laying, 14 days incubation, 12 days nestling period) in which incubation begins with the penultimate egg. Age of nests at the time they were discovered was calculated by forward- or backward-dating of nests in relation to known dates of nest building, laying, or hatching.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for models reflecting *a priori* hypotheses and questions regarding the effect of habitat

TABLE 1. Description of surrounding land-use cover types and percentage of total land-use cover (means, with ranges in parentheses) within 400 m of Least Bell's Vireo nests ($n = 195$) at the San Luis Rey River and Pilgrim Creek, California, 1999–2000.

Land use	Description	Percentage of total land-use cover	Percentage of nests adjacent to land use	Data type
Willow riparian	All areas within the riparian system, including the river, washes, and disturbed and restored riparian areas.	49.5 (11.6–85.6)	100	Continuous
Disturbed upland	Areas containing a combination of shrubs and disturbed grasslands.	13.5 (0.0–46.0)	96	Continuous
Urban	Areas with more than one house per 0.4 ha, commercial areas, schools.	8.5 (0.0–56.9)	64	Discrete
Grassland	Areas of non-native grasslands and grazed land.	5.3 (0.0–36.1)	60	Discrete
Coastal sage scrub	Areas of intact or relatively intact native habitat. Highly disturbed areas were included in "disturbed upland."	5.2 (0.0–31.4)	52	Discrete
Wetland	Both freshwater marshes and brackish areas containing salt marsh species. Standing water may or may not be present.	4.1 (0.0–54.0)	16	Discrete
Golf course–park	Golf courses and manicured parks.	2.6 (0.0–35.9)	24	Discrete
Agriculture	Usually, but not exclusively, tomato fields.	2.9 (0.0–69.3)	19	Discrete
Roads	Highways, major (more than two lanes) and paved rural roads. Roads in urban areas were recorded as "urban" unless they were major roads.	2.2 (0.0–7.6)	91	Continuous
Dirt roads–trails	Single-lane dirt roads with low traffic use, and manicured or worn dirt trails.	2.1 (0.0–7.3)	95	Continuous
Cleared	Areas completely cleared of vegetation for development.	2.0 (0.0–20.0)	32	Discrete
Rural	Areas with fewer than one house per 0.4 ha. Includes all areas with buildings and apparent borders of yards.	1.3 (0.0–32.5)	29	Discrete
Orchards	Areas planted in groves, whether actively farmed or not, including citrus, avocado, and walnut groves.	0.7 (0.0–14.5)	15	Discrete

variables on DSR. At the fine and intermediate scales, we predicted that DSR would increase with increases in nest concealment, percent understory, percent canopy, and distance from habitat and acting edges. We expected nest height to influence DSR according to one of two alternative hypotheses: (1) DSR would increase with increasing nest height because of reduced accessibility of nests to ground predators, or (2) DSR would decrease with increasing nest height as a result of greater exposure to avian predators. We questioned whether certain plant species consistently provide conditions that allow nests to escape predation and used our analysis to search for associations between the species of plant supporting vireo nests and DSR. At the broad scale, we reasoned that disturbed and developed habitats (disturbed upland, urban, golf course–park, agriculture, cleared, orchards, and rural) would differ from “natural” habitats (willow riparian, coastal sage scrub, and wetland) in their effect on DSR. We considered two alternative hypotheses: (1) if prey densities and, consequently, predator densities are reduced in disturbed habitats, predation on vireo nests may be lower in or near these areas than in natural habitats supporting higher predator densities; or (2) if predators are attracted to disturbed habitats, particularly urbanized areas where subsidized natural and domestic predator species can achieve high densities (Crooks and Soulé 1999), predation may be higher there—and DSR, thus, lower—than in natural habitats. We predicted that increased cover of dirt roads and trails near vireo nests would reduce DSR by providing ground predators access to nesting habitat.

We used logistic regression with a logit link to build a series of models of increasing spatial scale. First, we generated a constant survival model to serve as a reference for the effect of habitat variables on DSR. We then modeled the effects of fine- and moderate-scale covariates individually and evaluated support for each model in relation to the constant survival model and each other. In addition, we modeled the effect of year on DSR to search for any temporal differences across our study. We then combined variables in the models with the strongest support to determine whether the resultant multivariate models improved the best univariate model. In an analogous manner, we considered uni- and multivariate models describing the effect of the 13 broad-scale habitat types on DSR, including interaction terms in our candidate multivariate models. Finally, we considered support for models combining the best fine- and moderate-scale models with the best broad-scale model.

Nine of the 13 land-use types exhibited extreme right-skewed distributions with a majority of zeroes and a long tail; these land uses occurred at <65% of the nests. To better analyze these variables, we treated them as discrete (Table 1) and scored each land-use type as present ($\geq 5\%$ cover) or essentially absent (<5% cover) in relation to each nest. The 5% cutoff is arbitrary but was chosen to avoid counting as “present” very small amounts of cover that were predicted to have little or no effect on nest outcome.

The use of a 400-m-radius area within which to characterize adjacent land use often resulted in overlap of circular land-use-measurement areas among nests, creating the potential for spatial non-independence among the explanatory variables. We assessed both independence and spatial distribution of DSR and explanatory variables for each year using Wald-Wolfowitz runs (Wald and Wolfowitz 1940, Zar 1999), a test of serial autocorrelation for binary data. We used this test because the one-dimensional

spatial distribution of nests along the length of the river made testing for serial autocorrelation identical to testing for spatial autocorrelation.

RESULTS

We monitored 231 vireo nests in the present study: 108 in 1999 and 123 in 2000. Apparent nest predation was similar in both years (53% in 1999 and 48% in 2000; $\chi^2 = 0.53$, $df = 1$, $P = 0.47$). Of the 231 nests, 195 had sufficient data for nest-survival analyses. These latter nests were monitored for a total of 3,127 exposure days over a 105-day interval in both years (14 April–29 July). Nest age in days on the day nests were found averaged 4.0 ± 4.7 (SD; day 1 = first day of laying).

Fine- and moderate-scale factors.—Nest height ranged from 0.3 to 1.7 m, with an average height of 0.9 ± 0.3 m. Vireos used 18 different plant species for placement of their nests. The three species most frequently used were Arroyo Willow (36%, $n = 71$), Mule Fat (22%, $n = 42$), and Sandbar Willow (18%, $n = 35$). Plants supporting the remaining nests (24%, $n = 47$) included Goodding’s Willow (*S. gooddingii*), White Alder (*Alnus rhombifolia*), Fremont Cottonwood (*Populus fremontii*), Elderberry (*Sambucus mexicana*), tamarisk (*Tamarix* sp.), Wild Rose (*Rosa californica*), and various other native and non-native shrubs and herbs. The index of nest concealment within 1 m of the nest averaged 2.6 ± 0.7 , and cover-class values for percent understory and percent canopy within 15 m of nests averaged 3.7 ± 0.7 and 2.7 ± 1.0 , respectively. Nests ranged in distance to the nearest habitat edge from 1 to 230 m, with 47% ($n = 92$) of all nests within 50 m of the edge. Distance from each nest to the closest acting edge within the riparian habitat ranged from 1 to 160 m, with 65% ($n = 127$) of nests within 50 m of this edge.

None of the univariate models for the effects of fine- and intermediate-scale variables on DSR improved the predictive power of the constant survival model (Akaike’s Information Criterion [AIC]; $\Delta AIC_c = 0.00$, $w = 0.18$). Of the seven habitat covariate models, that including nest concealment received the greatest support ($\Delta AIC_c = 0.25$, $w = 0.16$). Models combining nest concealment and percent understory ($\Delta AIC_c = 1.32$, $w = 0.09$), nest concealment and distance to acting edge ($\Delta AIC_c = 1.94$, $w = 0.07$), percent understory and percent canopy ($\Delta AIC_c = 5.85$, $w = 0.01$), and nest concealment, percent understory, and percent canopy ($\Delta AIC_c = 5.40$, $w = 0.01$) did not yield an improvement over the univariate nest-concealment model. Year, like the habitat covariates, received less support as a predictor of nest success than the model for constant survival ($\Delta AIC_c = 1.99$, $w = 0.07$).

Broad-scale factors.—The 13 surrounding land uses were distributed throughout the study area (Table 1), with disturbed uplands and urban land making up most of the nonriparian habitat surrounding vireo nests. The number of land-use types, including riparian, around each nest averaged 5.5 ± 1.1 and ranged from 3 to 9. When analyzed separately from the fine- and intermediate-scale covariates, only 7 of the 13 land-use variables appeared in models receiving more support than the constant-survival model: golf course–park, coastal sage scrub, urban, wetland, dirt roads–trails, willow riparian, and cleared (in ascending order of ΔAIC_c). Systematic combination of these variables yielded models in which golf course–park, urban, wetland, and coastal sage scrub appeared in the models receiving substantial support (Table 2).

TABLE 2. Logistic regression models for the effects of fine-, intermediate-, and broad-scale factors on nest survival of Least Bell's Vireos at the San Luis Rey River and Pilgrim Creek, California, 1999–2000. Models are ranked from best to worst on the basis of Akaike's Information Criterion (AIC) for small samples (AIC_c), ΔAIC_c , and Akaike weights (w). AIC_c is based on $-2 \times \log_e$ likelihood (L) and the number of parameters (K) in the model. GCP = golf course–park, and CSS = coastal sage scrub. Eight univariate models (seven habitat covariates and year) with less support than the constant model are not shown.

Model	$-2(L)$	K	AIC_c	ΔAIC_c	w
GCP + urban + wetland + GCP \times urban + nest concealment	508.02	6	520.05	0.00	0.411
GCP + urban + wetland + GCP \times urban	510.37	5	520.39	0.34	0.347
GCP + CSS + urban + wetland + GCP \times urban	509.41	6	521.57	1.52	0.192
GCP + CSS + urban + wetland	516.29	5	526.31	6.26	0.018
GCP + CSS + urban	518.41	4	526.42	6.37	0.017
GCP + CSS + urban + wetland + dirt roads–trails	516.29	6	528.32	8.27	0.007
GCP + urban + wetland	521.28	4	529.30	9.25	0.004
GCP + urban	524.96	3	530.97	10.92	0.002
GCP	528.68	2	532.68	12.63	0.001
CSS + urban	527.97	3	533.98	13.93	<0.001
CSS	530.79	2	534.79	14.74	<0.001
Urban	535.32	2	539.33	19.28	<0.001
Wetland	535.44	2	539.45	19.40	<0.001
Dirt roads–trails	535.49	2	539.50	19.45	<0.001
Willow riparian	535.57	2	539.57	19.52	<0.001
Cleared	535.58	2	539.58	19.53	<0.001
Constant	537.61	1	539.61	19.56	<0.001

Inclusion of an interaction between golf course–park and urban, derived from a *post hoc* examination of the relationship between these variables, yielded an improved model in which coastal sage scrub no longer appeared. Addition of nest concealment as a fine-scale variable produced a model for which support increased slightly, which we therefore analyzed further as the best model describing the effects of habitat variables on vireo DSR. The univariate model for an effect of year on DSR received virtually no support in relation to this model ($\Delta AIC_c = 21.55$, $w < 0.001$), so we did not consider it further.

Confidence intervals for the odds ratios of two of the variables in the best model, urban and nest concealment, included 1, which indicates that these variables did not significantly affect the likelihood of nest survival (Table 3). Nests within 400 m of golf course–park habitat were only 20% as likely to survive as nests distant from these habitats, and nests near wetland were 2.39 \times more likely to survive than nests distant from wetland. Although urban land use, by itself, did not affect nest survival, it interacted with

TABLE 3. Parameter estimates (β), standard error (SE), odds ratios, and 95% confidence intervals (CI) for the best-supported fine-, intermediate-, and broad-scale model explaining daily survival rate of Least Bell's Vireo nests at the San Luis Rey River and Pilgrim Creek, California, 1999–2000.

Effect	β	SE	Odds ratio	95% CI
Golf course–park	-1.62	0.30	0.20	0.11–0.36
Urban	-0.06	0.26	0.94	0.57–1.57
Wetland	0.87	0.41	2.39	1.07–5.33
Nest concealment	-0.23	0.15	0.79	0.59–1.07

golf course–park habitat such that in urban settings, the proximity to golf course–park tended to have a positive effect on nest survival, whereas in nonurban settings the effect was negative.

Spatial distributions.—Spatially, golf course–park, urban, and wetland habitats were clustered in both years (Table 4), which reflects their occurrence as large expanses of contiguous habitat.

TABLE 4. Results of Wald Wolfowitz runs analyses used to determine the spatial distribution of daily survival rate (DSR) and predictor variables of DSR of Least Bell's Vireos along the San Luis Rey River and Pilgrim Creek, California, 1999–2000.

	DSR	Golf course–park	Urban	Wetland	Nest concealment
1999					
Average run length	2.2	13.3	8.0	20.0	3.0
Number of runs	36	6	10	4	27
Z-test (P value)	-1.08 (0.28)	-6.88 (<0.001)	-6.71 (<0.001)	-7.78 (<0.001)	-0.62 (0.57)
Pattern	None	Clustered	Clustered	Clustered	None
2000					
Average run length	2.6	14.6	6.5	19.5	2.3
Number of runs	45	8	18	6	50
Z-test (P value)	-2.37 (0.02)	-8.32 (<0.001)	-7.36 (<0.001)	-8.05 (<0.001)	-1.57 (0.12)
Pattern	Clustered	Clustered	Clustered	Clustered	None

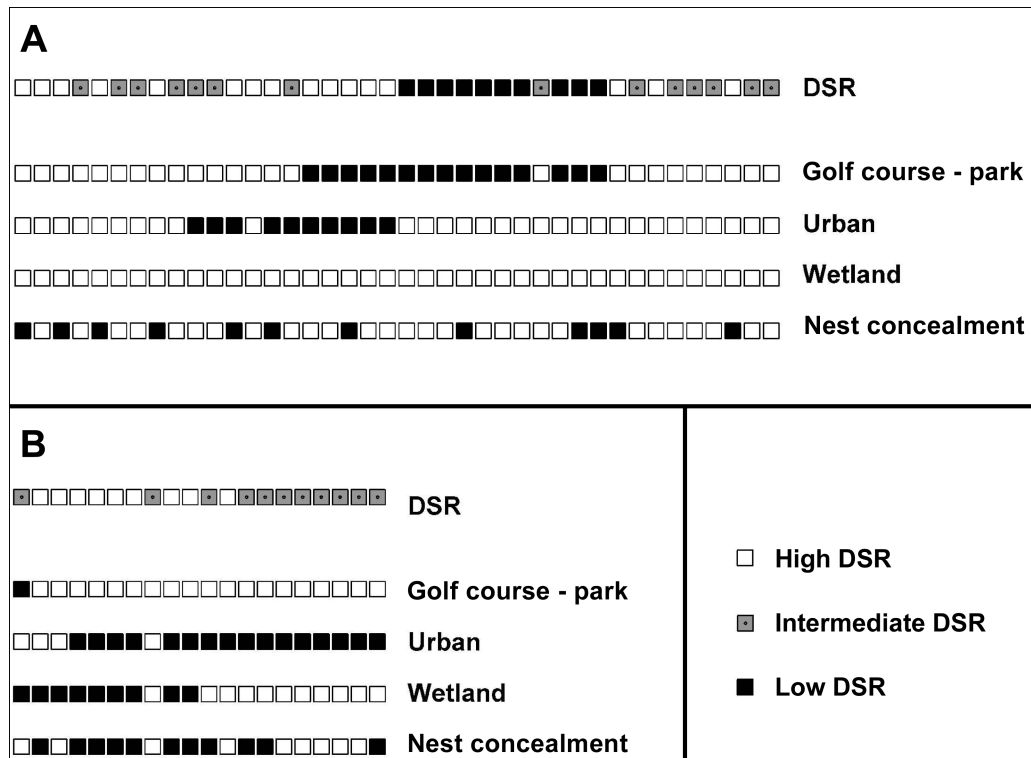


FIG. 1. Spatial patterns of predictor variables and daily nest survival (DSR) for a subset of Least Bell's Vireo nests in 2000, along two reaches of the study area near a golf course (top) and wetland (bottom). Squares represent nests placed in latitudinal order. Black squares represent "present" for golf course-park, urban, and wetland; white squares represent "absent." Daily nest survival is divided into tertiles, with white, gray, and black squares representing high, intermediate, and low DSR, respectively. Nest concealment is divided in relation to the midpoint of the range of values, with white representing high concealment and black representing low.

No pattern in spatial distribution of nest concealment was evident in either year. Overall, DSR appeared to be spatially random in 1999 and weakly clustered in 2000, as evidenced by the shortness of the average run length in 2000 compared with those of the clustered broad-scale habitat types. The weak spatial clustering of DSR is a reflection of the association between DSR and the habitat types influencing it, particularly golf course-park and wetland (Fig. 1). A long run of low DSR is apparent for nests along the length of a golf course in the eastern part of the study area (Fig. 1, top); this run abruptly switches to one of high DSR along a region of the golf course in urban habitat, which illustrates the interaction between these land-use variables. Another long run of high DSR is apparent in the vicinity of a wetland in the western part of the study area (Fig. 1, bottom). Similar patterns in DSR in relation to proximity to golf course-park and wetland habitats were observed in 1999, though overall DSR in 1999 was spatially random. Outside of regions near golf course-park and wetland, DSR showed no spatial pattern.

DISCUSSION

We found nest predation in Least Bell's Vireos to be unrelated to habitat features at fine and intermediate spatial scales. Nests varied with regard to height, supporting plant species, percent

understory, percent canopy, and distance to edge, but these variables were poor predictors of nest survival. Nest concealment appeared to contribute to the best model describing habitat effects on DSR but was determined, by inspection of odds-ratio confidence intervals, not to significantly influence nest survival. Only at the landscape scale did we detect habitat effects on predation risk, with proximity to golf course-park increasing risk and proximity to wetland reducing it. Our findings indicate that predation at our study site was spatially random at the fine and intermediate scales, as has been reported for other species, including Northern Cardinal (*Cardinalis cardinalis*; Filliater et al. 1994) and Acadian Flycatcher (*Empidonax vireescens*; Wilson and Cooper 1998), but nonrandom at the landscape scale, which suggests the latter as the appropriate scale at which to manage nest predation.

Nest concealment has been shown in some studies to be a predictor of predation (Martin and Roper 1988, Martin 1992, Hoover and Brittingham 1998), whereas in others it has been found to be unrelated to predation risk (Howlett and Stutchbury 1996, Burhans and Thompson 1998, Ricketts and Ritchison 2000, Peak 2003). None of our measurements of nest concealment, taken within 1 m and within 15 m of nests, affected the likelihood of predation. By contrast, Sharp and Kus (2006), in a parallel study at the same site and during the same years as our study, found that increasing cover within 5 m of vireo nests significantly decreased

brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). It is possible that some predators are deterred by high nest-concealment, whereas others are not, resulting in no net effect on predation risk.

Nest predation on vireos did not decrease with increasing distance to the habitat edge or gaps within the habitat (acting edge). The hypothesis that nest predation decreases with distance from edge has been debated since Gates and Gysel's (1978) study, and the empirical evidence relative to edge effects on predation is mixed (Paton 1994, Tewksbury et al. 1998, Lahti 2001). Nearly all the studies in North America that demonstrate edge effects have been conducted in eastern forests, which differ in structure from western riparian forests such as the one we studied. Unlike the comparatively large, intact stands of eastern forests, western riparian habitat is narrow, linear, and naturally patchy. Our failure to detect an edge effect on vireo nest depredation suggests either that no such effect exists or that virtually all habitat at our site is, functionally, edge habitat.

Despite great differences in land use adjacent to vireo nesting habitat, nest survival was not found to be related to surrounding habitat type, with the exception of golf course-park and wetland. These findings suggest either the absence of a biological effect of other land uses or an inability to detect an effect within the constraints of our study. For example, it is possible that the heterogeneous mix of land-use types at our site interacted with nest predation in a way that prevented us from detecting associations that might be evident in areas with larger and more homogeneous expanses of land types. This is particularly possible for land types such as orchards and rural areas, which at our site contributed little to overall cover but may have detectable and potentially strong effects on nest survival in other settings where they are more widespread. This possibility warrants further investigation; in the meantime, our results indicate that the current configuration of land uses adjacent to our study population is not associated with differential survival of vireo nests.

We found substantial support for a model of nest predation in which proximity to golf course-park increased the odds of predation and proximity to wetland decreased them. Moreover, we found no corresponding patterns in any of the fine- and intermediate-scale explanatory variables that could account for these broad-scale effects. In particular, we cannot explain the high predation near golf courses in nonurban settings and cannot rule out that a single predator could be responsible for the effect. We detected the association between golf courses and low DSR at both of two golf courses in our study area in both years of the study, which suggests that something other than the activities of a single predator was responsible. However, in both years, the relationship was driven primarily by the effect of one large golf course adjacent to a dense concentration of vireo territories (Fig. 1); therefore, we advise caution in interpreting these results until the study can be replicated in another setting. Meanwhile, we propose that differences in predator regimes across broad-scale habitat types and the boundaries between them may be responsible for the observed patterns in predation risk. Our results suggest that a comparative examination of predator communities associated with our broad-scale land-use characterizations would be a productive next step toward identifying and understanding habitat effects on depredation of vireo nests.

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