

# Factors Influencing the Incidence of Cowbird Parasitism of Least Bell's Vireos

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## Abstract

Least Bell's vireo (*Vireo bellii pusillus*) is a federally endangered subspecies of Bell's vireo subject to high levels of brood parasitism by brown-headed cowbirds (*Molothrus ater*). Brood parasitism greatly reduces the reproductive success of the vireo. We examined the relationship of vegetation structure surrounding nests and of activity near the nest to the incidence of brood parasitism by brown-headed cowbirds of least Bell's vireos. We examined vegetation structure at 3 spatial scales: microhabitat (0–1 m from a nest), mesohabitat (1–11.3 m from a nest), and macrohabitat (greater than 11.3 m from a nest). Nests with high microhabitat cover and mesohabitat cover within 5 m of the nest had a lower incidence of parasitism than those with low cover at these scales. Unparasitized nests had fewer trees greater than 8-cm diameter at breast height (dbh) within 11.3 m, and they had less canopy cover within 5 m than parasitized nests. Cowbirds parasitized nests farther from the edge of the riparian habitat more often than nests near the edge. Activity near the nest did not differ significantly between parasitized and unparasitized nests. We suggest that microhabitat cover is the most important habitat feature influencing the incidence of brood parasitism of least Bell's vireos, and we conclude that cover near the nest reduces the chance that a cowbird will observe nesting activity. We suggest that habitat management for improved breeding success of least Bell's vireos focus on increasing the density of understory vegetation. (JOURNAL OF WILDLIFE MANAGEMENT 70(3):682–690; 2006)

## Key words

behavior, brood parasitism, brown-headed cowbird, host-activity, least Bell's vireo, *Molothrus ater*, nest-concealment, perch-proximity, riparian woodland, San Diego County, vegetation, *Vireo bellii pusillus*.

Least Bell's vireo is a federally endangered subspecies of Bell's vireo (*V. bellii*) that breeds in southern California, USA, and northern Baja California, Mexico. Knowledge of this subspecies' breeding ecology in Mexico is sparse, but the primary reasons for its decline in California are loss of habitat and brood parasitism by brown-headed cowbirds (Franzreb 1989; Kus 1999, 2002). Rates of parasitism of least Bell's vireo were high ( $37 \pm 10\%$  over 11 years, Kus 2002), and parasitism accounted for between 58 and 71% of the variability in seasonal productivity of young in 3 populations of least Bell's vireos in San Diego County, California (Kus and Whitfield 2005). Although brood parasitism has adversely affected least Bell's vireo, we do not know what factors most influence the incidence of parasitism within this subspecies. Such information is invaluable to the development of an effective recovery plan for least Bell's vireo.

Hypotheses regarding factors that might influence rates of brood parasitism in hosts are numerous and varied. Some such factors include host nest densities (Lowther and Johnston 1977, Zimmerman 1983, Barber and Martin 1997), host quality (Sealy and Bazin 1995, Soler et al. 1995, Kozlovick et al. 1996, Burhans and Thompson 2000, Grant and Sealy 2002), timing of nesting (Finch 1983, Kus 1999), landscape features (Hahn and Hatfield 1995, Tewksbury et al. 1998, Gustafson et al. 2002), and host aggression directed at cowbirds, as in the nest-cue hypothesis (Robertson and Norman 1976, 1977; Smith 1981; Clotfelter 1998; Grief and Sealy 2000). To examine every potential factor influencing rates of parasitism in a single study would be a daunting task. We addressed 3 hypotheses: nest-concealment, perch-proximity, and

host-activity. The nest-concealment hypothesis predicts that nests with greater vegetative cover surrounding them have a lower probability of parasitism than those with sparse cover (Burhans 1997, Larison et al. 1998, Clotfelter 1998, Grief and Sealy 2000, Budnik et al. 2002, Saunders et al. 2003). The perch-proximity hypothesis suggests that nests near perches from which cowbirds may survey for nests have a higher probability of parasitism than those far from perches (Anderson and Storer 1976, Clotfelter 1998, Hauber and Russo 2000, Saunders et al. 2003). The host-activity hypothesis purports that the activity level of host parents during early stages of the nesting cycle influences their detection by nearby cowbirds, thus influencing the chance that their nest is parasitized (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001, Robinson and Robinson 2001).

Knowledge and assumptions regarding the manner in which cowbirds search for host nests form the basis for the above hypotheses. Several studies in forested landscapes indicate that brown-headed cowbirds prefer edge habitat to interior habitat (Brittingham and Temple 1983, Johnson and Temple 1990, Gates and Giffen 1991, Paton 1994, Burhans 1997, Gustafson et al. 2002); however, other studies found no support for this edge effect (e.g., Paton 1994, Hahn and Hatfield 1995, Tewksbury et al. 1998). Edge habitat includes the transition zone from one type of habitat to another, as well as openings created by river channels. Cowbirds move between foraging and breeding habitats on a daily basis (Rothstein et al. 1984, Thompson 1994); thus, they may occur at a greater density near the edge of a breeding habitat. We assumed that cowbirds enter a breeding habitat at its edge and disperse from there. We also assumed that it is easier for cowbirds to find nests near an edge than to penetrate interior habitat in search of nests (sensu Brittingham and Temple 1983).

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Few studies quantitatively address the manner by which brown-headed cowbirds search for nests of host species once they enter breeding habitat of their hosts. However, several authors report that cowbirds begin their search by perching in trees and watching activity of potential hosts (Mayfield 1961; Norman and Robertson 1975; Thompson and Gottfried 1976, 1981). Norman and Robertson (1975) describe female cowbirds walking on the ground in search of nests and systematically moving through vegetation to flush potential hosts from their nests. Given these findings, we assume that cowbirds move from the habitat edge to a nest in a somewhat stepwise fashion. That is, cowbirds enter breeding habitat from a habitat edge, search for nests from suitable perches within the habitat, and move through vegetation to nests once they identify the approximate location of a nest.

Numerous studies have investigated the relationship between rates of brood parasitism and vegetation structure surrounding host nests (e.g., Beuch 1982, Brittingham and Temple 1996, Burhans 1997, Larison et al. 1998). Although these studies considered similar vegetation characteristics, they report different results with regard to which vegetative features influence rates of parasitism. For example, Burhans (1997) found that the incidence of parasitism was lower at nests of indigo buntings (*Passerina cyanea*) that had relatively dense vegetative cover within 1 m of them, whereas Brittingham and Temple (1996) found that ground cover was sparser and canopy cover denser at unparasitized nests of eastern forest species than at parasitized nests. Incongruent results in these similar studies suggest that factors influencing the incidence of parasitism are, to a considerable extent, habitat- and species-specific. This calls for examination of factors influencing parasitism in each host species rather than extrapolating results from studies of different host species.

Studies examining host behavior in relation to brood parasitism suggest that increased activity near the nest during early stages of the nesting cycle results in higher levels of parasitism (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001). Uyehara and Narins (1995) found that vocalization rates of pairs of southwestern willow flycatchers (*Empidonax trallii extimus*) were higher in parasitized versus unparasitized pairs. Likewise, vocalization rates of parasitized female red-winged blackbirds (*Agelaius phoeniceus*) were greater than those of unparasitized females (Clotfelter 1998).

Few studies have examined both host behavior and vegetation surrounding nest-sites (Clotfelter 1998, McLaren and Sealy 2003). Clotfelter (1998) suggested that more studies examine both behavior and habitat structure in relation to brood parasitism, as multiple facets of these factors could be operating simultaneously. We add to his suggestion that analyses include multiple spatial scales of habitat structure. We base our rationale for this suggestion on the manner in which cowbirds search for host nests, as described above. Our study examines the nest-concealment and perch-proximity hypotheses at 3 spatial scales and the host-activity hypothesis in relation to the incidence of brood parasitism of least Bell's vireos. We offer suggestions of how to apply our findings to management of this federally endangered subspecies.

## Study Area

Our study site was a 16-km stretch of the San Luis Rey River in northern San Diego County, California, USA. Nest monitoring and cowbird trapping programs began at this site in 1985 and 1988, respectively, as part of the recovery plan for least Bell's vireo (Kus 1999, 2002; Kus and Whitfield 2005). However, from 1999 through 2003, there was no cowbird trapping at the site, providing a unique opportunity to study rates of cowbird parasitism of least Bell's vireo without cowbird management. Overall parasitism rates at the study site were 46% of nests in 1999, 31% in 2000, and 56% in 2003.

The riparian corridor at the site ranged in width from 50 to 500 m and contiguous land included golf courses, housing developments, roads, and agricultural and commercial areas. Common trees and shrubs in the area included arroyo willow (*Salix lasiolepis*), red willow (*S. laevigata*), black willow (*S. gooddingii*), sandbar willow (*S. exigua*), Fremont cottonwood (*Populus fremontii*), western sycamore (*Platanus racemosa*), and mule fat (*Baccharis glutinosa*). Least Bell's vireos typically place their nests in one of these host plants (rarely in *P. racemosa*) within 1 m of the ground. The population of least Bell's vireos within the study site ranged from 100 to 125 breeding pairs during the 3 seasons of our study.

## Methods

### Nest Monitoring

We monitored nests of least Bell's vireos in 1999, 2000, and 2003 as part of an ongoing study of vireo breeding ecology (Kus 1999, 2002; Peterson et al. 2004; Sharp and Kus 2004). Field crews located and checked nests every 5 to 8 days to determine the status of nests. A parasitized nest was one in which a brown-headed cowbird laid an egg. An unparasitized nest was one that reached the midpoint of incubation (day 7 of incubation) without being parasitized. We used this point in the nesting cycle as our cut-off because cowbirds rarely parasitize nests later than this stage in the cycle (Friedmann 1963, Lowther 1993, Sharp and Kus 2004). We did not classify nests as unparasitized if they were depredated (but not parasitized) before day 7 of incubation because they may have been parasitized later. We conducted this study under animal protocol SDSU APF#02-04-011K, "Distribution and demography of least Bell's vireos and southwestern willow flycatchers."

### Measures of Vegetation Surrounding Nests

We used 27 measurements to characterize the vegetation surrounding nests of least Bell's vireos in 1999 (the pilot year) and 2000 (Table 1). We modified most of our vegetation measurements from the BBIRD (Breeding Biology Research and Monitoring Database) Protocol of Martin et al. (1997). We sampled vegetation after nests had failed or fledged young.

**Macrohabitat.**—For our study, the macrohabitat scale extended from the nest to the edge of the riparian woodland. We measured the distance between each nest and the edge of the riparian woodland and between the nest and the nearest water channel. We defined the riparian edge as the point within the floodplain at which vegetation typical of riparian habitat was no longer present. We defined a water channel as the point at which riparian vegetation was replaced by semi-aquatic vegetation, such as

**Table 1.** Vegetation variables, separated by the scales at which they were measured (height and edge measurements in meters); results of single variable logistic regression models with unparasitized as the response condition and parasitized as the reference; and loadings of variables on component 1 of principle components analysis. We collected data at nests of least Bell's vireos located along the San Luis Rey River in San Diego County, Calif., USA, in 1999 and 2000.

Variable	Parasitized mean SE	Unparasitized mean SE	IQR <sup>a</sup>	OR <sup>b</sup>	95% CI for OR	P	Component 1 loading
Macrohabitat							
Distance to riparian edge	83.6 10.7	56.5 5.9	65	0.6	0.3–0.9	0.03 <sup>c</sup>	-0.13
Distance to river channel	88.6 19.7	126.3 26.7	134	0.9	0.5–1.6	0.65	-0.46*
Mesohabitat							
Trees 2.5–8 cm dbh, <11.3 m of nest	27.1 3.7	26.8 3.0	34	0.9	0.5–1.7	0.75	-0.10
Trees >8 cm dbh, <11.3 m of nest	8.4 1.1	6.2 1.0	10	0.5	0.2–0.9	0.03 <sup>c</sup>	-0.58*
Total trees within 11.3 m of nest	35.5 4.1	33.0 3.3	33	0.8	0.5–1.4	0.45	-0.26
Hits 1–11.3 m lateral to nest	40.6 3.4	40.7 2.3	25	1.0	1.0–1.0	0.86	0.37
Hits 1–3 m, upper diagonal from nest	3.1 0.4	2.8 0.3	4	0.7	0.4–1.3	0.27	0.04
% concealment 11.3 m lateral to nest	95.8 2.4	94.6 1.7	2	0.9	0.7–1.2	0.58	0.23
% ground cover within 5 m of nest	75.6 2.5	79.4 1.5	15	1.3	0.9–2.1	0.17	0.02
% ground cover within 11.3 m of nest	66.7 2.6	69.5 1.8	20	1.3	0.7–2.3	0.36	0.10
% canopy cover within 5 m of nest	72.8 3.9	63.0 3.0	38	0.5	0.3–1.0	0.04 <sup>c</sup>	-0.47*
% canopy cover within 11.3 m of nest	59.0 3.2	52.9 2.6	31	0.7	0.4–1.2	0.15	-0.50*
Max. canopy ht within 11.3 m of nest	7.7 0.3	7.4 0.3	3	0.8	0.5–1.3	0.36	-0.44*
Microhabitat							
Hits 0–1 m above nest	5.8 0.5	7.1 0.6	5	1.5	0.9–2.5	0.12	0.33
Hits 0–1 m below nest	2.3 0.4	2.6 0.3	3	1.3	0.8–2.0	0.34	0.41*
Hits 0–1 m lateral to nest	3.3 0.4	4.2 0.4	3	1.3	0.9–2.0	0.18	0.55*
Hits 0–1 m, upper diagonal from nest	2.2 0.3	3.2 0.4	2	1.5	1.0–2.3	0.04 <sup>d</sup>	0.74*
Hits 0–1 m, lower diagonal from nest	2.1 0.4	2.7 0.3	3	1.3	0.9–2.1	0.20	0.73*
% concealment 1 m lateral to nest	13.4 2.1	20.2 1.9	18	2.2	1.2–4.1	0.01 <sup>d</sup>	0.74*
% concealment 1 m on upper diagonal from nest	13.0 2.4	16.8 1.8	15	1.5	1.0–2.4	0.08 <sup>d</sup>	0.63*
% concealment 1 m on lower diagonal from nest	7.5 1.3	12.6 2.0	10	1.6	1.0–2.7	0.06 <sup>d</sup>	0.76*
Nest placement							
Nest height	0.89 0.05	0.84 0.03	0.4	0.8	0.5–1.4	0.41	-0.31
Host plant species	$\pi_{OT} = 0.54^e$	$\pi_{SALI} = 0.76^e$	N/A	2.7	1.1–6.9	0.03 <sup>d</sup>	0.24
Host plant height	2.8 0.4	3.0 0.2	2.3	1.3	0.8–2.2	0.34	-0.17
Host plant diameter	0.36 0.10	0.75 0.16	0.4	1.8	1.1–3.0	0.03 <sup>d</sup>	-0.08
Edge host plant	0.11 0.04	0.21 0.04	0.02	2.7	1.2–5.9	0.01 <sup>d</sup>	0.06
Edge host clump	6.5 1.2	6.1 1.1	5.5	0.9	0.6–1.4	0.72	-0.17

\* Indicates a loading with an absolute value greater than 0.4.

<sup>a</sup> IQR = interquartile range.

<sup>b</sup> OR = odds ratio.

<sup>c</sup>  $P < 0.10$ , an increase in these variables results in a decrease in the probability of avoiding parasitism

<sup>d</sup>  $P < 0.10$ , an increase in these variables results in an increase in the probability of avoiding parasitism

<sup>e</sup> For the logistic regression model with the independent variable of host species we designated *Salix* spp. as 1 and all other species as 0;  $\pi_{SALI}$  = proportion of nests placed in large *Salix* spp. that were unparasitized,  $\pi_{OT}$  = proportion of nests placed in all other host plants that were unparasitized

cattails (*Typha* spp.), along the riverbed. We recorded both distances because we have observed cowbirds traveling along both habitat edges and water channels when searching for nests.

**Mesohabitat.**—We counted the number of tree stems within 11.3 m of each nest as an estimate of potential cowbird perches surrounding a nest. We categorized trees as small (2.5–8 cm diameter at breast height [dbh]) and large (>8 cm dbh) to determine whether a relationship existed between probability of parasitism and tree size, and between probability of parasitism and number of trees. We used an 11.3-m radius to allow comparison of our results with other studies that used this distance (e.g., Brittingham and Temple 1996, Martin et al. 1997, Larison et al. 1998).

We measured the number of vegetation hits on a 2.5-cm diameter PVC pipe along 11.3-m radii lateral to the nest, at nest height, in the 4 cardinal directions. We recorded a hit each time a piece of vegetation (leaf, branch, or stem) touched a pipe-transect.

We divided the 11.3-m transect into segments from 1–3, 3–5, and 5–11.3 m. We also recorded number of hits along a 45° angle above each nest (upper diagonal) in the 4 cardinal directions. We chose the 45° angle as the best estimate of the angle between a nest placed low to the ground and a cowbird searching for nests. We sampled the upper diagonal only to a distance of 3 m due to logistical difficulties of taking this measurement.

We stood along each of the 4 transects radiating from a nest and looked toward the nest from 3, 5, and 11.3 m away. We placed a 25-cm diameter paperboard against the side of the nest (concealing the nest from our view), facing the direction where we stood. We visually estimated the percentage of the board covered by vegetation from our position to the nearest 5%, unless coverage was within 5% of 0 or 100%, in which case we estimated to the nearest 1%. We did not estimate cover from the 3-m upper diagonals, for it was impractical to carry a ladder through riparian habitat to make this estimate.

We also visually estimated percent ground cover and canopy cover within 5- and 11.3-m radii surrounding each nest. We defined ground cover as any portion of ground covered by vegetative growth, at least 1 m in height, and we defined canopy cover as growth >2 m in height. We chose 1 m as the minimum height for ground cover as least Bell's vireos usually place their nests within 1 m of the ground; thus, our definition of ground cover was any growth high enough to conceal a vireo nest. Our minimum for canopy height was 2 m, as the canopy in our riparian system was relatively low (especially compared to that of eastern deciduous forests), and we observed cowbirds perched as low as 2 m. We also visually estimated the maximum canopy height within 11.3 m of each nest.

**Microhabitat.**—We measured vegetation hits within 1 m directly above and below the nest, lateral to the nest, and at a 45° angle above (upper diagonal) and below (lower diagonal) the nest. We used the 45° angle below the nest as we considered it the best estimate of the angle between a nest and a cowbird searching for nests from the ground. We took 1 measurement above and below a nest. We took 4 measurements for each of lateral, upper diagonal, and lower diagonal cover—1 measurement in each of the 4 cardinal directions.

We estimated percent cover using the 25-cm diameter paperboard at distances of 1 m from each nest. We made 4 estimates for lateral, upper diagonal, and lower diagonal cover. We did not estimate percent cover above and below nests because of the difficulty of viewing the nest from these directions.

**Nest placement.**—We measured the height of each nest from the ground to the highest part of the nest rim. We recorded the plant species in which the nest was placed (host plant) and measured host plant height and widest diameter at nest height. We also measured the distance of each nest to the edge of the host plant and to the edge of the host clump. We drew boundaries of a clump where leaves and/or branches of neighboring plants no longer overlapped at nest height.

### **Host Behavior at the Nest**

We recorded host vocalizations at nests during 1-hr intervals between 0600 and 1200 (most between 0600 and 0900). We made recordings at these times as cowbirds are in host breeding areas during morning hours, especially early morning (Rothstein et al. 1984, Thompson 1994). We made recordings from the time of nest building to the middle of the incubation stage of the nesting cycle—the period over which female cowbirds locate and lay eggs in host nests (Friedmann 1963, Lowther 1993, Sealy 1995, Sharp and Kus 2004).

We collected behavioral data using audio and video recorders. We used 2 different types of video camera systems—5 Fuhrman Microcams (Fuhrman Diversified, Seabrook, Texas) and 2 Christensen Sentinel systems (Sandpiper Technologies, Manteca, California). We used Maxell GX-Silver 6- and 8-hour videotapes to make recordings. We placed camera lenses within 1 m of nests and camouflaged these by surrounding vegetation. We connected the camera by cable to the recorder, which we hid in vegetation approximately 20 m away from a nest. We then recorded behavior continuously with a time-lapse VCR. As sound did not record well in time-lapse mode, we periodically switched the recorder to real-time mode to make clear recordings of vocalizations.

If a video recorder was not available, or we were not able to properly conceal and/or support a camera near a nest, we used an audio recorder to sample vocal behavior. We used Radio Shack Optimus audio recorders and TDK IEC I/TYPE I 120-min (60 min per side) audiotapes. We concealed an individual recorder in vegetation directly below a nest. The tape stopped automatically upon reaching its end, and we returned later the same day to retrieve the recorder.

We noted all least Bell's vireo vocalizations recorded on tape. Bell's vireo's song consists of 2 distinct phrases, described as "cheedle-cheedle-chee?" and "cheedle-cheedle-chew!" (Peterson 1990). Because vireos do not always give both phrases of their song consecutively, we tallied song vocalizations as individual phrases.

During the first review of an audiotape, we set the volume of the recorder to the loudest volume level to ensure that we heard all vocalizations. Once we tallied all vocalizations, we replayed the tape a second time and recorded the decibel level of each individual vocalization. We placed a Radio Shack digital sound level meter 5 cm from the speaker of the recorder (both meter and recorder on a level desk) and noted the decibel reading for each vocalization. During the second playback period, we set the volume of the recorder to 70% maximum volume. This setting kept all vocalizations between decibel levels that the sound level meter was able to measure (60–120 dB).

We used decibel level as an objective manner by which to gauge the conspicuousness of a nest location. We assumed that louder vocalizations were more likely to attract a cowbird to the nest than softer vocalizations. We could not tell the distance of the bird from the nest when vocalizing. However, a loud vocalization away from the nest could register as "soft" on our recorder but still be consistent with our assumption in that it conveyed less information about nest location than a loud vocalization near the nest.

We also gathered data on movements of parents at the nest for those nests at which video recordings were made of vocal behavior. The behaviors noted were number of visits to and departures from the nest and any other movement while on the nest. Other movements included adjusting eggs, preening, and shaking the nest.

We collected behavioral data in 2000 and returned to the field in 2003 to augment the 2000 sample.

### **Statistical Analyses**

We analyzed data for nests: 1) in which egg laying began on or after the date of the first parasitism event of the season, 2) that reached the midpoint of incubation or received a cowbird egg before this point, and 3) at which we gathered information for all vegetation variables. We transformed all estimates of percent cover and percent nest concealment using arcsine-square root transformation to normalize skewed distributions. We transformed any other variables that exhibited a right-skewed distribution of raw data using the square root or natural log, whichever was appropriate, to normalize distributions before analyses. All *t*-tests used in analyses were 2-tailed, 2-sample tests. If a variable did not meet the assumptions necessary for application of a *t*-test, we used a Mann-Whitney *U*-test. The dependent variable for all logistic regression models was nest-fate with the reference condition

parasitized and the response condition unparasitized. We set statistical significance at  $P < 0.10$ .

**Vegetation surrounding nests.**—We conducted 2 separate analyses of measurements taken in the 4 cardinal directions; 1 using the mean of the 4 measurements, and the other using the minimum value. A nest could have dense cover on 3 sides, but be open on the fourth. We assume a cowbird most likely discovers a nest from the direction with the least concealment; thus, we used minimum cover as well as the mean in analyses.

We tested for differences in vegetation variables between 1999 and 2000 using Mann-Whitney  $U$ -tests in light of the large difference in sample sizes between years ( $n_{1999} = 11$ ,  $n_{2000} = 91$ ). We placed host plant species into 2 categories: SALI or OT. The SALI's included large *Salix* species: *S. lasiolepis*, *S. laevigata*, and *S. gooddingii*; OT's were all others: *S. exigua*, *Platanus racemosa*, *Populus fremontii*, *Baccharis glutinosa*, *Artemisia douglasiana*, and *Typha* sp. We chose these 2 categories as we can generalize them as large host plants (SALI's) and small host plants (OT's). (*P. racemosa* and *P. fremontii* can grow to be rather large; however, least Bell's vireo nests placed in these species were either in very young, small trees or were in low branches of a large tree far from the tree's trunk, thus effectively acting more like a low-lying shrub than a tall tree.) We eliminated vegetation variables that differed significantly between years from further analyses. We combined 1999 and 2000 data on remaining variables for subsequent analyses.

Before analyzing data for vegetation measurements, we tested for differences between the 2 nest-fate groups with respect to potentially confounding variables of 1) date egg laying began (lay date) and 2) measurement lag—that is, the elapsed time (in days) between when a nest became inactive and when we took nest measurements. The latter variable could influence results if vegetation changed (i.e., senesced or grew) over time (Burhans and Thompson 1998). In general, riparian habitat does not change noticeably over the course of 1 breeding season, with the exception of herbaceous plants, which grow and senesce over the season. We assumed that any changes in vegetation were consistent between parasitized and unparasitized nests. However, a difference in measurement lag between the 2 groups could violate this assumption.

We used individual vegetation measures described above as independent variables in logistic regression models in which nest-fate (parasitized or unparasitized) was the dependent variable. Single variable logistic regression models are similar to independent samples  $t$ -tests and are useful for identifying predictors of binary variables. We used odds ratios (see Kleinbaum et al. 1988) to evaluate the change in the likelihood of avoiding parasitism as a function of incremental increases in the independent variables. An odds ratio above one means the chance of avoiding parasitism increases with an increase in the independent variable, whereas an odds ratio below one indicates a reduction in the chance of avoiding parasitism with an increase in the independent variable. We adjusted odds ratios for logistic regression (Kleinbaum et al. 1988) so they represented the odds of avoiding parasitism when the value for respective variables changes at the same magnitude as the difference between the quartile 3 (Q3) value and the quartile 1 (Q1) value for the variable. The range from Q1 to Q3 is the

interquartile range (IQR), which includes the middle 50% of data points for a given variable. A change from Q1 to Q3 represents a transition from the median of the lower 50% of values for a variable to the median of the upper 50% of values. Adjusting odds ratios in this manner standardizes them in a biologically relevant manner, allowing for easy interpretation of the ratios.

We used backward stepwise logistic regression, with  $P < 0.15$  as the criterion for inclusion of a variable in the model to identify the combined effect of vegetation variables. This method identified the multivariate model that best predicted nest-fate.

We used principal components analysis (PCA) with varimax rotation to identify correlations between variables and to reduce those variables to a smaller set of uncorrelated components. We then used component scores as the independent variable in a logistic regression model; again, with nest-fate as the dependent variable.

**Host behavior near the nest.**—Before comparing behaviors between parasitized and unparasitized nests, we tested for differences in potential confounding variables between nest-fate groups. These variables included date of recording, time of day of recording, and day of nesting cycle at time of recording. For 2000 data, we also compared vocalization rates between recordings made with audio recorders and those made with video recorders, and we tested for a difference in which type of device we used to make recordings at parasitized and unparasitized nests. We used the outcome of these tests to determine whether pooling of audio and video samples was acceptable. We did not collect audio data with video recorders in 2003.

For nests at which we recorded more than 1 sample, we used the sample taken earliest in the nesting cycle for analyses. We had hoped to use means from multiple samples for each nest in analyses, but we were unable to collect a sufficient number of samples to make such an analysis possible. We chose the earliest sample because cowbirds typically parasitize nests early in the nesting cycle (Friedmann 1963, Lowther 1993, Sealy 1995). We used loud song phrases, soft song phrases, and total vocalizations in analyses. We used ANCOVAs (analysis of covariance) to compare vocalization rates per hour in each category and movements at the nest between parasitized and unparasitized nests.

**Vegetation and behavior combined.**—We used PCA scores on component one from the PCA conducted with vegetation variables as an index for all vegetation measurements. We used total vocalizations per hour as the index of behavior near the nest. We then used these 2 variables in logistic regression analysis to identify the combined effects of vegetation and behavior on incidence of parasitism.

## Results

### Vegetation Surrounding Nests

We sampled vegetation surrounding 11 nests that could be classified as parasitized or unparasitized in 1999 ( $n_{UP} = 8$ ,  $n_P = 3$ ), and 91 such nests in 2000 ( $n_{UP} = 55$ ,  $n_P = 36$ ). We found no differences between years for vegetation variables; thus, we combined data for both years for subsequent analyses.

When examining variables that could potentially confound results of comparisons between nest-fate groups, we found no differences in Julian lay date (mean<sub>UP</sub> = 140.6, mean<sub>P</sub> = 146.8,  $t =$

-1.53,  $P = 0.13$ ). We did find that measurement lag was greater for unparasitized nests than for parasitized nests (mean<sub>UP</sub> = 76.5, mean<sub>P</sub> = 61.0,  $t = 2.96$ ,  $P = 0.004$ ). Consequently, we regressed each variable against measurement lag to find if any vegetation variable related to lag. We found significant relationships between measurement lag and edge of clump ( $t = -1.97$ ,  $df = 1$ ,  $P = 0.05$ ,  $r^2 = 0.04$ ), and canopy cover within 5 m ( $t = -2.52$ ,  $df = 1$ ,  $P = 0.01$ ,  $r^2 = 0.06$ ), and within 11.3 m of nests ( $t = -2.02$ ,  $df = 1$ ,  $P = 0.05$ ,  $r^2 = 0.04$ ). Based on the  $r^2$  values, measurement lag explained only 4 to 6% of the variation in the variables considered. This low explanatory value indicated that the relationships are very weak; thus, we considered these relationships negligible and did not address them in further analyses.

We found no differences between nest-fate groups when comparing means of vegetation variables. Therefore, further analyses involved only the minimum value for measurements taken in the 4 cardinal directions.

We found no differences between nest-fate groups in hits or percent cover at any of the distances into which we subdivided the mesohabitat scale (hits: 1–3 m,  $t = 1.43$ ,  $P = 0.16$ ; 3–5 m,  $t = -0.16$ ,  $P = 0.87$ ; 5–11.3 m,  $t = -0.44$ ,  $P = 0.66$ ; 1–5 m,  $t = 0.97$ ,  $P = 0.34$ ; 3–11.3 m,  $t = -0.29$ ,  $P = 0.77$ ; percent cover: 3 m,  $t = 1.09$ ,  $P = 0.28$ ; 5 m,  $t = -0.20$ ,  $P = 0.84$ ). Therefore, we used the undivided mesohabitat data (1–11.3 m) in subsequent analyses to reduce the number of total variables in multivariate analyses.

We identified 10 vegetation variables with odds ratios significantly different from one. Three of these variables decreased the probability of avoiding parasitism with an increase in the value of the variable, and 7 variables increased the probability of avoiding parasitism with an increase in the value of the variable (Table 1).

In principal components analysis, we identified 1 component with a considerably large eigenvalue, which was interpretable biologically. The eigenvalue for component 1 was 4.91 after varimax rotation with  $\gamma = 1$ . Variables that loaded heavily on component 1 included: 1) microhabitat cover, 2) distance to river channel, 3) trees greater than 8 cm dbh, 4) percent canopy cover, and 5) maximum canopy height (Table 1). Nests with high scores on component 1 had greater microhabitat cover, lesser canopy cover at the mesohabitat scale with few large trees, and were close to the river channel. Given these features, we expected that unparasitized nests would have higher scores on this component than parasitized nests. This was the case: the odds ratio for the logistic regression model with PCA scores on component 1 as the independent variable indicated a 2.1-fold increase in the likelihood of avoiding parasitism with a 1.2 unit increase in the score on component 1 ( $Q_1 = -0.67$ ,  $Q_3 = 0.51$ , chi-square comparing this model to the constants only model:  $\chi^2 = 7.4$ ,  $df = 1$ ,  $P = 0.007$ ).

The multivariate model that best discriminated between parasitized and unparasitized nests included: 1) host plant diameter at nest height, 2) percent nest concealment 1 m lateral to nests, 3) distance to edge of riparian habitat, 4) ground cover within 5 m of nests, and 5) number of vegetation hits within 1 m directly above a nest (chi-square comparing this model to the constants only model:  $\chi^2 = 27.3$ ,  $df = 5$ ,  $P < 0.001$ ; Table 2). This model correctly classified 64.3% of nests as parasitized or unparasitized.

For every 0.4 m increase in host plant diameter, the likelihood of avoiding parasitism increased 2.1-fold. Likewise, an 18% increase in percent cover lateral to a nest at the microhabitat scale resulted in a 2.3-fold increase in the probability of avoiding parasitism, and a 20% increase in percent ground cover within 5 m of a nest increased the probability of avoiding parasitism 1.8-fold. An increase of 5 vegetation hits within 1 m above a nest increased the probability of avoiding parasitism 1.9-fold. Distance to the edge of the riparian habitat was the only variable in this model for which an increase in the variable decreased the probability of avoiding parasitism; this probability decreased 50% with a 65-m increase in distance to habitat edge.

### Cover and Host Plant Species

Nests in large *Salix* spp. had a lower probability of parasitism than those placed in other host plant species (Table 1). This finding suggests that some measures of cover may relate to host species. If this were the case, differences in cover between nest-fate groups could be a function of the host plant and not a function of cover in general. To test this idea, we added host species to the best logistic regression model. We found no difference between the 6-variable and 5-variable models ( $\chi^2 = 0.99$ ,  $df = 1$ ,  $P = 0.32$ ). Similarly, the logistic regression model that contained only host plant species did not improve upon our multivariate model, as the  $P$ -values for the respective models were 0.03 and  $< 0.001$ .

### Host Behavior at the Nest

Of the 73 recordings we made of vocalization behavior in 2000, 29 met the criteria described under Nest Monitoring (above) for inclusion in analyses. We made these recordings at 16 nests of 13 different pairs of least Bell's vireos. We recorded nest-visitation (and departure) rates and adult movements while on the nest at 6 of these nests (3 parasitized, 3 unparasitized). In 2003, 21 of 21 audio recordings from 20 nests of 20 different vireo pairs met the criteria.

**Movements of adults at the nest.**—We found no evidence for an effect of time of day ( $t = 0.72$ ,  $P = 0.52$ ), nor stage of nesting cycle ( $t = 0.20$ ,  $P = 0.85$ ) on rates of movements of adults at parasitized and unparasitized nests ( $n_{UP} = 3$ ,  $n_P = 3$  for all comparisons of movements). Unparasitized nests in this sample had significantly later dates of recording ( $t = 3.39$ ,  $P = 0.03$ ) than parasitized nests; therefore, we used this variable as a covariate for further analyses. We found no difference in number of visits to (and departures from) nests per hour between groups (ANCOVA:  $F = 3.87$ ,  $P = 0.14$ ,  $df = 1, 3$ ; mean<sub>UP</sub> = 2.7, mean<sub>P</sub> = 3.3), nor number of other movements on the nest per hour (ANCOVA:  $F = 0.002$ ,  $P = 0.97$ ,  $df = 1, 3$ ; mean<sub>UP</sub> = 6.6, mean<sub>P</sub> = 2.8).

**Vocalization behavior.**—Multiple studies cite a difference in host behavior over the nesting cycle (e.g., Greig-Smith 1982, Howes-Jones 1985, Eens et al. 1994). In our study, the difference in day of nesting cycle approached  $P = 0.10$  (see below). Considering these 2 points, we used day of nesting cycle as a covariate in further analyses.

There was no difference in vocalization rates for recordings made with audio or video recorders with respect to soft song phrases (ANCOVA:  $F = 1.28$ ,  $P = 0.27$ ,  $df = 1, 26$ ; mean<sub>A</sub> = 155.3, mean<sub>V</sub> = 101.0). However, the difference in loud song phrases approached  $P = 0.10$  (ANCOVA:  $F = 2.92$ ,  $P = 0.14$ ,  $df =$

1, 26;  $\text{mean}_A = 131.4$ ,  $\text{mean}_V = 82.6$ ) and the difference for total vocalizations was significant (ANCOVA:  $F = 3.12$ ,  $P = 0.09$ ,  $df = 1, 26$ ;  $\text{mean}_A = 301.0$ ,  $\text{mean}_V = 187.9$ ;  $n_A = 20$ ,  $n_V = 9$  for all comparisons, 2000 season only). There was no difference in how often each type of recording device was used at unparasitized and parasitized nests ( $\chi^2 = 0.60$ ,  $df = 1$ ,  $P = 0.44$ ). Given these results, we used type of recording device as a covariate for further analyses.

We found no evidence for an effect of date of recording ( $t = 1.22$ ,  $P = 0.23$ ), time of day ( $t = 0.61$ ,  $P = 0.55$ ), nor day of nesting cycle ( $t = 1.51$ ,  $P = 0.14$ ) on vocalization rates between parasitized and unparasitized nests ( $n_{UP} = 15$ ,  $n_P = 21$  for all comparisons of vocalization rates). We found differences between years with regard to soft song phrases ( $t = 2.33$ ,  $P = 0.03$ ) and total vocalizations ( $t = 2.54$ ,  $P = 0.02$ ), and the difference with regard to loud song phrases approached  $P = 0.10$  ( $t = 1.59$ ,  $P = 0.12$ ). Therefore, we used year as a covariate for further analyses.

We found no difference between parasitized and unparasitized nests in soft song phrases per hour (ANCOVA:  $F = 0.64$ ,  $P = 0.43$ ,  $df = 1, 31$ ;  $\text{mean}_{UP} = 148.80$ ,  $\text{mean}_P = 84.10$ ); loud song phrases per hour (ANCOVA:  $F = 2.63$ ,  $P = 0.12$ ,  $df = 1, 31$ ;  $\text{mean}_{UP} = 122.93$ ,  $\text{mean}_P = 68.48$ ); nor in total vocalizations per hour (ANCOVA:  $F = 1.60$ ,  $P = 0.22$ ,  $df = 1, 31$ ;  $\text{mean}_{UP} = 281.73$ ,  $\text{mean}_P = 165.29$ ). Although the trends are not significant, the average vocalization rates for parasitized nests were actually 45% lower than unparasitized nests.

### **Vegetation and Behavior Combined**

We gathered behavioral and vegetation data at 15 nests (7 parasitized, 8 unparasitized, all sampled in 2000). The logistic regression model combining scores on component 1 with total vocalizations per hour was not significantly different from the constants only model ( $\chi^2 = 2.92$ ,  $df = 2$ ,  $P = 0.23$ ). Thus, we found no relationship between the combined effects of vegetation and behavior and the incidence of brood parasitism.

## **Discussion**

### **Vegetation Surrounding Nests**

Our results support the nest-concealment hypothesis at the microhabitat scale, and at the 5-m distance within the mesohabitat scale. Support for the influence of microhabitat and mesohabitat cover on parasitism from other studies varies. Burhans (1997) found that unparasitized nests of indigo buntings had greater microhabitat cover than parasitized nests in old-field habitat. Staab and Morrison (1999) found that nests with greater cover around, and specifically below, the nest had a lower probability of parasitism. Uyehara and Whitfield (2000) found that unparasitized nests of southwestern willow flycatchers had more cover immediately around the nest and within 11.3 m of the nest than parasitized nests. Larison et al. (1998) did not find cover within 1 m of nests to differ between parasitized and unparasitized song sparrow (*Melospiza melodia*) nests; however, they did find that cover 0–1 m above the ground within 11.3 m of nests was greater at unparasitized nests. The authors suggest that cover at this height and scale is important because it conceals activity of song sparrows around their nests, not just at the nest. Conversely, Brittingham and Temple (1996) found that unparasitized nests of several eastern forest species had less cover 0–0.5 m from the ground within 11.3 m of nests than parasitized nests. This

difference may be a result of the fact that Brittingham and Temple (1996) studied eastern forest species that nested well above the ground. Cover low to the ground would not conceal nests of these high nesters whereas it would do so in low nesters, such as indigo buntings, song sparrows, and Bell's vireos. Activity that is close to or on the nest is more likely to lead a cowbird to a nest than activity further from the nest. Greater microhabitat cover better conceals a nest from the view of searching cowbirds, and, thus, such nests may be better able to escape parasitism.

We found no support for this hypothesis between the 5 and 11.3-m distance of the mesohabitat scale. The lack of a relationship is most likely a function of the riparian habitat at our study site. This habitat is relatively patchy when compared to an eastern deciduous forest, for example. The canopy is relatively sparse and, generally, only low-growing understory plant species grow between patches of canopy. These understory species also occur in a patchy distribution. Least Bell's vireos place their nests in the latter patches. Because these patches generally are not surrounded by contiguous vegetation at the height of the nest (and this holds true throughout the riparian habitat), mesohabitat cover to 11.3 m does not influence the incidence of parasitism.

We also found evidence that the number of trees and extent of canopy cover surrounding nests influenced the incidence of parasitism, although the evidence for this relationship is weaker than that for microhabitat cover. Clotfelter (1998) found that nests of red-winged blackbirds placed close to perches suitable for brown-headed cowbirds had a greater incidence of parasitism than nests further from such perches. Hauber and Russo (2000) found similar results when studying song sparrows, as did Staab and Morrison (1999) in a study of 4 common hosts in a riparian system in central Arizona. We did not specifically measure perch-proximity. Instead, we used number of trees greater than 8 cm dbh and percent canopy cover as surrogates for perch proximity. A greater number of trees indicates a greater number of perches, and these trees provide canopy cover in addition to perches.

Brittingham and Temple (1996) found the opposite of our results—parasitized nests had fewer trees within 11.3 m of them. We suggest, again, that this difference is a result of the different habitats in which we executed our studies. Brittingham and Temple (1996) carried out their study in eastern forests with numerous large trees and a well-developed canopy. The dense canopy of eastern forests may indeed prevent cowbirds from finding nests below the canopy. In western riparian systems, such as the one in which we conducted our study, the larger trees were much smaller than those of eastern forests and the canopy was much more open. In our study, nests with greater canopy cover surrounding them and with more large trees near them were those that were close to more perches from which cowbirds could survey for nests. Thus, our findings support the perch-proximity hypothesis.

The final vegetation-related variable that played a role in separating parasitized and unparasitized nests was distance to the riparian edge. We expected this measure to be an important determinant of parasitism; however, our results were in the opposite direction of our prediction: parasitized nests were actually farther from the edge than unparasitized nests. Thus, our study adds to the number of studies that found no support for an edge effect in relation to the incidence of parasitism (Paton 1994, Hahn

and Hatfield 1995, Tewksbury et al. 1998). The best explanation we can offer for our finding is that cowbirds easily permeate riparian woodland (see Thompson et al. 2000, Cavitt and Martin 2002). Riparian woodland is very different from the eastern forests from which the concept of an edge effect in relation to cowbird parasitism was developed. Eastern forests have large, densely packed trees and a higher, denser canopy relative to western riparian habitat, which has numerous open spaces within the canopy, including the river channel itself (which can be a large break in many sections of otherwise continuous canopy). Peterson (2002) also illustrated the contrast between eastern deciduous forests and western riparian woodland with regard to the role of habitat edge. She found no relationship between distance to edge and likelihood of nest predation at the same study site where we conducted our research.

### **Movements of Parents and Vocalization Behavior**

We found no support for the host-activity hypothesis with regard to nest visitation rates or movements while on the nest. Nest visitation behavior and behavior while on the nest are a function of incubation behavior, which is relatively consistent across individuals of the same species; thus, one might expect there to be no difference between parasitized and unparasitized nests with respect to these behaviors. As in our study, McLaren and Sealy (2003) found no relationship between movement on the nest and the incidence of parasitism. However, in the only other study to report the relationship between parasitism rates and nest visitation, Banks and Martin (2001) found that, within 4 host species, unparasitized females had higher visitation rates than parasitized females.

We found no support for the host-activity hypothesis with regard to vocalization rates near nests, although vocalization rates were higher at unparasitized nests than parasitized nests. This finding differs from studies that found direct relationships between vocalization rates and the likelihood of parasitism (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001). It is possible that, although unparasitized pairs of vireos were more vocal than parasitized pairs, they had greater cover surrounding their nests, which better concealed their conspicuous behavior. Our finding that unparasitized nests had greater microhabitat cover and mesohabitat cover within 5 m than parasitized nests supports this possibility; however, given that statistical tests were not significant, observed differences could simply be due to random chance.

### **Vegetation and Behavior Combined**

Analyses combining vegetation and behavior data had very low power because the difficulty in obtaining data on behavior

precluded a large sample size. However, we maintain that addressing behavior and vegetation structure in the same study is an important issue that merits further investigation.

### **Management Implications**

We suggest management to reduce parasitism of least Bell's vireos focus on increasing microhabitat cover. As vireos nest approximately 1 m above the ground, this increase in cover should focus on riparian understory. Managing for a dense understory may reduce parasitism rates without the need to alter canopy cover. Although the link between nest host species and microhabitat cover is unclear, we found a higher proportion of unparasitized nests in large *Salix* species versus other host plants. Therefore, one way to increase cover may be to increase the number of large *Salix* species (*S. lasiolepis*, *S. laevigata*, *S. gooddingii*) in habitat restoration sites. These trees do grow tall, but they also grow wide and dense low to the ground, providing the type of microhabitat cover that may lower the incidence of parasitism. We encourage exploration of methods to enhance understory cover combined with experimental testing of their effectiveness in reducing parasitism. We propose that recovery efforts focus on habitat management strategies with the intention of their eventually taking the place of cowbird control programs. As with any species-specific management recommendations, managers should examine potential effects on other species as well.

### **Acknowledgments**

We thank P. Beck, B. L. Peterson, and D. A. Kisner for monitoring nests of least Bell's vireos; B. L. Peterson and M. Wellik for assisting with camera set up and the changing of batteries to run cameras; and K. J. Burns, D. H. Deutschman, P. Pryde, B. L. Peterson, P. Beck, J. Wells, K. Ferree, D. A. Kisner, and J. W. Rourke for assisting in development of the project. J. Guarderas, R. Figueroa, V. Mestas-Romero, S. Sullivan, R. A. del Rio, M. Giometti, J. Mascarin, D. Evans, and B. Langan provided additional field assistance. Earlier versions of this manuscript benefited from comments of A. J. Banks, C. Bodnar, S. G. Sealy, M. L. Morrison, and 3 anonymous reviewers. A. Atkinson provided an invaluable statistical review. We thank the Bureau of Reclamation and Arizona Game and Fish Department for the loan of 5 camera systems used in this study. The California Department of Transportation, District 11, and grants to the senior author from the Garden Club of America (c/o Cornell Laboratory of Ornithology), the American Museum of Natural History, Sigma Xi, Los Angeles Audubon Society, and the San Diego State University Evolutionary Biology Program Area provided funding for this investigation.

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Associate Editor: Morrison.