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COWBIRD PARASITISM OF ARIZONA BELL'S VIREOS (*VIREO BELLII ARIZONAE*) IN A DESERT RIPARIAN LANDSCAPE: IMPLICATIONS FOR COWBIRD MANAGEMENT AND RIPARIAN RESTORATION

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Abstract. We determined microhabitat characteristics associated with both nest-site selection by the Arizona Bell's Vireo (*Vireo bellii arizonae*) and discovery of vireo nests by Brown-headed Cowbirds (*Molothrus ater*) on the Bill Williams River National Wildlife Refuge, Arizona, during the 1994 and 1995 breeding seasons. Nest sites had greater foliage cover than random sites, particularly in the low canopy layer (0.7–4.5 m high). This may have concealed nests and/or parental activity from predators and brood parasites. The probability of nest discovery by cowbirds was a function of distance to a mature cottonwood or willow tree. Nests that were 5–12 m from a mature cottonwood or willow tree were 4.5 times more likely to be discovered by cowbirds than nests with a mature cottonwood or willow tree within 5 m. However, nests that were 12–30 m and >30 m from a mature cottonwood or willow tree were 1.3 and 3.2 times less likely to be discovered by cowbirds, respectively, than nests with a mature cottonwood or willow tree within 5 m. We also conducted point counts and monitored parasitization rates and nesting success in 1994, 1995, and 1997. The proportion of Bell's Vireo nests parasitized ranged from 88% to 93% from late April to early July 1994 and 1995. Parasitization rates in 1997 were 38% for the entire breeding season and 58% for nests initiated after 29 April. The lower parasitization rate in 1997 may be related to several factors, including the initiation of cowbird control on the refuge in 1996 and decreased forage availability for Brown-headed Cowbirds with the temporary cessation of ranching operations upriver. The leading cause of nest failure was nest abandonment in 1994 and 1995, and predation in 1997.

Key Words: Arizona Bell's Vireo, parasitization rates, riparian restoration, vegetation management, *Vireo bellii arizonae.*

Habitat loss and high parasitization rates by Brown-headed Cowbirds (*Molothrus ater*) are often related factors in the decline of songbird populations (e.g., Terborgh 1989, Rosenberg et al. 1991, Rothstein 1994). While cowbird parasitism has been implicated in the near extirpation of several species, including Least Bell's Vireo (*Vireo bellii pusillus*; Franzreb 1990) and Kirtland's Warbler (*Dendroica kirtlandii*; Walkinshaw 1972), habitat loss is the ultimate cause behind these population declines. Cowbird control via live-decoy trapping has been used successfully to manage small populations of neotropical migratory songbirds with narrow geographic ranges (Robinson et al. 1993). However, habitat restoration on the breeding grounds through vegetation management may be a better option for permanently reducing parasitization rates and increasing nest success (Laymon 1987, Robinson et al. 1993, Larison et al. 1998, Staab and Morrison *this volume*).

The relationship between vegetation features, Brown-headed Cowbird abundance, and brood parasitization rates is well documented. However, past studies have primarily focused on landscape-level effects, such as total forest area, distance to edge, and level of habitat fragmentation (e.g., Robinson 1992, Paton 1994). Few studies have addressed the relationship between microhabitat features at nest sites and brood parasitization rates (Robinson et al. 1995a), and few have considered the potential this information has as a management tool.

Our study focused on identifying microhabitat characteristics associated with (1) nest-site selection by Arizona Bell's Vireos (*Vireo bellii arizonae*) and (2) discovery of vireo nests by Brown-headed Cowbirds in the lower Colorado River Valley, Arizona. Many riparian-obligate songbirds have experienced population declines in this region since the turn of the century (Rosenberg et al. 1991). The Arizona Bell's Vireo (hereafter, Bell's Vireo) has declined dramatically since the 1950s and is currently listed as endangered at the state level by the California Department of Fish and Game (Rosenberg et al. 1991).

Bell's Vireos have been heavily parasitized in the lower Colorado River Valley since the early 1900s (Brown 1903, Grinnell 1914) without experiencing population declines until recently (Rosenberg et al. 1991). The destruction of gallery cottonwood (*Populus fremontii*)-willow (*Salix gooddingii*) forests in the valley since the turn of the century has likely increased the vulnerability of the Bell's Vireo to cowbird parasitism (Rosenberg et al. 1991). With the exception of the cottonwood-willow and mesquite

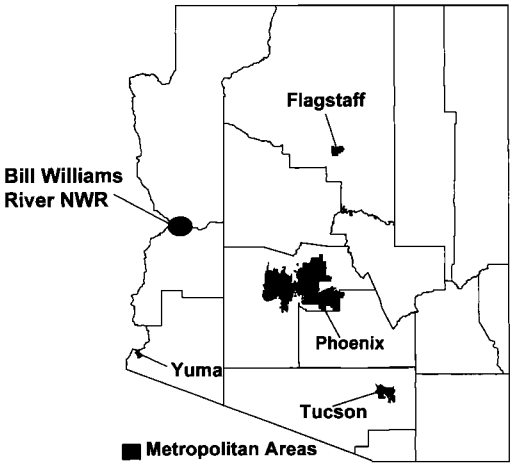

FIGURE 1. Bill Williams River National Wildlife Refuge, Mohave and La Paz Counties, Arizona.

(*Prosopis* spp.) woodlands of the Bill Williams River drainage, the Bell's Vireo is no longer a common summer resident in the lower Colorado River Valley. To restore native vegetation (i.e., cottonwood, willow, and mesquite), revegetation efforts were initiated along the lower Colorado River in the 1970s (Rosenberg et al. 1991). As of 1997, few bird species nested in these revegetation sites, and those that did experienced high parasitization and predation rates (A. Averill-Murray and S. Lynn, unpubl. data). Therefore, identification of vegetation features in cottonwood-willow forest associated with nests discovered by cowbirds may be useful in designing and managing revegetation sites.

STUDY AREA

Our study was conducted on the Bill Williams River National Wildlife Refuge (BWRNWR) located in the Sonoran Desert, La Paz and Mohave counties, Arizona (Fig. 1). The Bill Williams River is one of the principal tributaries of the lower Colorado River and is the site of the largest remaining stand of cottonwood-willow forest in the lower Colorado River Valley. However, the cottonwood-willow community has been altered by extended flooding, fire, and the introduction of saltcedar (*Tamarix ramosissima*; Rosenberg et al. 1991). Though natural regeneration of cottonwoods and willows occurs along the Bill Williams River drainage, few old trees remain.

Common understory species of the cottonwood-willow forest included saltcedar, mesquite (*Prosopis glandulosa*), arrowweed (*Pluchea sericea*), *Baccharis veminosa,* and cattail (*Typha latifolia*). Surrounding vegetation was typical of the lower Colorado River biome; desert uplands were characterized by creosote bush (*Larrea tridentata*), cholla cacti (*Opuntia* spp.), and saguaro (*Carnegiea gigantea*), and desert arroyos were characterized by ironwood (*Olneya tesota*), catclaw acacia (*Acacia greggii*), paloverde (*Cercidium* spp.), mesquite, and quail bush (*Atriplex lentiformis*). Several non-functional ranches bordered the riparian forest of the Bill Williams River, including one that temporarily ceased operations in 1994. These areas were typified by fallow fields bordered by a narrow band of mesquite trees.

METHODS

Avian Community Surveys

We conducted 5-min point counts at 200-m intervals along transects established in the riparian zone of the Bill Williams River. We surveyed 83 point-count stations in 1994 and 1995 and 45 point-count stations in 1997. Data presented here are for point-count stations that were surveyed in all three years. We used the variable circular plot method (Reynolds et al. 1980) to estimate the abundance of Brown-headed Cowbirds, Bell's Vireos, and other cowbird host species. We truncated data at 60 m to increase the chance of detecting most birds while decreasing the chance of double counting birds at neighboring point-count stations. We conducted three surveys between late April and late June in 1994, 1995, and 1997. We calculated the ratio of Brown-headed Cowbirds to suitable hosts, defined as species that accept cowbird eggs and feed their young insect diets (Rogers et al. 1997).

Rates of Brood Parasitization and Nest Success

We searched for Bell's Vireo nests from late April to early July 1994 and 1995 and early April through June 1997. In 1994 and 1995, we searched for nests within 50 m of point-count transects, concentrating on areas where Bell's Vireos were heard singing during early-morning surveys. Additional nest-searching transects were established in areas characterized primarily by mesquite. In 1997, we established nine 5-ha nest-searching plots along point-count transects. We located nests by systematically searching vegetation and observing adult behavior (Martin and Guepel 1993). We monitored nests approximately every five days to determine brood parasitization rates and nest failure.

We calculated brood parasitization rates as the percent of all nesting attempts that were discovered by cowbirds. We considered a nest "discovered" if we found one or more cowbird eggs or nestlings in the nest or cowbird eggs on the

ground below the nest. We defined successful brood parasitism as those instances in which the cowbird egg was deposited early in a vireo's nesting attempt (i.e., egg-laying or early incubation) and unsuccessful brood parasitism as those instances in which the cowbird egg was deposited in the nest during late incubation or subsequent to hatching. We considered a brood unparasitized if the nesting attempt did not fail prior to incubation and there were no cowbirds in the nest. This assumption is probably valid because (1) host species with small bills, such as Bell's Vireos, probably do not eject cowbird eggs due to the large cost associated with this behavior (Rohwer and Spaw 1988), and (2) nests found during the brooding stage often contained three or four vireo nestlings (a full clutch size). We calculated the intensity of brood parasitization as the average number of cowbird eggs per discovered nest.

We calculated nest success as the proportion of nests that successfully fledged at least one host young. We assumed that a nest was successful if fledglings were seen near the nest, if the nest had a flattened rim and fecal matter on the edge, or if the nest had large nestlings close to fledging age at the time of the last nest check and there was no subsequent evidence of depredation. We assumed that the number of fledglings was equivalent to the number of nestlings present in the nest at the last visit, as long as these nestlings were within a few days of fledging. We attributed nest failure to complete predation (loss of entire clutch or brood), parasitization (raising only cowbird young), abandonment following partial predation (in nests with or without cowbird eggs), abandonment of nests containing only cowbird eggs (no evidence of partial predation), abandonment during nest building, and unknown factors (Rogers et al. 1997).

We calculated parasitization and nest success rates in 1997 for (1) all nests and (2) nests found after 29 April to allow comparison with 1994 and 1995 data. Cowbird control was initiated on BWRNWR in 1996. In 1997, we trapped cowbirds on two-thirds of the nest-searching plots, and we addled cowbird eggs on half of these plots. Ongoing research will examine the relationship between parasitism, nest success, and varying levels of cowbird control.

Vegetation Sampling at Nest and Random Sites

We measured vegetation characteristics associated with nest sites at the end of the 1994 and 1995 breeding seasons to quantify differences between nests that were and were not discovered by cowbirds. The location of each nest was broadly classified as being in either the cottonwood-willow riparian zone or the mesquite woodland-desert wash zone. We measured specific vegetation features at the nest and within a 5-m radius circular plot centered on the ground below the nest (Appendix; Martin and Roper 1988). We also measured vegetation characteristics within randomly placed 5-m radius circular plots to determine which vegetation features were associated with nest-site selection for Bell's Vireos. We examined nest-site selection within the general vegetation types associated with Bell's Vireo nests by stratifying random plots among the nest-searching transects, one random plot per nest plot (Martin and Roper 1988). We established a random plot for each nest found on a transect, including nests of other bird species, resulting in a larger number of random plots than Bell's Vireo nest plots. We located plots by generating two random numbers, the first of which determined the distance along the transect and the second of which determined the distance away from the transect (0–50 m) at which to place each plot. We spun a compass to determine which side of the transect the plot would be located. On random plots we measured a subset of the variables measured at nest plots: distance to nearest shrub, distance to nearest mature tree, canopy cover, ground cover, and vertical height diversity within a 5-m radius circle (Appendix).

We calculated shrub and tree dispersion, plant species composition by height class, percent canopy and ground cover, and average nest concealment for use in vegetation analyses (Appendix). We used logistic regression to build two models, a model that would discriminate between nest and random sites (hereafter, nest-site selection model) and a model that would discriminate between nests discovered and undiscovered by cowbirds (hereafter, parasitism model). For the purpose of the model, we limited "discovered" nests to those containing successfully parasitized broods; "undiscovered" nests included those nests in which no cowbird eggs or nestlings were found and those containing unsuccessfully parasitized broods. We decided on this grouping because nests discovered by cowbirds late in a vireo's nesting attempt had a success rate closer to undiscovered nests than nests discovered by cowbirds early in a vireo's nesting attempt (Averill 1996). This grouping also lessened the disparity between sample sizes of discovered and undiscovered nests. Nests initiated before the onset of cowbird breeding were considered unavailable for brood parasitism and were not included in the parasitism model.

We screened vegetation variables with univariate analyses prior to logistic regression mod-

TABLE 1. PARASITIZATION RATES AND NESTING SUCCESS FOR THE BELL'S VIREO, BILL WILLIAMS RIVER NATIONAL WILDLIFE REFUGE, 1994–1995 AND 1997

Variable description	1994	1995	1997[a]
Number of nests studied	49	86	43 (26)
Proportion of nests discovered by cowbirds	0.88	0.93	0.38 (0.58)
Proportion of broods successfully parasitized	0.81	0.81	0.33 (0.54)
Cowbird eggs per discovered nest[b]	1.66 ± 0.83	1.94 ± 0.97	1.40 ± 0.63
Cowbird eggs per successfully parasitized brood[b]	1.75 ± 0.84	2.07 ± 0.98	1.46 ± 0.66
Size of unparasitized clutches[b]	3.50 ± 0.58	3.20 ± 0.45	3.62 ± 0.50
Size of parasitized clutches[b]	2.71 ± 0.92	2.25 ± 0.95	2.77 ± 0.93
Proportion of nests succeeding	0.11	0.11	0.66 (0.48)
Proportion of nests failing due to:			
Complete predation	0.31	0.22	0.16 (0.24)
Abandonment after partial predation in nests containing cowbird eggs	0.29	0.29	0.08 (0.14)
Abandonment with cowbird eggs in nest, no evidence of partial predation	0.13	0.15	0.03 (0.05)
Abandonment with only host eggs in nest, no evidence of partial predation	0.00	0.00	0.03 (0.00)
Abandonment during nest building	0.04	0.11	0.00
Raised only cowbird young	0.09	0.07	0.05 (0.10)
Unknown causes	0.03	0.05	0.00
Vireos fledged per nest[b]	0.31 ± 0.97	0.24 ± 0.78	1.41 ± 1.37 (1.00 ± 1.35)
Vireos fledged per successful nest[b]	2.80 ± 1.30	2.50 ± 0.93	2.29 ± 1.00 (2.44 ± 0.88)

[a] In 1997, nest-searching efforts began three weeks earlier than 1994–1995. The first number includes all nests found in 1997. The number in parentheses includes only nests found after 29 April, which is directly comparable to efforts in 1994–1995.
[b] Means ± SD.

eling (Hosmer and Lemeshow 1989). We tested for significant differences between (1) nest and random sites, and (2) discovered and undiscovered nests with the Chi-square test for categorical variables and the Mann-Whitney U test (corrected for ties) for continuous variables. The significance level for entry into logistic regression was set at 0.25 (Hosmer and Lemeshow 1989). Independent variables were also screened for high intercorrelation. Only one of each pair of variables with a Pearson's correlation coefficient $\geq |0.80|$ was selected for entry into the model. We used forward stepwise variable selection with variables entered into the model if the score statistic was <0.10 and removed from the model if the likelihood ratio was >0.11. There was a large disparity between sample sizes of discovered and undiscovered nests in the parasitism model. Therefore, we ran 50 logistic regression analyses by subsampling from the larger outcome category (i.e., discovered nests).

RESULTS

AVIAN COMMUNITY SURVEYS

In 1994–1995, the predominant songbird species in rank order of decreasing abundance were Brown-headed Cowbird, Yellow-breasted Chat (*Icteria virens*), Song Sparrow (*Melospiza melodia*), Abert's Towhee (*Pipilo aberti*), and Bell's Vireo. The ratio of Brown-headed Cowbirds to suitable host species was 0.28. In 1997, the predominant songbird species in rank order of decreasing abundance were Yellow-breasted Chat, Bell's Vireo, Blue Grosbeak (*Guiraca caerulea*), Common Yellowthroat (*Geothlypis trichas*), and Verdin (*Auriparus flaviceps*). The ratio of Brown-headed Cowbirds to suitable host species was 0.07. Potential nest predators that were detected on point counts included Bewick's Wren (*Thryomanes bewickii*), Marsh Wren (*Cistothorus palustris*), Cactus Wren (*Campylorhynchus brunneicapillus*), Great-tailed Grackle (*Quiscalus mexicanus*), Greater Roadrunner (*Geococcyx californianus*), and Common Raven (*Corvus corax*).

RATES OF BROOD PARASITIZATION AND NEST SUCCESS

The proportion of Bell's Vireo nests discovered by cowbirds in 1994–1995 ranged from 88% to 93% (Table 1). The proportion of successfully parasitized broods was slightly lower (81%). However, this sample consisted mainly of nests initiated after April, with the earliest recorded parasitism event occurring on 2 May. In 1997, discovery rates were lower: 38% for all nests (including those initiated in early April) and 58% for nests found after 29 April. We found no cowbird eggs prior to 8 May in 1997. Fifty percent of discovered nests received more than one cowbird egg in 1994, and 61% received

TABLE 2. RESULTS OF UNIVARIATE AND FORWARD STEPWISE LOGISTIC REGRESSION ANALYSES FOR BELL'S VIREO NEST-SITE SELECTION AND PARASITISM MODELS[a]

Variable	Mann-Whitney U		Logistic regression		
	U Statistic	P-value	Coeff. (B) ± SE	Wald statistic	P-value
Nest site selection model[b]					
Foliage cover, 0.7–4.5 m high	5377.5	<0.01	0.021 ± 0.005	16.28	<0.01
Total mesquite foliage cover	8122.5	<0.01	0.019 ± 0.005	14.36	<0.01
Saltcedar cover, 4.6–7.5 m high	7716.0	<0.01	0.022 ± 0.009	5.91	0.02
Mean distance to tree >8 cm dbh	7210.5	<0.01	−0.042 ± 0.022	3.66	0.06
Total saltcedar foliage cover	7689.5	<0.01	0.009 ± 0.005	3.11	0.08
Parasitism model[c]					
Distance to cottonwood or willow tree >8 cm dbh	514.0	0.02	−0.015 ± 0.006	5.47	0.02

[a] Variables that were included in forward stepwise logistic regression models.
[b] Model $\chi^2 = 76.01$, $P < 0.01$.
[c] Model $\chi^2 = 6.09$, $P = 0.01$.

multiple cowbird eggs in 1995, with an average of 1.66 and 1.94 cowbird eggs per nest in 1994 and 1995, respectively. In 1997, the percent of nests with multiple cowbird eggs was lower (33%).

Clutch size (i.e., the number of vireo eggs per clutch) was significantly lower in discovered than undiscovered nests in all but one year (1994: U = 16.0, P = 0.07; 1995: U = 40.5, P = 0.02; 1997: U = 46.0, P = 0.01; Table 1). Success rates were also significantly lower for parasitized broods in all but one year, despite the fact that we addled cowbird eggs in 40% of the parasitized broods in 1997 (Fisher's Exact Test; 1994: P = 0.08; 1995: P < 0.01; 1997: P < 0.01). All of the parasitized broods that successfully fledged vireo young in 1997 were located in nest-searching plots in which cowbird eggs were addled. The proportion of nests that fledged vireo young was very low in 1994 and 1995 compared to 1997, even if only nests initiated after 29 April are considered. The leading cause of nest failure in 1994 and 1995 was nest abandonment (approximately half of all nests were abandoned, either during nest building, egg laying, or incubation). The majority of abandoned nests appeared to be discovered and partially depredated by cowbirds prior to desertion. Complete predation was the leading cause of nest failure in 1997, accounting for 16% of nest loss (24% for nests found after 29 April). In 1994 and 1995, 31% and 22% of nests, respectively, failed due to complete predation.

NEST-SITE SELECTION MODEL

We measured vegetation at 129 Bell's Vireo nests and 154 random sites. Sixty-seven percent of nests were located in the cottonwood-willow riparian zone, and 33% were located in the mesquite-desert wash zone. Seven plant species were used as nest substrates: 52% of nests were in saltcedar, 28% were in mesquite, 10% were in arrowweed, 6% were in cottonwood or willow trees, and the remaining 4% were in either *Baccharis* sp. or quail bush. Vegetation structure at nest and random plots was significantly different (P < 0.25) for 16 variables, all of which were used in the forward stepwise logistic regression procedure. These variables included distance to the closest shrub and mature tree; canopy and ground cover within 5 m; foliage cover in all height categories except >7.5 m; and cottonwood-willow, saltcedar, mesquite, arrowweed, and total shrub foliage cover within 5 m.

Five variables were significant predictors of nest-site selection (Table 2). These variables are listed in Table 2 in rank order of their relative contribution to the model. Nest sites had greater foliage cover in the low tree canopy layer (0.7–4.5 m high) than random sites. Nest sites were also characterized by greater mesquite and saltcedar foliage cover and a shorter average distance to a tree >8 cm dbh (Fig. 2).

PARASITISM MODEL

Vegetation structure at discovered and undiscovered nests was significantly different (P < 0.25) for ten variables, all of which were used in the forward stepwise logistic regression procedure (Table 3). Only one variable, distance to cottonwood or willow tree >8 cm dbh, met the criteria for entry into the model when all cases were considered. Nests discovered by cowbirds were generally closer to a mature cottonwood or willow tree than undiscovered nests (Fig. 3). When we transformed this continuous variable into a categorical variable based on quartile ranges (Hosmer and Lemeshow 1989), a specific pattern emerged. Nests that were 5–12 m from a mature cottonwood or willow tree were 4.5 times more likely to be discovered by cowbirds than nests with a mature cottonwood or willow

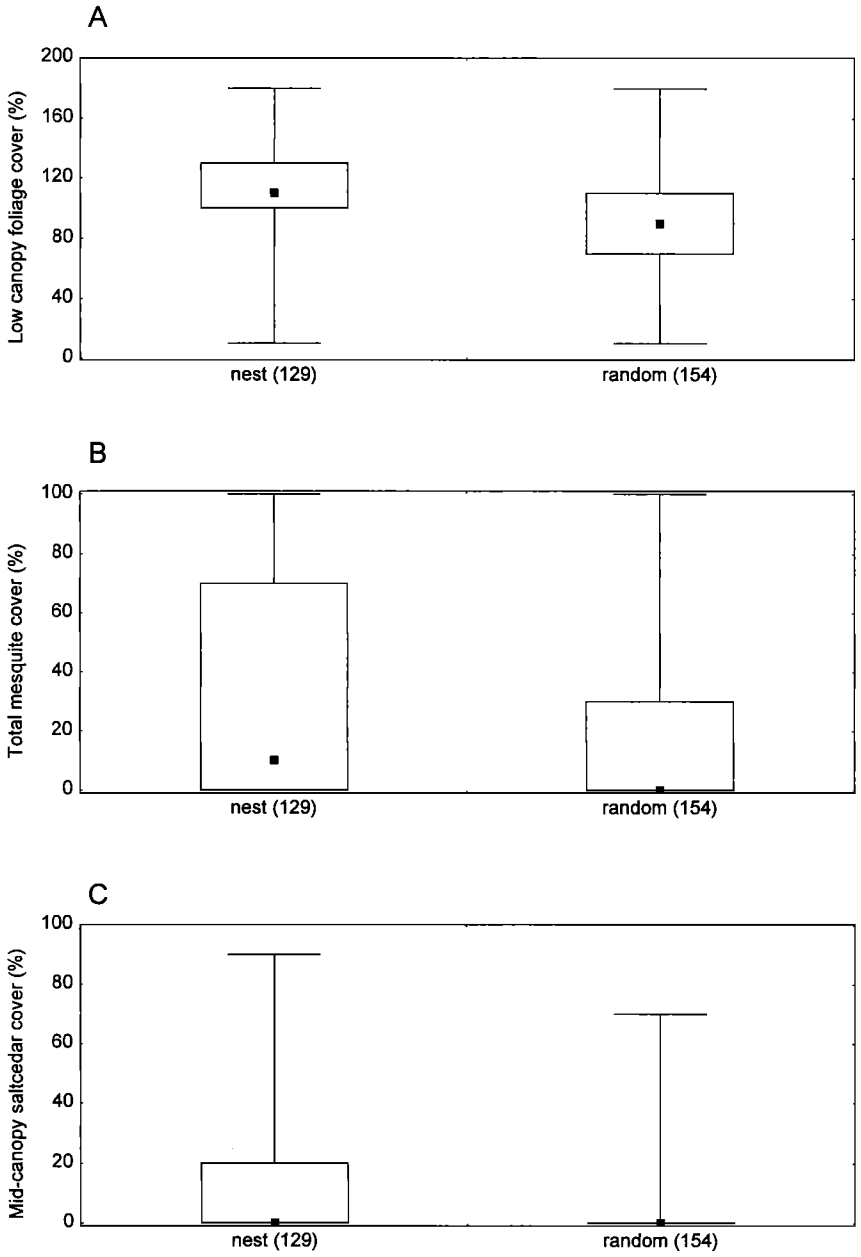

FIGURE 2. Box and whisker plots for variables included in the nest-site selection model: (A) Percent foliage cover, 0.7–4.5 m high, within 5 m of nest; (B) Total mesquite foliage cover within 5 m of nest; (C) Saltcedar foliage cover, 4.6–7.5 m high, within 5 m of nest; (D) Mean distance to the closest tree >8 cm dbh; (E) and Total saltcedar foliage cover within 5 m of nest. Box and whiskers represent 25th and 75th percentile values and minimum and maximum values, respectively. Dark square represents median value. Figure continued next page.

tree within 5 m. However, nests that were 12–30 m and >30 m from a mature cottonwood or willow tree were 1.3 and 3.2 times less likely to be discovered, respectively, than nests with a mature cottonwood or willow tree within 5 m. No nests that were placed within a cottonwood or willow tree were discovered by cowbirds, whereas 83% of nests in saltcedar, 88% of nests in mesquite, and 67% of nests in shrubs (arrowweed, quail bush, and *Baccharis* sp.) were dis-

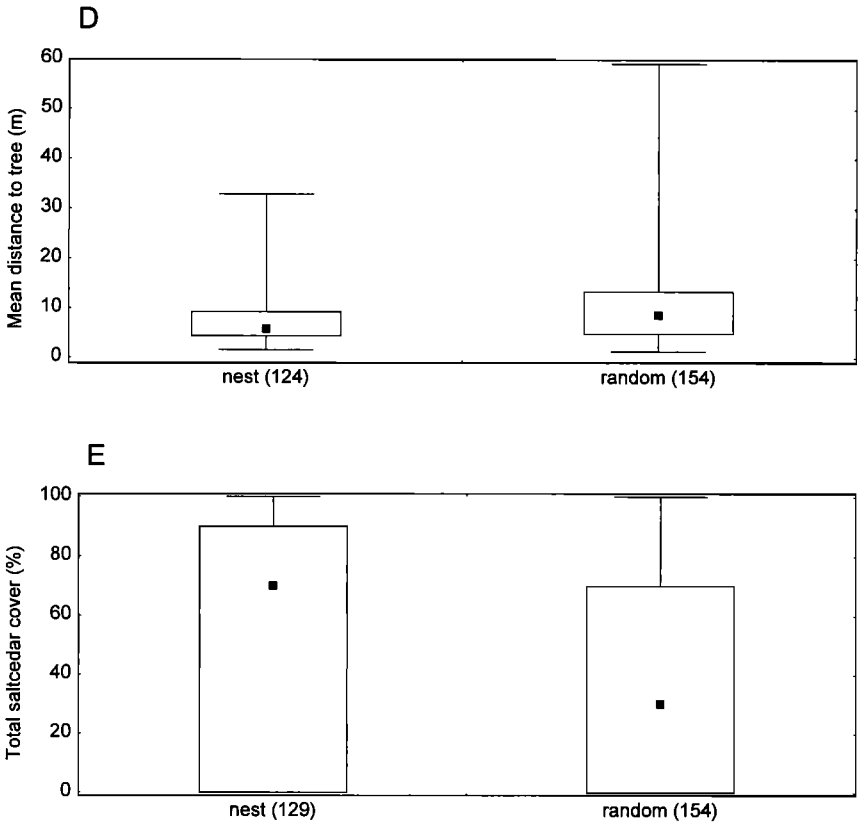

FIGURE 2. Continued.

covered by cowbirds ($\chi^2 = 3.80$, P = 0.28). Additionally, there was not a significant difference (Fisher's exact test, P = 0.41) in the proportion of nests discovered by cowbirds in the cottonwood-willow riparian zone (92%) and the mesquite-desert wash zone (89%).

When regression models were built by subsampling from the discovered nest category, all ten

TABLE 3. VEGETATION VARIABLES USED IN LOGISTIC REGRESSION ANALYSES FOR BELL'S VIREO PARASITISM MODEL, BILL WILLIAMS RIVER NATIONAL WILDLIFE REFUGE, 1994–1995

Variable[a]	U statistic	P-value	Percent of LR models in which variable was included[b]
Distance to cottonwood or willow tree >8 cm dbh	514.0	0.02	36
Nest height	576.5	0.05	24
Average lateral concealment at nest	525.5	0.09	24
Total cottonwood and willow foliage cover	646.5	0.11	14
Total shrub foliage cover	639.0	0.12	10
Canopy cover within nest patch	632.5	0.14	18
Foliage cover, 0.0–0.6 m high	646.0	0.15	8
Mean distance to shrub	612.5	0.19	12
Cottonwood and willow cover, 4.6–7.5 m high	688.0	0.22	6
Cottonwood and willow cover, 0.7–4.5 m high	690.0	0.23	4

[a] Variables used in forward stepwise logistic regression modeling based on univariate screening at P < 0.25.
[b] Percent of forward stepwise logistic regression models in which variable was included when 50 analyses were run by subsampling from larger outcome group (successfully parasitized broods).

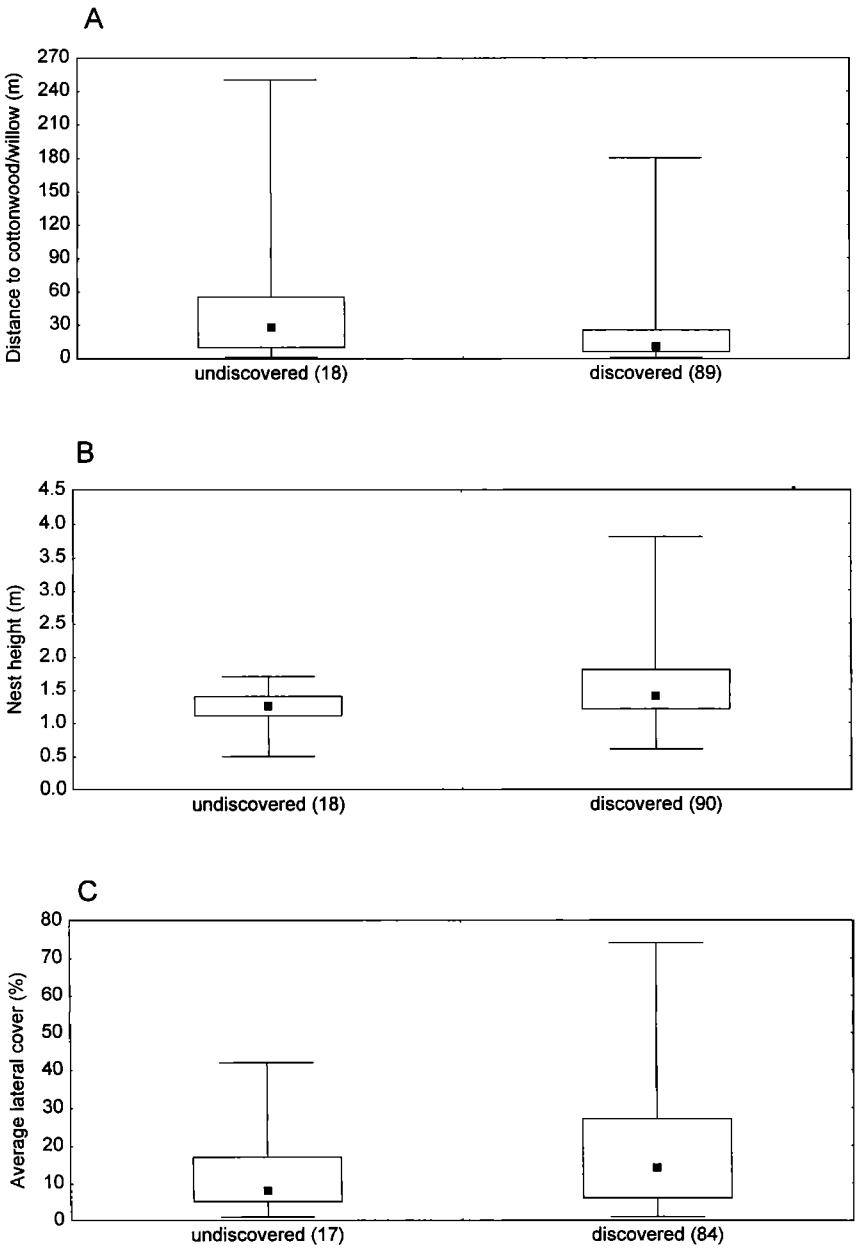

FIGURE 3. Box and whisker plots for variables included in >20% of the parasitism models built by subsampling: (A) Distance to the closest cottonwood or willow tree >8 cm dbh; (B) Nest height; and (C) Average lateral cover at the nest. For purposes of this model, "discovered" refers to nests that were found by cowbirds early in a vireo's nesting attempt (egg-laying or early incubation); "undiscovered" refers to nests that were never found by cowbirds or were found late in a vireo's nesting attempt (mid-incubation or later). See Fig. 2 legend for details on box and whisker plots.

vegetation structure variables were included in at least two models (Table 3). However, only three variables—distance to cottonwood or willow tree, nest height, and average lateral concealment at the nest—were included in more than 20% of the subsampled models. Nests discovered by cowbirds were placed higher and had greater lateral concealment than undiscovered nests (Fig. 3).

DISCUSSION

Parasitization Rates and Nesting Success

Years of high cowbird abundance: 1994–1995

The Brown-headed Cowbird was the most abundant passerine species on BWRNWR between late April and late June, 1994 and 1995. There were 11 suitable host species breeding on the refuge, and the ratio of cowbirds to suitable hosts was 0.28. Ratios above 0.10 have been associated with high levels of brood parasitism in other regions (Donovan et al. in press, Thompson et al. in press, cited in Rogers et al. 1997). On BWRNWR, 88–93% of Bell's Vireo nests found between late April and early July 1994 and 1995 had at least one cowbird egg or nestling, and over half of these had more.

Bell's Vireos typically arrive in the lower Colorado River Valley in mid-March and begin breeding in late March to early April (Rosenberg et al. 1991, A. Averill-Murray, pers. obs.). Therefore, parasitization and nest success rates in 1994 and 1995 are not representative of the entire breeding season (i.e., early-season nests and first brood attempts are under-represented). In 1997, the parasitization rate for late-season broods was 20% higher than the parasitization rate for the entire breeding season. This suggests that parasitization rates may also have been lower in April 1994 and 1995, before we started nest searching.

Parasitization rates along the Bill Williams River were high relative to other locales along the Colorado River. Brown (1994) reported parasitization rates of 7% for the Bell's Vireo (N = 57) in Grand Canyon National Park. On the other hand, parasitization rates $\geq$ 50% have also been documented for the Kirtland's Warbler (Walkinshaw 1983), Black-capped Vireo (*Vireo atricapillus*; Gryzbowski, unpubl. data, Tazik and Cornelius, unpubl. data, cited in Robinson et al. 1995a), and Least Bell's Vireo (Goldwasser et al. 1980, Franzreb 1989a) prior to cowbird control. These species breed in a wide range of habitats, ranging from jack pine (*Pinus banksiana*) forest to scrub vegetation to riparian woodland. However, all require or prefer early successional stages for breeding (Robinson et al. 1995a).

Bell's Vireos experienced low nesting success on BWRNWR between late April and early July, 1994 and 1995. Cowbird parasitism directly or indirectly accounted for the failure of approximately 50% of nests in 1994 and 1995. Barlow (1962) also reported that brood parasitism by Brown-headed Cowbirds was the primary cause of low nest success for Bell's Vireos. Approximately 43% of vireo nests along the Bill Williams River were abandoned shortly after they were discovered by cowbirds. Nest desertion is a common rejection behavior in small host species (Friedmann 1963, Graham 1988). Though nest abandonment may lower total reproductive success by limiting the number of broods a female successfully rears, this strategy may be preferable for small host species that incur a higher fitness by raising one unparasitized brood rather than two parasitized broods (Petit 1991). Bell's Vireos rarely fledge their own young from parasitized broods (Mumford 1952, A. Averill-Murray, pers. obs.). This may partly explain the high desertion rate of parasitized broods observed in this species.

Twenty-two to 31% of nests failed due to complete predation in 1994 and 1995. The majority of depredated nests were undisturbed (i.e., the nest was not missing or torn and the nest lining was not pulled up; A. Averill-Murray, unpubl. data) suggesting that snakes may be a common nest predator in this region. In fact, common kingsnakes (*Lampropeltis getula*) were seen near nests on more than one occasion.

Year of low cowbird abundance: 1997

In 1997, the ratio of Brown-headed Cowbirds to suitable host species was lower than 0.10, and this was correlated with lower parasitism rates on Bell's Vireos (38% of nests discovered by cowbirds, 58% of nests found after late April). The incidence of multiple parasitism was also substantially lower. Several factors may have contributed to the lower number of cowbirds on BWRNWR in 1997: (1) cowbird trapping efforts removed a total of 264 female cowbirds in 1996–1997; (2) temporary cessation of ranching operations upriver in 1994 may be limiting forage availability for cowbirds; and (3) unknown factors on the wintering grounds and during migration may be contributing to a decline in cowbird numbers. The shift in rank relative abundance of other avian species on the BWRNWR may be attributable, in part, to random variation and interobserver variability. In addition, the actual change in abundance of any particular host species relative to other host species between study years was small. For example, Bell's Vireos comprised 12% of the detections of suitable cowbird host species in 1994–1995 (0.50 vireos/point) and 15% of the detections in 1997 (0.53 vireos/point).

Nest success was high in 1997, 66% overall and 48% for nests found after 29 April. This is also high compared to values reported for passerine species in other studies. Martin (1992) reviewed published reports of nesting success for 32 species from 35 different studies or locations and found an average nest success of 44% based on fraction estimates (the number of successful

nests divided by the total number of nests studied). Complete predation was the primary nest mortality agent for Bell's Vireos along the Bill Williams River in 1997, as is typical for many species in other locales (Martin 1992). Nest abandonment dropped dramatically, from 55% in 1995 to 14% in 1997.

On BWRNWR, there were several occasions where cowbird eggs were found on the ground below a nest, pierced on a branch near a nest, or broken inside a nest. This frequently coincided with the appearance of another cowbird egg, suggesting that female cowbirds with overlapping laying areas may remove the eggs of competing cowbirds. In addition, the partial brood reduction of a Yellow-breasted Chat nest in 1997 coincided with the appearance of a cowbird egg. A bloody chat nestling was discovered dangling from the nest. Nestling removal by cowbirds has also been documented by other researchers (Scott and McKinney 1994, Sheppard 1996).

Bell's Vireo populations in the lower Colorado River Valley have been heavily parasitized since the turn of the century (Brown 1903, Grinnell 1914); however, this species is still found in isolated pockets, including the Bill Williams River delta (Rosenberg et al. 1991). Rothstein (1994) suggested that parasitization rates reported by early researchers may apply only to the nests most easily located (i.e., those on the edge of dense riparian forest). The landscape of the lower Colorado River Valley has changed dramatically since 1900: the riparian corridor is narrow and fragmented with little interior forest remaining (Robinson et al. 1993). Along the Bill Williams River, Bell's Vireos were not typically found in dense, interior cottonwood-willow stands but were common in forest edges, early successional stands of cottonwood and willow, and shrubby mesquite groves. Bell's Vireos may be persisting along the Bill Williams River because some birds arrive early enough to produce first broods before the cowbird breeding season fully commences. There is evidence that first broods in 1994 and 1995 experienced low parasitization rates; we found no cowbird eggs in April, and there were sightings of vireo fledgling groups during May, 1994 and 1995.

Bell's Vireos may still be in danger of regional extirpation if brood parasitization remains at the current level. Parasitization rates >25% (Robinson et al. 1993) or >30% (Laymon 1987) could threaten the persistence of local populations of host species. Though cowbird control may lower parasitization rates in the lower Colorado River Valley (A. Averill-Murray and M. L. Morrison, unpubl. data), it is not a permanent solution and may not be effective over large, fragmented landscapes with agricultural areas that provide cowbirds with numerous feeding grounds. Habitat restoration through revegetation of native plant species may be the key to maintaining many local breeding bird populations. Determining vegetation features associated with nest-site selection by sensitive songbird species and nest discovery by cowbirds will aid in the planning of revegetation sites along the lower Colorado River.

Vegetation Features Associated with Nest-site Selection and Parasitism

In the lower Colorado River Valley, Bell's Vireos were most abundant in cottonwood-willow forest (A. Averill-Murray and S. Lynn, unpubl. data). Within this general vegetation type, percent cottonwood-willow foliage cover did not differ ($P > 0.15$) between nest and random plots. However, Bell's Vireos selected nest sites with greater saltcedar foliage cover than random sites, especially in the middle canopy layer (4.6–7.5 m high). The majority of nests (52%) were in saltcedar while only 6% of nests were in cottonwood or willow trees. Therefore, saltcedar may be an important understory component for shrub-nesting species along the Bill Williams River. On the other hand, monotypic stands of saltcedar do not attract and support many birds in the lower Colorado River Valley, although this tree species is heavily used in other areas of the southwest (Hunter et al. 1988). This regional difference is attributed to saltcedar's lack of structural complexity and inability to provide shelter from the extreme summer heat typical of the lower Colorado River Valley. However, saltcedar may provide suitable nesting sites when an overstory of cottonwood or willow provides shelter from the extreme summer heat.

The nest-site model further indicated that Bell's Vireos may be selecting mesquite. Twenty-eight percent of Bell's Vireo nests were placed in mesquite trees; 33% of nests were located in areas typified by mesquite and other desert wash vegetation. Of 12 general vegetation types found in the lower Colorado River Valley, Bell's Vireos were abundant in mesquite vegetation, second only to the cottonwood-willow association (A. Averill-Murray and S. Lynn, unpubl. data).

Bell's Vireo nests were associated with vegetation features that potentially affect nest concealment. For example, nest plots had higher percent foliage cover in the low canopy layer (0.7–4.5 m high) than random plots. This corresponds to the height at which most Bell's Vireo nests were placed (0.5–3.8 m). High foliage cover in the low canopy layer may have concealed nests or parental activity from predators and brood parasites and may be indicative of a

high number of potential nest sites nearby. This could lower predator or parasite search efficiency by increasing the number of sites that must be searched (Martin 1988). Likewise, Staab (1995) and Staab and Morrison (*this volume*) found that greater vegetation volume near the nest significantly reduced the likelihood of parasitization for several host species breeding in a riparian area of central Arizona.

Tall cottonwood or willow trees near vireo nests may have aided nest discovery by cowbirds. Cowbirds use tall trees as perches from which to survey the surrounding area for nests to parasitize (Norman and Robertson 1975), and parasitization rates have been shown to increase with proximity of tall trees (Alvarez 1993) and snags (Anderson and Storer 1976). Tall trees with adjacent open areas may allow cowbirds to observe the movements and behaviors of potential hosts more easily than when host activities are confined to more interior, dense patches of vegetation. Brittingham and Temple (1996) found that parasitized broods occurred in nests characterized by a more open subcanopy (3–10 m) and canopy (>10m) than nests with unparasitized broods. This may have enabled cowbirds to find elevated perches with unobstructed views of host activity in the understory vegetation.

Bell's Vireo nests discovered by cowbirds had greater lateral concealment than undiscovered nests. However, vireo nests were typically placed within a small clearing in the shrubby undergrowth and were rarely well concealed from close range. Brittingham and Temple (1996) suggested that host species that nest in shrubs within small openings may be particularly vulnerable to parasitism, especially when potential cowbird perches are nearby. In addition, Bell's Vireos are not secretive around their nest but rather sing and scold aggressively. Therefore, host behavior may have further aided cowbird nest-searching efforts.

In conclusion, we have identified vegetation characteristics associated with cowbird nest discovery in cottonwood-willow forest that could be useful in designing and managing revegetation sites. High vegetation volume in the low canopy layer may be an important component of breeding habitat for many shrub-nesting species by concealing nests from predators and brood parasites. Saltcedar is the predominant woody species providing foliage cover at nests along the Bill Williams River. Therefore, removal of saltcedar *per se* is not a preferred management technique unless dense, native vegetation (e.g., willow, mesquite) is reestablished. Additionally, revegetation efforts that focus on planting rows of cottonwoods without providing for a dense understory could actually enhance the ability of cowbirds to locate nests by providing elevated survey perches with unobstructed views.

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APPENDIX 1. VEGETATION VARIABLES MEASURED AT NEST AND RANDOM PLOTS AND CALCULATED VARIABLES USED IN LOGISTIC REGRESSION ANALYSES

Variable	Description
Measured variables	
Nest substrate type	Plant species in which nest was located.
Height of nest	Measured with a pole calibrated to decimeters or a tape measure.
Height of nest substrate	Measured with a pole calibrated to decimeters. If the plant substrate was >6.5 m, substrate height was visually estimated using the pole as a reference.
Nest concealment	Vegetation cover below, above, and lateral to nest. Lateral nest concealment was measured one meter from the nest in each of the four cardinal directions. A 25-cm diameter circle was projected onto the nest and the percent of the circle obscured by vegetation was estimated (Martin and Roper 1988, Ralph et al. 1993). Concealment above and below the nest was the percent obscurement of a 25-cm diameter circle centered on the nest and projected to the ground and through the canopy.
Distance to closest shrub and mature tree[a]	Distance to the closest shrub/sapling (woody plant >0.6 m tall and <2.5 cm dbh) and tree (>8 cm dbh) in each of four quadrants formed by extending perpendicular lines in the cardinal directions from a point directly below the nest or random site. Measured with a tape measure or estimated by pacing.
Distance to closest mature cottonwood or willow tree	Distance from nest to closest cottonwood or willow tree >8 cm dbh. Measured with a tape measure or estimated by pacing.
Cottonwood and willow tree density	Estimated as the number of cottonwood or willow trees >8 cm dbh within 30 m of the nest.
Vertical height diversity within 5 m[a]	Estimated using the point-intercept method (Bonham 1989). Two 5-m radii were established, centered on the nest/random site and oriented in the east-west direction. At meter intervals, we recorded the plant species whose foliage intercepted an imaginary vertical line that was divided into four height categories following Anderson and Ohmart (1986): 0.0–0.6 m, 0.7–4.5 m, 4.6–7.5 m, and >7.5 m. Estimates were aided by the use of an ocular tube (James and Shugart 1970).
Canopy and ground cover within 5 m[a]	Estimated by sighting up and down through an ocular tube and recording presence or absence of vegetation cover where the crossthreads intersect. Measurements taken at meter intervals along east-west radii.
Calculated variables	
Average lateral concealment at nest	Average percent lateral concealment from the four cardinal directions.
Total nest concealment	Sum of lateral, above, and below nest concealment.
Minimum and mean distance to closest shrub and mature tree	1) Distance to the closest shrub and tree >8 cm dbh and 2) average distance to the closest shrub and mature tree in four quadrants formed by extending perpendicular lines in the cardinal directions from a point directly below the nest or random site.
Dispersion index for shrubs and mature trees	Coefficient of Variation {(standard deviation/mean) × 100} for distance to closest shrub and mature tree
Percent live foliage cover by height class within 5 m	The number of times foliage was recorded in a particular height interval divided by the total number of sample points.
Percent plant species composition within 5 m	The percent of sample points within 5 m of nest/random site at which each plant species was recorded. Percent cover by plant species was also calculated for each of the four height categories.
Percent ground and canopy cover within 5 m	Percent of sample points at which ground or canopy cover was recorded.

[a] Vegetation characteristics measured at random sites.