

NESTING HABITAT AND REPRODUCTIVE SUCCESS OF SOUTHWESTERN RIPARIAN BIRDS¹

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Abstract. Vegetation structure and floristic composition strongly influence the structure of bird communities. To assess the influence of vegetation and other environmental characteristics on songbirds, we quantified nest-site characteristics and reproductive success of a riparian songbird community in Arizona. Although we found interspecific variation in characteristics associated with nest sites, we identified two suites of species that chose sites with similar characteristics. These “nest groups” were explained largely by nest height and characteristics of nest trees. Overall, nest success was low for songbirds in this community, and averaged 23%. The most common cause of nest failure was predation (81%), although brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) was highest at nests of Bell’s Vireos (*Vireo bellii*) (29%). No vegetation or environmental features were associated with the likelihood of cowbird parasitism for any species; nest success for Bell’s Vireos was negatively associated with the amount of netleaf hackberry (*Celtis reticulata*) in the understory. Arizona sycamore (*Platanus wrightii*) and netleaf hackberry trees contained 41% and 17% of all nests, respectively, and therefore provide critically important nesting substrates for birds in this rare yet diverse vegetation community.

Key words: Bell’s Vireos, bird community, habitat structure, *Molothrus ater*, nesting habitat, *Platanus wrightii*, reproductive success.

INTRODUCTION

Although many environmental factors affect the structure of bird communities, vegetation characteristics have been found consistently influential (James 1971). In particular, richness and abundance of bird species increase with increased floristic diversity (Rice et al. 1984, Strong and Bock 1990) and vegetation structure (MacArthur and MacArthur 1961, Roth 1976).

Many studies have focused on the contribution of foraging strategy in determining community structure (MacArthur 1958, Sabo and Holmes 1983). Increasingly, however, focus has shifted to nesting habitat as another organizing force during the breeding season, because nest sites may be more limiting than food in many areas during this time (Rosenberg et al. 1982). Subsequently, researchers have contrasted features of nest sites chosen by members of songbird communities (Stauffer and Best 1986, Martin 1998). This community-based approach is useful in identifying resources that maintain or promote bird diversity during the breeding sea-

son. The quality of breeding habitat, however, can only be assessed using demographic measures, such as reproductive success, that exert strong selective pressures that affect selection of breeding habitat.

Predation and brood parasitism are the most common causes of nest failure in songbirds, and have resulted in population declines for various species and populations (Ricklefs 1969, Brittingham and Temple 1983, Robinson et al. 1995). Natural selection will favor individuals that can mitigate these negative forces by selecting nest sites that are less likely to be discovered by predators and brood parasites (Martin 1998). Although many factors can affect the susceptibility of nests to these pressures, successful conservation of songbird communities requires identifying characteristics of high-quality breeding habitat. The need to identify these critical habitat characteristics is heightened by population declines observed in many bird species in North America in recent decades (Robbins et al. 1989).

Birds that rely on riparian vegetation in the arid southwestern United States may be particularly vulnerable to population declines because these areas often comprise <0.5% of the landscape, yet support disproportionately high bird di-

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versity and abundance (Szaró 1980, Rosenberg et al. 1991). Furthermore, riparian areas in much of the southwest and adjacent Mexico have decreased in size and quality because of climate change and habitat destruction (Rosenberg et al. 1991).

Our objectives were to identify nest-site characteristics and assess reproductive success of songbirds inhabiting riparian and adjacent desert-scrub areas in southern Arizona. We contrasted habitat characteristics among species to identify those characteristics that were important for this community, and sought to identify characteristics associated with differential reproductive success, predation, and brood parasitism for a subset of species.

METHODS

STUDY AREA

We studied the songbird community of Brown Canyon (111°35'N, 31°47'W), a part of the Buenos Aires National Wildlife Refuge, in the Baboquivari Mountains in southern Arizona. The study site encompassed two distinct life zones. The lower canyon was Sonoran desert-scrub, dominated by velvet mesquite trees (*Prosopis velutina*) and spinescent shrubs such as desert hackberry (*Celtis pallida*), mimosa (*Mimosa* spp.), and acacia (*Acacia* spp.). The riparian area in this zone contained dense thickets of shrubs including gray thorn (*Ziziphus obtusifolia*), desert olive (*Forestiera shrevei*), wolfberry (*Lycium* spp.), and seep willow (*Baccharis salicifolia*), and was dominated by Arizona sycamore (*Platanus wrightii*) and netleaf hackberry (*Celtis reticulata*) trees. The upper canyon was Madrean evergreen woodland dominated by three species of oak: Arizona white (*Quercus arizonica*), Mexican blue (*Q. oblongifolia*), and Emory (*Q. emoryi*), as well as Arizona walnut (*Juglans major*) and sycamore. Most of our research was focused in the lower riparian and desert-scrub areas of the canyon.

NEST SEARCHING

During the breeding seasons of 1997 and 1998, we searched for nests of the seven most abundant non-cavity nesting songbirds: Bell's Vireos (*Vireo bellii*), Verdins (*Auriparus flaviceps*), Phainopeplas (*Phainopepla nitens*), Summer Tanagers (*Piranga rubra*), Northern Cardinals (*Cardinalis cardinalis*), Blue Grosbeaks (*Guiraca caerulea*), and Hooded Orioles (*Icterus cu-*

cullatus). We concentrated our efforts within 75 m of the creek channel and searched all accessible areas uniformly to avoid biasing locations of nest sites.

We assessed reproductive success of the three most abundant species (Bell's Vireos, Phainopeplas, and Northern Cardinals). Once we located a nest, we checked it every 3–5 days to record its contents and ultimate fate. To reduce our impact on nest outcomes, we used a series of precautionary measures (Martin and Geupel 1993).

VEGETATION SAMPLING

After each nesting attempt was completed, we measured habitat characteristics at and around the nest. We recorded nest height, nest-plant height, species, and diameter at breast height (dbh). We measured the distance the nest was placed from the middle of the primary stream channel and percent hill slope within 10 m of the nest. We estimated nest concealment (percent obscured by foliage at 50 cm) from above, below, and in each cardinal direction around the nest, and averaged these scores. We measured percent canopy cover with a spherical densiometer centered vertically at the nest (plot-center), and took measurements at four cardinal directions within 1 m of the plot-center. We estimated percent herbaceous cover within a 1-m radius circle centered on the nest.

We used a 5-m radius circular plot (0.008 ha) centered on the nest to describe vegetation of the nest-patch. Here, we counted stem densities of shrubs (<8 cm dbh) and trees (>8 cm dbh). We then delineated three height strata (0–1.5 m = understory, >1.5–4 m = midstory, and >4 m = overstory) within which we quantified the following structural and floristic vegetation characteristics. We estimated percent vegetation volume by extending an imaginary cylinder from the bottom to top of each strata, then estimated the percent vegetation volume within each cylinder, excluding herbaceous cover and tree trunks. We estimated percent horizontal vegetation coverage of all woody plant species in each strata by sketching the area covered by each species onto circles on data sheets (one for each strata) on which we overlaid a grid (40 dots cm⁻², 1,000 dots total) and counted the number of dots covered by each species. Because of the large number of plant species encountered (47), we grouped less common species according to

life-form, floristic, and habitat similarities, creating 13 composite groups (Powell 1999). We maintained all dominant tree species in separate groups except oaks, which we combined. In addition to quantifying coverage of each species or group of species, we quantified total vegetation coverage by combining coverages for all species in each height strata. Lastly, we quantified vegetation coverage and volume separately because they capture slightly different attributes of vegetation structure. For example, mesquite has less vegetation volume than does sycamore and likely provides a different level of protection from thermal radiation and predators.

DATA ANALYSES

Habitat characteristics. We first tested for differences in habitat characteristics of nest sites among species for individual vegetation characteristics with analysis of variance (ANOVA). We transformed variables (natural log or square-root) when necessary to better meet assumptions of parametric tests.

To identify species that used nesting habitats with similar characteristics, we used minimum-variance cluster analysis based on mean values for all measured variables. We compared vegetation characteristics between these groups using two-sample *t*-tests. We also used stepwise discriminant function analysis (DFA; $P < 0.20$ to enter, $P < 0.05$ to stay) to identify subsets of variables that best revealed differences among species and between groups based on nest-site characteristics. We then used canonical coefficients to determine the influence of environmental variables on each discriminant function. We used standard deviation of canonical scores as a measure of species breadth along each discriminant axis.

We performed three sets of DFAs to investigate habitat relationships among species. First, we examined all seven species together. Second, we combined species within each group (from cluster analysis) and compared groups. For these analyses we omitted variables measured at the nest site (i.e., nest concealment and diameter of nest-branch) as we were interested in identifying larger-scale environmental characteristics separating species or groups. Third, we compared species within each group to identify characteristics that differentiated group members. For these analyses we included all variables.

Reproductive success. We estimated nest suc-

cess using the Mayfield method (Mayfield 1975, Hensler and Nichols 1981) for all species except Phainopepla where we found all nests during the building stage and knew their outcomes. Nests that were destroyed or abandoned before egg laying were excluded from reproductive estimates. We classified each nest as successful (fledged at least one host young), failed (fledged no host young), parasitized (contained at least one Brown-headed Cowbird [*Molothrus ater*] egg or nestling, regardless of outcome), or unknown outcome. In addition, we classified failed nests as depredated (eggs or nestlings missing within 80% of time from expected fledgling date, using minimum number of days to fledging; Ehrlich et al. 1988), abandoned (eggs or nestlings left unattended), parasitized successfully (fledged only cowbird young), or unknown (abandoned or depredated prior to laying). For each species, we used logistic regression to compare habitat characteristics between failed and successful, depredated and successful, and parasitized and nonparasitized nests. We first examined each variable individually for inclusion ($P < 0.15$) into final models.

RESULTS

HABITAT CHARACTERISTICS

We found 162 nests (Table 1), 41% of which were located in sycamores and 17% in netleaf hackberries. Hooded Orioles (97%) and Blue Grosbeaks (94%) nested in sycamores almost exclusively. Phainopeplas nested in mesquites (80%), and Bell's Vireos and Northern Cardinals nested in a variety of plant species, but each used netleaf hackberries for 39% of nest sites.

Habitat characteristics differed among all species for all variables (one-way ANOVAs, $P < 0.001$) except for percent herbaceous cover ($F_{6,161} = 0.4$, $P = 0.90$) (Table 2). However, two groups of species consistently used habitat resources similarly. A "high-nesting" group composed of Summer Tanagers, Blue Grosbeaks, and Hooded Orioles, nested high in large trees with few shrubs and trees within the nest-patch, and in areas with high nest concealment, vegetation volume, and total vegetation coverage in the overstory (Table 2). In contrast, a "low-nesting" group composed of Bell's Vireos, Verdins, and Northern Cardinals, nested low in small trees or shrubs and in areas with high densities of shrubs and trees within the nest-patch, and

TABLE 1. Number of nests found and nest-plant species used by songbirds, Brown Canyon, Baboquivari Mountains, Arizona, 1997–1998.

Bird species	Plant species							Total
	Arizona sycamore	Netleaf hackberry	Velvet mesquite	<i>Lycium</i> spp.	Desert hackberry	Oak spp.	Other ^a	
Bell's Vireo	5	17	1	7	5		9	44
Hooded Oriole	30						1	31
Northern Cardinal	3	9		2	6	1	2	23
Summer Tanager	10		1			6	1	18
Blue Grosbeak	17		1					18
Phainopepla	1		12			2		15
Verdin		1		5	3		4	13
Total	66	27	15	14	14	9	17	162

^a See Powell (1999).

high total vegetation coverage and volume in the understory (Table 2). Nesting habitat of Phainopeplas was unique and therefore did not fit into either group. All habitat characteristics we measured differed between these groups (two-sample, two-tailed *t*-tests, all $t_{145} > 2.0$, $P < 0.001$) except for percent canopy cover ($t_{145} = 0.5$, $P = 0.65$) and percent herbaceous cover ($t_{145} = 0.01$, $P = 0.98$).

HABITAT DIFFERENCES

Among species. Nest-tree dbh (canonical score [CS] = 0.92), nest height (0.90), and vegetation volume in the understory (−0.69) best distinguished all species along the first discriminant axis, which represented a gradient from large trees and high nest placement to lower nest placement and dense vegetation in the understory (Fig. 1). Bell's Vireos, Verdins, and Northern Cardinals tended to nest low in small trees and shrubs in areas with more vegetation in the understory. Summer Tanagers, Blue Grosbeaks, Hooded Orioles, and to a lesser extent Phainopeplas, tended to nest high in large trees with less vegetation in the understory (Fig. 1). Species varied considerably in habitat breadth along this axis; Northern Cardinals showed the widest breadth and Verdins, Phainopeplas, and Hooded Orioles the narrowest (Fig. 1).

Sycamore coverage in the overstory (CS = −0.68), nest distance from creek (0.67), and succulent coverage in the understory (0.62) best distinguished nest sites among species along the second discriminant axis, which represented a gradient from riparian (mesic) to upland (xeric) vegetation types (Fig. 1). Blue Grosbeaks and Hooded Orioles nested consistently in the ripar-

ian area, whereas Phainopeplas, and to a lesser extent Verdins, nested farther from the riparian area in the desert-scrub vegetation that was typified by the presence of succulents.

Between groups. Nest-tree dbh (CS = 0.94) and nest height (0.91) best distinguished between low- and high-nesting groups. These habitat characteristics also contributed most to the separation of all species (Fig. 1).

Within groups. Diameter of nest branch (CS = 0.79) and sycamore coverage in the overstory (0.50) best distinguished species in the high-nesting group. Summer Tanagers differed most from other species as they placed nests on large limbs in both sycamores and oaks (Tables 1 and 2). Hooded Orioles hung their nests from small branches, whereas Blue Grosbeaks placed their nests on larger branches (Table 2). Nest concealment (0.74) and succulent coverage in the midstory (−0.45) best distinguished species in the low-nesting group. Verdins, which nested in more xeric areas with little nest concealment, differed most from Bell's Vireos and Northern Cardinals. Nest height (0.69) and nest concealment (0.50) best distinguished among low-nesting species along the second discriminant axis. Bell's Vireos were most distinct as they placed nests lower than the other species (Table 2).

REPRODUCTIVE SUCCESS AND COWBIRD PARASITISM

Reproductive success of Bell's Vireos was 20% (95% CI: 11–38%, $n = 41$ nests), Phainopeplas 27% ($n = 15$), and Northern Cardinals 23% (95% CI: 9–58%, $n = 19$). Predation accounted for 81% of all known nest failures ($n = 39$ of 48 nests; Table 3).

TABLE 2. Characteristics ($\bar{x} \pm SE$) at nest sites of songbirds, Brown Canyon, Baboquivari Mountains, Arizona, 1997–1998.

Characteristic	Low-nesting group			High-nesting group			
	Bell's Vireo	Verdin	Northern Cardinal	Summer Tanager	Blue Grosbeak	Hooded Oriole	Phainopepla
Nest-branch diameter (cm)	0.6 ± 0.1	1.0 ± 0.2	1.5 ± 0.2	5.0 ± 0.7	2.9 ± 0.3	0.8 ± 0.1	4.8 ± 0.3
Nest concealment (%)	21.0 ± 2.1	9.3 ± 1.6	42.3 ± 4.2	46.2 ± 3.5	50.2 ± 3.9	53.1 ± 3.4	19.0 ± 2.6
Nest height (m)	0.9 ± 0.1	2.1 ± 0.2	1.9 ± 0.5	8.5 ± 0.8	7.1 ± 0.9	6.9 ± 0.7	3.5 ± 0.6
Nest-plant							
dbh (cm)	3.1 ± 0.4	2.3 ± 0.3	15.2 ± 5.6	55.2 ± 7.0	46.8 ± 6.2	42.5 ± 2.1	19.4 ± 3.2
height (m)	2.8 ± 0.2	2.4 ± 0.2	5.5 ± 1.3	12.3 ± 1.0	13.0 ± 1.2	13.8 ± 0.8	5.1 ± 0.7
Shrubs	54.4 ± 5.7	41.5 ± 6.1	42.8 ± 6.5	23.3 ± 4.8	21.7 ± 4.3	21.2 ± 3.1	49.9 ± 6.3
Trees	2.3 ± 0.4	1.8 ± 0.4	2.9 ± 0.7	1.7 ± 0.3	1.2 ± 0.4	0.8 ± 0.2	2.7 ± 0.4
Vegetation volume (%)							
understory	58.2 ± 1.4	40.8 ± 2.2	50.0 ± 2.7	19.2 ± 1.0	20.8 ± 1.8	22.7 ± 1.4	35.7 ± 1.3
midstory	47.8 ± 1.7	38.1 ± 1.2	40.4 ± 2.4	28.6 ± 1.7	24.4 ± 1.9	22.9 ± 1.5	32.7 ± 1.6
overstory	21.5 ± 1.7	16.1 ± 2.0	26.5 ± 2.3	44.7 ± 1.9	38.9 ± 2.0	39.2 ± 1.2	7.3 ± 1.2
Vegetation coverage (%)							
understory	65.3 ± 3.8	48.3 ± 4.9	49.0 ± 5.8	23.2 ± 4.0	25.4 ± 4.6	24.1 ± 3.2	39.8 ± 5.2
midstory	57.6 ± 4.5	54.4 ± 5.3	59.7 ± 6.7	53.3 ± 6.9	33.5 ± 5.7	36.2 ± 4.8	57.6 ± 4.9
overstory	39.7 ± 6.2	34.4 ± 7.5	57.8 ± 10.7	81.9 ± 6.2	65.4 ± 7.7	64.4 ± 4.1	19.3 ± 8.5
Canopy (%)	64.0 ± 3.8	48.8 ± 3.8	62.8 ± 5.0	69.5 ± 3.6	61.1 ± 5.2	59.9 ± 2.7	44.9 ± 3.6
Slope (%)	5.2 ± 0.6	9.3 ± 3.9	11.0 ± 2.3	5.3 ± 1.6	3.6 ± 0.6	2.7 ± 0.3	13.2 ± 2.0
Distance from creek (m)	18.3 ± 2.6	18.1 ± 4.1	20.8 ± 4.9	12.8 ± 3.8	10.2 ± 3.6	5.7 ± 1.8	67.5 ± 18.8

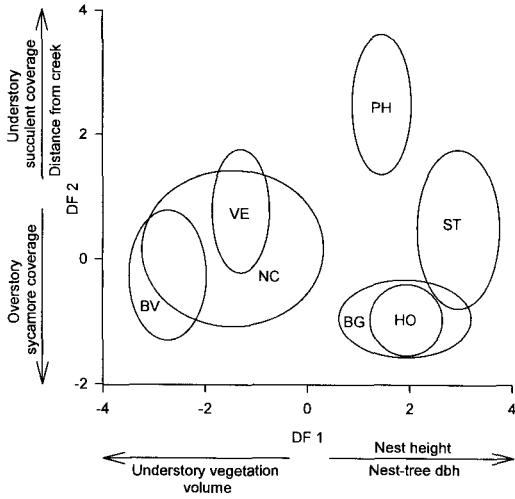


FIGURE 1. Distribution of nest scores showing separation of all species along first two discriminant axes (DF1 and DF2). Arrows indicate direction of increasing values for characteristics strongly influencing axes. Ellipses are standard deviations of nest scores along each axis and represent habitat breadth. Species codes: Bell's Vireo (BV), Verdin (VE), Northern Cardinal (NC), Summer Tanager (ST), Blue Grosbeak (BG), Hooded Oriole (HO), and Phainopepla (PH).

Odds of predation on a Bell's Vireo nest increased 1.2 times for each 1% increase in netleaf hackberry in the understory, after accounting for vegetation volume, total vegetation coverage and mesquite coverage in the midstory, and netleaf hackberry coverage and sycamore coverage in the overstory ($\chi^2_1 = 4.5, P = 0.03$). Similarly, odds of nest failure for a Bell's Vireo nest was 1.5 times greater with netleaf hackberry in the understory than without hackberry, after accounting for vegetation volume and total coverage in the midstory and canopy cover ($\chi^2_1 = 4.4, P = 0.04$). No habitat characteristics were associated with nest predation or failure of Phainopepla or Northern Cardinal nests ($P < 0.10$, for all variables).

Parasitism by Brown-headed Cowbirds was restricted largely to Bell's Vireos, with 29% ($n = 12$ of 41) of their nests being parasitized. Five Bell's Vireo nests fledged cowbirds and no vireo young, one nest fledged both vireos and cowbirds, and six nests were depredated. No habitat characteristics were associated with parasitism of Bell's Vireo nests ($P > 0.10$, for all variables). Only 1 of 19 Northern Cardinal nests was parasitized and no Phainopepla nests were par-

TABLE 3. Fates of songbird nests, Brown Canyon, Baboquivari Mountains, Arizona, 1997-1998.

Species	n	Failed ^a				Parasitized ^g
		Successful ^b	Depredated ^c	Successful parasitism ^d	Abandoned ^e	
Bell's Vireo	44	12	19	5	2	12
Phainopepla	15	4	10		1	
Northern Cardinal	24	5	10		1	1
Total	83	21	39	5	4	13

^a Fledged no host young.
^b Fledged at least one host young.
^c Eggs, nestlings, or nest disappeared within 80% of time from expected fledging date.
^d Fledged only cowbird young.
^e Eggs or nestlings left unattended.
^f Abandoned or depredated before evidence of laying.
^g Contained one cowbird egg or nestling.

asitized. All parasitized nests contained one cowbird egg.

DISCUSSION

A number of characteristics consistently explained differences in nesting habitat among species; foremost were nest-tree species and size, and nest height (Fig. 1, Table 2). Characteristics of the nest-patch (within 5 m of nests) also were important, especially understory structure and understory and overstory floristics (Tables 1 and 2). Interestingly, all species nested in locations with high total vegetation coverage within the height strata in which they typically nested (Table 2).

Local distribution, abundance, and diversity of birds are explained largely by floristic resources (Rice et al. 1983, Strong and Bock 1990). Accordingly, we found plant species composition to be an important determinant of this breeding bird community (Table 1, Fig. 1). In particular, sycamores, and to a lesser extent netleaf hackberries, both riparian obligate trees, were used heavily by many species (Table 1) and their abundance explained habitat differences among species (Fig. 1).

Riparian trees with large volume and complex growth form provide birds with a substrate for foraging and nesting and support a large prey base (Bock and Bock 1984). They are critical in areas where adjacent vegetation communities have little vertical structure, such as in arid regions of the southwestern U.S. (Carothers et al. 1974, Szaro and Jakle 1985). Hence, sycamores are vital for maintaining bird diversity in these regions. They were used as a nesting substrate for 133 of 300 nests in this area, and 18 of 37 bird species built >50% of their nests in sycamores (Powell 1999). In general, diverse and heterogeneous vegetation structure in these ecotones contributed to the diversity of the nesting bird community we studied, because each species nested in areas with unique structural characteristics (Table 2).

Nest height was an important characteristic distinguishing habitat use among species (Fig. 1). Compared to other site-specific life-history characteristics such as foraging, singing, and perching, vertical nest position is one of the most predictable characteristics of bird habitat; dramatic differences across a songbird species' geographic range are rare (Martin 1988). However, we found evidence of a systematic change

in nest height by Blue Grosbeaks that typically nest close to the ground in riparian areas with dense understory vegetation and little canopy cover (Bent 1968, Rosenberg et al. 1991, Averill 1996). In our study area, however, they nested high in large sycamores in areas with little understory vegetation (Table 2). In contrast, we found that Bell's Vireos nested within the same narrow height range and in vegetation similar to individuals in other parts of their range (Bent 1965).

Floristic and structural diversity, although important to promoting local bird diversity, also affects the diversity and distribution of nest predators (Bider 1968), the main cause of nest failure in our study and elsewhere (Ricklefs 1969). Nest density in the riparian zone we studied was high, which may increase the likelihood of nest predation because predators may find their chance of locating food to be greater. Indeed, the amount of netleaf hackberry, found only along narrow riparian areas, was negatively associated with nesting success for Bell's Vireos, suggesting that predators cued into these areas.

Overall, reproductive success for Phainopepla, Bell's Vireos, and Northern Cardinals represented some of the lowest reported reproductive success for birds in the southwest (23%). The most abundant diurnal nest predators in the study area were probably Sonoran whipsnakes (*Masticophis bilineatus*) and Mexican Jays (*Aphelocoma ultramarina*); we observed two predation events by each of these species during the study.

Nest predation is an important factor influencing breeding bird communities (Martin 1998). Because nest success has such important fitness consequences, birds will likely select nest sites to reduce chances of predation. Nest concealment by vegetation is an important criterion in nest-site selection because it can affect the ability of predators and brood parasites to locate nests visually (Joern and Jackson 1983). Martin (1992) reviewed 11 studies that correlated nest success with concealment in passerines; in 7 studies predation was lower at nests with more concealment. We found no association between nest predation and concealment, suggesting this microsite habitat characteristic may not have been important in the predation process in this area. Instead, features of the nest-patch (such as the amount of netleaf hackberry) or larger-scale habitat features seemed more important.

Although cowbirds were uncommon in our study area (an estimated 10 females in both 1997 and 1998), reproductive success of Bell's Vireos was impacted strongly by cowbird parasitism (Table 3). Parasitism rates of Bell's Vireos in Arizona range from 90% (118 of 131 nests) in the lower Colorado River valley (Averill 1996) to 7% (4 of 57 nests) in the Grand Canyon (Brown 1994), although Brown probably underestimated parasitism rates. Cowbirds were a major factor in the decline of the Least Bell's Vireo (*Vireo bellii pusillus*) in California and pose a serious threat to its chances of recovery (Goldwasser et al. 1980).

Although Northern Cardinals and Bell's Vireos used similar nesting habitats (Fig. 1) and were equally abundant (unpubl. data), only one cardinal nest was parasitized. Northern Cardinals are parasitized heavily in some parts of their range (Ehrlich et al. 1988, Eckerle and Breitwisch 1997) but may not be impacted seriously by parasitism because they can mitigate its effects by raising their own young along with cowbirds or through renesting (Eckerle and Breitwisch 1997). In a study of cowbird parasitism of Black-capped Vireos (*V. atricapillus*), White-eyed Vireos (*V. griseus*), and Northern Cardinals, vireos suffered three to four times higher rates of parasitism than cardinals (Barber and Martin 1997). The authors believed that vegetation components were unimportant in the disparate rates of parasitism.

Species in the genus *Vireo* are often heavily or disproportionately parasitized (Averill 1996, Barber and Martin 1997). Bell's Vireos are conspicuous at nest sites; males sing incessantly when near the nest but stop when on the nest. Knowing this pattern, we were often able to locate nests without ever observing individuals, and because locating host nests is vital for cowbird fitness, they may also cue into these predictable patterns.

The lack of apparent habitat features associated with nest predation and parasitism suggests that processes determining these phenomena can be difficult to identify or are incidental. Despite these difficulties, successful conservation of songbirds will require identification and promotion of resources that favor high reproductive success.

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