

**BREEDING HABITAT AND REPRODUCTIVE SUCCESS OF  
SOUTHWESTERN RIPARIAN BIRDS**

**A REPORT TO  
BUENOS AIRES NATIONAL WILDLIFE REFUGE**

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## ABSTRACT

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Identifying habitat characteristics that influence selection of nest-sites and reproductive success provides insight into the structure of bird communities and can help identify critical environmental features to target for conservation efforts. We quantified relationships among vegetation characteristics, reproductive success, and patterns of nest-site selection of a riparian songbird community in southeastern Arizona by examining 300 nests of 37 species. The most abundant species were Bell's vireos (*Vireo bellii*) ( $n = 44$  nests), verdins (*Auriparus flaviceps*) ( $n = 13$ ), phainopeplas (*Phainopepla nitens*) ( $n = 15$ ), summer tanagers (*Piranga rubra*) ( $n = 18$ ), northern cardinals (*Cardinalis cardinalis*) ( $n = 23$ ), blue grosbeaks (*Guiraca caerulea*) ( $n = 18$ ), and hooded orioles (*Icterus cucullatus*) ( $n = 31$ ). We compared nest-site habitat characteristics among species, to points chosen randomly near each nest, and to points chosen randomly within the canyon. Although we found considerable interspecific variation in vegetation characteristics associated with nest-sites, sycamore (*Platanus wrightii*) and netleaf hackberry (*Celtis reticulata*) trees were important nesting substrates for many species, containing 44% and 12% of all nests, respectively. We distinguished two groups of species that chose nest-sites with similar characteristics; these "nest groups" were distinguished largely by nest height and characteristics of their nest trees. Nest success was low for a subset of species we examined, and averaged 24%. The most likely causes for nest failure included predation and parasitism by brown-headed cowbirds (*Molothrus ater*). Parasitism occurred at 19% of nests, most notably at Bell' vireo nests (29%). Nest success for Bell's vireos was associated negatively with the amount of netleaf hackberry in the understory.

We compared characteristics at nests of the most abundant species to random characteristics at two spatial scales. Within the nest-patch, most species selected areas with more vegetation volume and coverage in the height strata where they nested. In general, we found verdins to be least selective, and hooded orioles and blue grosbeaks to be most selective of characteristics at the scale of the nest-patch. Within the canyon, riparian vegetation, particularly sycamore and hackberry, was rare and selected highly by most species. Subsequently, we suggest that these components, and the structural characteristics that they provide, are essential for maintaining species diversity in riparian areas of southern Arizona.

To determine the degree to which floristic diversity and vegetation structure influence distribution and abundance within bird communities, we investigated relationships between songbird communities and vegetation characteristics in three canyons of southern Arizona. We found distinct groups of bird species along two vegetation gradients, from oak woodland to mesquite/riparian vegetation and from open to closed vegetation canopy. All measures of bird abundance and diversity were associated positively with high volume of understory woody vegetation and associated negatively with the density of velvet mesquite (*Prosopis velutina*).

Finally, we make management and future research recommendations specific to Brown Canyon on the Buenos Aires National Wildlife Refuge.

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## PREFACE

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Riparian areas in the arid southwestern United States are rare, yet vital for maintaining diversity of breeding birds in the region. Although previous research has investigated relationships of southwest riparian bird communities, such as density and diversity and characteristics of the environment, few studies have focused on the actual resources used by members of a bird community. This information is necessary for land managers interested in maintaining diverse riparian bird communities.

This report summarizes the findings from two studies during the breeding season of 1997 and 1998. The main focus of our work was the riparian bird community in Brown Canyon on the Buenos Aires National Wildlife Refuge. Specifically, we characterized nest-site habitat for some of the most common songbird species in the canyon and compared these characteristics to random sites at two spatial scales. Additionally, we monitored a subset of these species to assess reproductive success. Our main objectives were to determine environmental characteristics that were the most important nesting habitat component(s) to members of the community and to determine associations between environmental characteristics and reproductive success. We also used morning bird counts to compare abundance and diversity of the breeding bird community in Brown Canyon to two nearby canyons. Our main objective was to associate characteristics of the bird communities with characteristics of the environment to determine which influenced bird community structure most.

### Report organization

In *Nest-site Characteristics and Reproductive Success* we quantify nesting habitat and reproductive success of common songbird species in Brown Canyon. In *Nest-site Selection* we compare nest-site habitat of seven focal species to random characteristics. In *Canyon-level Habitat Associations* we describe general characteristics of three riparian bird communities and compare these characteristics to environmental attributes.

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## STUDY AREAS

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In *Nest-site Characteristics and Reproductive Success* and *Nest-site Selection* we studied nesting habitat of birds in Brown Canyon (1200-1550 m), 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 spinecint shrubs such as desert hackberry (*Celtis pallida*), mimosa (*Mimosa* spp.), acacia (*Acacia* spp.), grey thorn (*Zizyphus obtusifolia*), and desert olive (*Forestiera shrevei*). The riparian area in this zone was dominated by sycamore (*Platanus wrightii*) and netleaf hackberry (*Celtis reticulata*) and the uplands were a relatively open canopy of shrubs and perennial grasses. The upper canyon was Madrean Evergreen Woodland dominated by three species of oak: Arizona white oak (*Quercus arizonica*), Mexican blue oak (*Q. oblongifolia*), and Emory oak (*Q. emoryi*), as well as Arizona walnut (*Juglans major*) and sycamore. The creek is perennial; no above-ground water flowed in 1997, but some was present in 1998.

In *Canyon-level Habitat Associations* we studied birds in Brown and nearby Lone Dog and Ramonote Canyons in the Atascosa Mountains. Canyons were similar in elevation (1200 to 1700 m), aspect, and topography. Ramonote (1300-1525 m) and Lone Dog (1350-1490 m) Canyons were similar in vegetation composition, though less diverse than Brown Canyon, and dominated by relatively closed canopy forests of oaks and alligator juniper (*Juniperus deppeana*). These canyons had few riparian trees or shrubs. Vegetation in upland areas was similar to those in Brown Canyon. No above-ground water flowed either year.

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## NEST-SITE CHARACTERISTICS AND REPRODUCTIVE SUCCESS

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### INTRODUCTION

Although many environmental factors influence the structure of bird communities, vegetation characteristics have proven to be one of the most important determinants (James 1971). In particular, bird species richness and abundance increase with vegetation structure (MacArthur and MacArthur 1961, James 1971, Roth 1976, Cody 1981, Kotliar and Weins 1990, Mills et al. 1991), and floristic diversity (Holmes and Robinson 1981, Rice et al. 1984, Strong and Bock 1990). Composition of the bird communities themselves, however, also may influence patterns of resource use.

Since MacArthur's (1958) work on partitioning of foraging habitat by warblers, many studies have focused on foraging as a major determinant of community structure (e.g., Terborgh and Weske 1975, James 1976, Sabo and Holmes 1983). Increasingly, attention has shifted to nesting habitat as another organizing force during the breeding season, because nest-sites are no longer assumed abundant (Lack 1971). Indeed, nest-sites may be more limiting than food during most breeding seasons in many vegetation types (Carothers et al. 1974, Tomoff 1974, Weins 1974, Rosenberg et al. 1982, Parker 1986). Accordingly, research has focused on community-wide patterns of nest-site features by contrasting vegetation characteristics among species (e.g., Collins 1981, MacKenzie et al. 1982, Stauffer and Best 1986, Gutzwiller and Anderson 1987, Brown and Trosset 1989, Martin 1998). This community-based approach is useful in identifying critical resources that maintain or promote bird diversity during the breeding season.

Identifying nest-site characteristics and the degree to which biotic and abiotic environmental components affect choice of nest-sites (*Nest-site Selection*) are important steps in defining habitat. The quality of breeding habitat, however, can only be assessed using demographic measures, such as survival and reproductive success, which will exert selective pressures affecting the choice of breeding habitat (Fretwell and Lucas 1969).

Predation and brood parasitism are the most common causes of nest failure in songbirds and have resulted in population declines for a number of species and populations (Ricklefs 1969, Brittingham and Temple 1983, Robinson et al. 1995). For many of these birds, decreasing nest success may be caused by human-induced changes to habitat and concomitant changes in predator communities and the distribution and abundance of brood parasites (Brittingham and Temple 1983, Rogers and Caro 1998). Natural selection has favored individuals that can mitigate the negative effects of predation and parasitism by nesting in areas that are less likely to be discovered by predators and brood parasites. Many factors can affect the susceptibility of nests to these pressures and successful conservation of songbird communities requires identification of characteristics that comprise high quality breeding habitat.

The need to identify important habitat characteristics associated with reproductive success is heightened by population declines observed in many bird species in North America in the last few decades (Robbins et al. 1989). Birds that rely on riparian and associated vegetation communities 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 high diversity and abundance of birds (Johnson et al. 1977, Rosenberg et al. 1991). Further, riparian areas in many parts of the southwest are decreasing in size and quality because of climatic change and habitat destruction (Rosenberg et al. 1991).

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Our objectives were to identify nest-site characteristics and determine reproductive success of species that co-occurred along a riparian area and adjacent desert-scrub in a canyon in southern Arizona. We compared habitat among species to identify characteristics that best explained differences and similarities among them and identified important vegetation components for the community. Finally, we attempted to identify vegetation characteristics associated with nest success, predation, and brood parasitism for a subset of species in the community.

## METHODS

### Nest searching

During the breeding seasons of 1997 and 1998, we searched for nests of all bird species within 75 m of the creek running through the canyon. We concentrated our search efforts on seven of the most abundant non-cavity nesting songbirds: Bell's vireo (*Vireo bellii*), verdin (*Auriparus flaviceps*), phainopepla (*Phainopepla nitens*), summer tanager (*Piranga rubra*), northern cardinal (*Cardinalis cardinalis*), blue grosbeak (*Guiraca caerulea*), and hooded oriole (*Icterus cucullatus*).

We monitored nests of three of the most abundant species (Bell's vireo, phainopepla, and northern cardinal) to assess reproductive success of a subset of the community. Once a nest was located, we checked it using a mirror pole or video monitoring device and recorded nest contents (number of eggs and/or nestlings). We returned to nests every few days to record their progress or ultimate fate. To reduce our impact on nest outcome, we used a series of precautionary measures (see Martin and Geupel 1993).

### Vegetation sampling

After each nesting attempt was completed, we measured habitat characteristics at and around nests. We recorded nest height, nest plant height, species, and diameter at breast height (dbh). We estimated nest concealment (percent of nest obscured by foliage when observed from 50 cm) from above, below, and in each cardinal direction around nests, and averaged these scores. To measure percent canopy cover we used a spherical densiometer, vertically centered 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 at plot-center.

We used a 5-m radius circular plot (0.008 ha), vertically centered at nests, to describe vegetation of the nest-patch. Within the nest-patch we counted stem densities of shrubs (<8 cm dbh) and trees (>8 cm dbh). We delineated three height strata (0-1.5 m = understory, 1.5-4 m = midstory, and >4 m = overstory) within which we quantified structural and floristic vegetation characteristics. We estimated percent vegetation volume (sensu McGarigal and McComb 1992) by extending an imaginary cylinder from the bottom to top of each strata, then estimated the percent vegetation 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 (one for each strata) on data sheets. We then overlaid a grid (40 dots/cm<sup>2</sup>, 1000 dots total) onto the circles and counted the number of dots covered by each species. Because of the large number of plant species in all samples (58), we grouped less common species according to life-form, floristic, and habitat similarities. We created 16 composite groups and maintained all dominant tree species in separate groups except oaks, which we combined (Appendix A). In addition to separating vegetation coverage for each plant species or group of species, we combined all species to quantify total vegetation coverage for each height strata.

We quantified vegetation coverage and volume separately because each characteristic captured slightly different attributes of vegetation structure. For example, velvet mesquite has less vegetation volume than does sycamore and therefore provides different levels of protection from thermal radiation and predators, two important factors for nesting birds (Ricklefs 1969, Austin 1976, Martin 1992).

We also recorded the distance the nest was placed from the middle of the primary stream channel and percent hill slope within 10 m of the nest. All vegetation was measured by one observer to reduce bias.

## Data analyses

### *Habitat dimensions*

Nests of each species located in 1997 and 1998 were combined for analyses as no obvious differences were evident in nest-site characteristics or reproductive success between years. Data were transformed with natural log, natural log+1, or square-root when necessary to meet assumptions of parametric tests. We tested for differences in vegetation characteristics among all seven species with analysis of variance (ANOVA).

We used minimum-variance cluster analysis (Ward 1963), using mean values of all vegetation variables, to combine the seven bird species into biologically meaningful groups. We identified two groups and compared vegetation characteristics between groups using two-sample *t*-tests. We used stepwise discriminant function analysis (DFA;  $P < 0.20$  to enter,  $P < 0.05$  to stay) to find subsets of variables that best revealed differences among species and between groups based on nest-site characteristics. We then ran canonical DFA on the subset of variables selected and used canonical coefficients to determine the influence of environmental variables on each discriminant function. We used standard deviation (SD) of DFA canonical scores for each species as a measure of their breadth along each axis.

We analyzed three sets of DFAs to investigate habitat relationships among species. We examined all seven species together as well as combined nests of species within each group (from cluster analysis) and compared groups. For these analyses we omitted variables immediately at the nest-site (i.e., nest concealment and diameter of nest branch) to identify gross environmental characteristics separating species or groups. Finally, we identified characteristics that differentiated among species within each group. For these analyses we included all variables.

### *Reproductive success*

We estimated nest success using the Mayfield method (Mayfield 1975, Hensler and Nichols 1981) for all species except phainopepla, for which we found all nests during the building stage and knew their outcomes. Nests that were destroyed or abandoned before evidence of laying were excluded from reproductive estimates. To determine habitat characteristics associated with different nest outcomes, 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*. Further, we classified each 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 evidence of laying).

For each species, we used logistic regression to compare habitat characteristics between failed and successful, depredated and successful, and parasitized and non-parasitized nests. We examined each variable separately for inclusion into final models ( $P < 0.15$  for inclusion).

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## RESULTS

### Habitat characteristics

We found 300 nests of 37 species in 1997 and 1998 (Table 1), 44% of which were located in sycamores. Oaks, netleaf hackberries, and velvet mesquites were used as nesting substrate for 14%, 12%, and 8% of nests, respectively. Eighteen species built  $\geq 50\%$  of their nests in sycamores and eight species built  $\geq 50\%$  of their nests in oaks. In total, 63% of all nests were in riparian obligate trees (sycamore, hackberry, and walnut). Hooded orioles (97%) and blue grosbeaks (94%) nested almost exclusively in sycamores (Table 1).

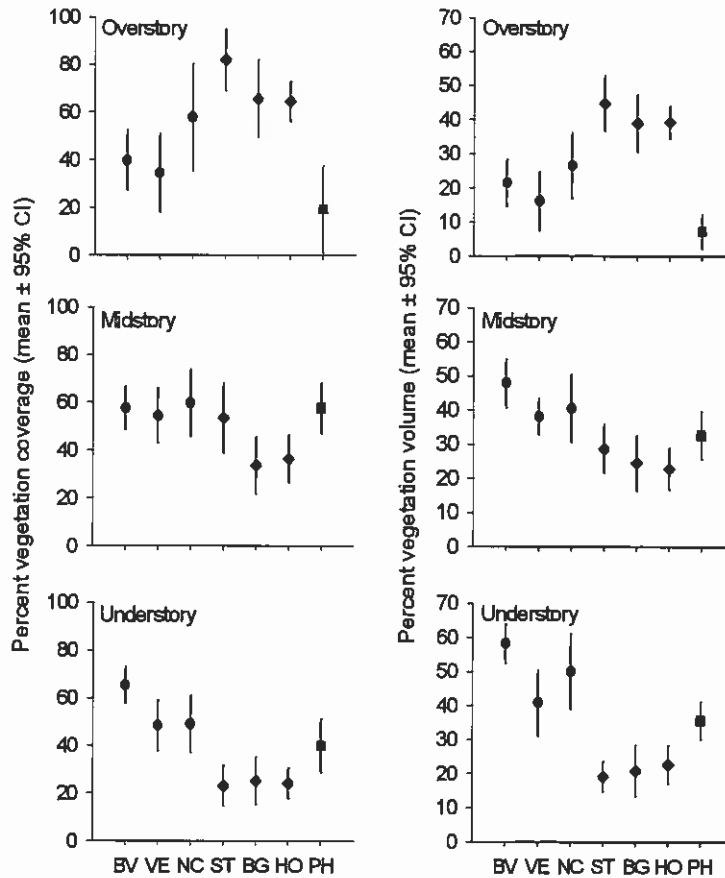
**Table 1.** Number of nests found and nest-plant species used for each nest, Brown Canyon, Baboquivari Mountains, Arizona, 1997 and 1998.

Species <sup>b</sup>	Plant Species <sup>a</sup>											Total
	Sycamore	Oak spp.	Netleaf hackberry	Mesquite	Lycium spp.	Desert hackberry	Cholla spp.	AZ walnut	Mimosa spp.	Desert olive	Other	
Bell's vireo	6		17	1	7	5				3	6	44
Hooded oriole	30						1					31
Northern cardinal	3	1	9		2	6			1		1	23
Summer tanager	10	6		1			1					18
Blue grosbeak	17			1								18
Phainopepla	1	2		12								15
Verdin			1		5	3	3		1			13
White-winged dove	3	1	3	3	2							12
Cactus wren			1				6		1		2	10
Broad-billed hummingbird	2	3	1						1		2	9
Cassin's kingbird	8											8
Solitary vireo	4	3									1	8
Blue-grey gnatcatcher	1	5						1			1	8
House finch	7										1	8
Bewick's wren	8											8
Bridled titmouse	1	4						1				6
Black-headed grosbeak	2	3										5
Ladder-backed woodpecker	3		1	1								5
Copper's hawk	3	1										4
Yellow-billed cuckoo	2	1	1									4
Hepatic tanager		3						1				4
Ash-throated flycatcher	4											4
Northern-beardless tyrannulet	4											4
Scott's oriole	1	2						1				4
Acorn woodpecker	2											2
Black-chinned hummingbird	1	1										2
Other <sup>c</sup>	9	9	3	6							1	28
<b>Total</b>	<b>133</b>	<b>41</b>	<b>37</b>	<b>23</b>	<b>16</b>	<b>14</b>	<b>9</b>	<b>6</b>	<b>4</b>	<b>3</b>	<b>17</b>	<b>300</b>

<sup>a</sup> See Appendix A for scientific name of plant species

<sup>b</sup> See Appendix D for scientific name of bird species.

<sup>c</sup> See Powell (1999) for other 11 bird species.



**Figure 1.** Nest-site habitat characteristics of species in low nesting group (●): Bell's vireo (BV), verdin (VE), northern cardinal (NC), high nesting group (◆): summer tanager (ST), blue grosbeak (BG), and hooded oriole (HO), and phainopepla (PH) (■) (not included in group analysis).

Habitat characteristics differed among the seven most abundant species (those with  $\geq 12$  nests) for all habitat variables (one-way ANOVAs,  $P < 0.01$ ) except for percent herbaceous cover ( $F_{6,161} = 0.42$ ,  $P = 0.90$ ). However, two groups of species used suites of resources similarly. 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 high vegetation volume and total coverage in the understory (Fig. 1). 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 and high vegetation volume and total coverage in the overstory (Fig. 1). Phainopeplas had unique nesting habitat and were therefore excluded from group analyses. All nest-site habitat characteristics differed between groups (two-sample  $t$ -tests,  $P < 0.001$ ,  $df = 145$ ) except for percent canopy cover (two-sample  $t$ -test,  $P = 0.45$ ,  $df = 145$ ) and percent herbaceous cover (two-sample  $t$ -test,  $P = 0.98$ ,  $df = 145$ ).

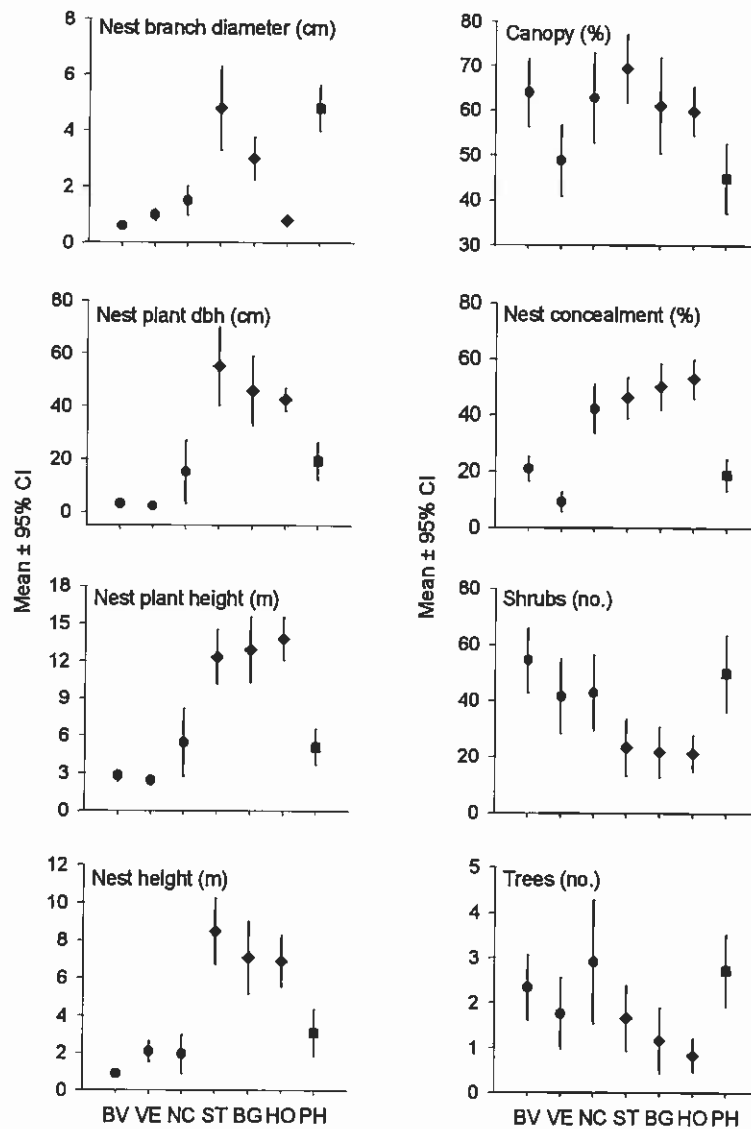


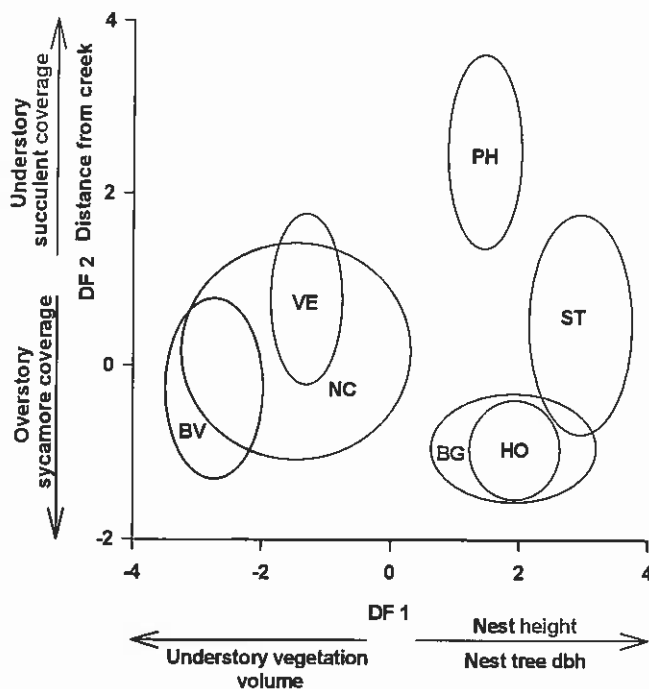
Figure 1. Continued.

### Habitat partitioning Among species

Nest tree dbh, nest height, and vegetation volume in the understory best distinguished among species along the first discriminant axis (Table 2). This axis represented a gradient from large trees and high nest placement to lower nest placement and dense vegetation in the understory (Fig. 2). Bell's vireos, verdins, and northern cardinals nested typically in small trees and shrubs in areas with high vegetation volume in the understory (Fig. 1). Summer tanagers, blue grosbeaks, hooded orioles, and to a lesser extent phainopeplas, nested typically 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. 2).

**Table 2.** Environmental characteristics that differentiated nest-site attributes between nesting groups, among all species, and within groups, from canonical discriminant function (DF) analysis. Low nesting group = verdin, Bell's vireo, and northern cardinal. High nesting group = hooded oriole, blue grosbeak, and summer tanager.

Characteristic	Comparison					
	Between Groups	Among All Species		Within Group		
		DF 1	DF 1	DF 2	High	Low
	DF 1	DF 1	DF 2	DF 1	DF 1	DF 2
Hill slope		-0.16	0.59	0.21		
Distance from creek		-0.25	0.67	0.33		
Nest tree dbh	0.94	0.92	-0.21			
Nest height	0.91	0.90	-0.19	0.22	-0.28	0.69
Total nest concealment					0.74	0.50
Diameter of nest branch				0.79		
Understory succulent coverage		-0.04	0.62			
Midstory succulent coverage					-0.42	0.22
Overstory sycamore coverage		0.54	-0.68	-0.50	0.27	0.15
Percent variance explained	100.0	74.8	15.0	95.3	70.0	30.0



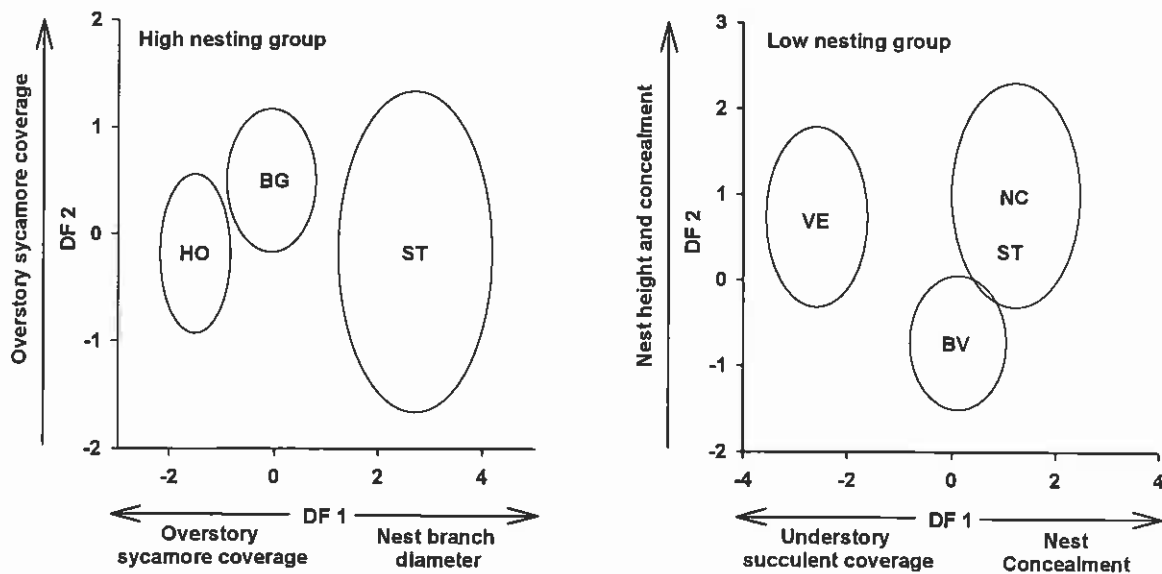
**Figure 2.** Distribution of nest scores showing separation of all species along first two discriminant axes (DF1 and DF2) based on all habitat characteristics except diameter of nest branch and nest concealment. Ellipsoids are SD of nest scores along each axis. Species codes as in Fig. 1.

Sycamore coverage in the overstory, nest distance from creek, and succulent coverage in the understory best distinguished among species along the second discriminant axis (Table 2). This axis represented a gradient from riparian (mesic) to upland (xeric) vegetation types (Fig. 2). Blue grosbeaks and hooded orioles nested consistently in sycamores (Table 1), whereas phainopeplas, and to a lesser extent verdins, nested typically away from the riparian area in the desert-scrub vegetation that is typified by the presence of succulents.

### *Between groups*

Nest tree dbh and nest height best distinguished between low and high nesting groups (Table 2). These variables also contributed most to the separation of all species (Fig. 2).





**Figure 3.** Distribution of nest scores for low and high nesting groups showing separation of species along first two discriminant axes (DF1 and DF2), based on all habitat variables. Species codes as in Fig. 1. Ellipsoids are SD of nest scores along each axis.

### *Within groups*

Diameter of nest branch and sycamore coverage in the overstory best distinguished among species in the high nesting group (Table 2). Summer tanagers showed the strongest departure from the other species as they placed nests on large limbs in both sycamores and oaks (Table 1, Figs. 1, 3). Hooded orioles and blue grosbeaks differed along this axis; hooded orioles used small branches from which to hang their nest whereas blue grosbeaks used larger branches upon which they placed their nests (Fig. 1).

Nest concealment and succulent coverage in the midstory best distinguished among species within the low nesting group along the first discriminant axis (Table 2). Verdins, which nested in more xeric areas with little nest concealment, differed clearly from Bell's vireos and northern cardinals along this axis (Figs. 1, 3). Nest height and nest concealment best distinguished among low nesting species along the second discriminant axis (Table 2). Bell's vireos were most distinct along this axis as they placed nests lower than the other species (Figs. 1, 3).

### **Reproductive success**

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 from 9 - 58%,  $n = 16$ ). Predation accounted for 72% of all known nest failures ( $n = 39$  of 54 nests) (Table 3). Brood parasitism by brown-headed cowbirds accounted directly for 9% of all nest failures ( $n = 5$  of 54) and was restricted largely to Bell's vireos with 29% ( $n = 12$ ) of nests parasitized. Five Bell's vireo nests fledged cowbirds and no vireo young, one nest fledged both vireos and cowbirds, and six nests were depredated. Only 1 of 19 northern cardinal nests was parasitized and no phainopepla nests were parasitized. All parasitized nests contained one cowbird egg.

**Table 3.** Fate of nests of songbirds, Brown Canyon, Arizona, 1997 and 1998.

Species	n	Successful <sup>b</sup>	Failed <sup>a</sup>					Unkn. outcome	Parasitized <sup>g</sup>
			Depredated <sup>c</sup>	Successful parasitism <sup>d</sup>	Abandoned <sup>e</sup>	Unkn. cause <sup>f</sup>	Unkn. outcome		
Bell's vireo	44	12	19	5	2	3	3	12	
Phainopepla	16	4	10		1				
Northern cardinal	24	5	10		1	3	5	1	
Total	83	21	39	5	4	6	8	13	

<sup>a</sup> fledged no host young

<sup>b</sup> fledged at least one host young

<sup>c</sup> eggs, nestlings, or nest disappeared within 80% of time from expected fledging date

<sup>d</sup> fledged only cowbird young

<sup>e</sup> eggs or nestlings left unattended

<sup>f</sup> abandoned or depredated before evidence of laying

<sup>g</sup> contained one cowbird egg or nestling

The odds of nest predation for a Bell's vireo nest was 1.2 times greater with netleaf hackberry in the understory than without hackberry, after accounting for vegetation volume, total coverage, and mesquite coverage in the midstory, and netleaf hackberry coverage and sycamore coverage in the overstory ( $X^2 = 4.5$ ,  $P = 0.03$ ,  $df = 31$ ). 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 ( $X^2 = 4.4$ ,  $P = 0.04$ ,  $df = 36$ ). No habitat characteristics were associated with nest predation or failure of phainopeplas or northern cardinals nor with parasitism of Bell's vireo nests ( $P < 0.10$ , logistic regression for all variables).

## DISCUSSION

A number of characteristics consistently explained differences among species, especially nest-tree species and size, and nest height (Table 2, Figs. 1, 2). Characteristics of the nest-patch were also important, especially understory structure and understory and overstory floristics (Table 2, Figs. 1-3). Finally, all species nested in locations with high vegetation volume and total coverage within the height strata(s) in which they nested (Fig. 1).

### Floristic and structural resources

The local distribution, abundance, and diversity of birds are explained in large part by floristic resources (Holmes and Robinson 1981, Rice et al. 1983, Strong and Bock 1990). Accordingly, we found plant species composition to be an important determinant of this breeding bird community (Tables 1, 2). In particular, sycamores and to a lesser extent netleaf hackberry, both riparian obligate trees, were used heavily by a wide range of species (Table 1) and were important characteristics distinguishing habitat among species (Table 2).

Riparian trees, with their large volume and complex physical structure, are thought to provide birds with more places for foraging and nesting, a larger prey base, and protection from predators (Bock and Bock 1984). These trees are critical for many bird species in arid and semi-arid environments (Carothers et al. 1974, Anderson and Ohmart 1977, Johnson et al. 1977, Stamp 1978, Bock and Bock 1984) and are preferred nesting habitat of a disproportionate number of species in many ecotonal vegetation communities containing both riparian and adjacent vegetation types (Carothers et al. 1974, Blancher and Robertson 1984, Bock and Bock 1984, Knopf 1985, Szaro and Jakle 1985, Finch 1989, McGarigal and McComb 1992). The importance of large riparian trees is even greater in communities where adjacent areas have little vertical structure, such as in arid regions of the southwestern U.S. (Szaro 1980). These ecotones promote high bird diversity by providing more areas in which birds can forage and nest (MacArthur and MacArthur 1961, Szaro and Jakle 1985, Gates and Gysel, Gates and Giffen 1991). Diverse and heterogenous vegetation structure were important determinants of the nesting bird community we studied, because each species nested in areas with unique structural characteristics (Fig. 1).

The combination of floristic and structural diversity are important factors that control and promote local bird diversity. However, these factors also affect the diversity and distribution of nest predators, the main cause of nest failure in songbirds (Ricklefs 1969). The abundance and diversity of predators is probably highest at these ecotones (e.g., Bider 1968). In the riparian zone we studied the density of nests was high with most sycamore and many netleaf hackberry trees containing at least one nest. This nest crowding can cause increases in the likelihood of nest predation in an area because predators may find their chance of locating food to be greater. Indeed, 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. Also, predators may use creek bottoms as movement corridors.

### Access to food

Most birds prefer specific plant species in which to forage (e.g., Holmes et al. 1979, Holmes and Robinson 1981) and by nesting near preferred foraging areas, individuals can reduce energy and time away from the nest (Rosenzweig 1981). We quantified insect abundance in three locations in the study area in 1998 and found that sycamores and velvet mesquites contained approximately the same numbers of insects (Appendix C). This suggests that forage availability probably had little influence on nest-site choice. Instead, birds were likely using sycamores and other species for their structural characteristics such as availability of nest-sites or protection from predators (see *Nest-site Selection*).

### Vertical nest separation

Nest height was an important characteristic separating species and groups of species (Table 2). Compared to other site-specific life-history functions such as foraging, singing, and perching (e.g., Klopfer 1963, Collins 1981, Collins 1983, Hutto 1985a), vertical nest placement is one of the most predictable characteristics of bird habitat and dramatic differences in vertical nest placement across a songbird species' geographic range are rare (Martin 1988). However, we found evidence of a systematic change in nest height by blue grosbeaks in the study area. Blue grosbeaks typically nest close to the ground in riparian areas with dense understory vegetation and little canopy cover (Bent 1968, Whitmore 1975, Ehrlich et al. 1988, Rosenberg et al. 1991, Staab 1995, Averill 1996). In my study area, however, they nested high in large sycamores in areas with little understory vegetation (Fig. 1). In contrast, Bell's vireos on my study area nested within the same narrow height range (Fig. 1) and in similar vegetation types as Bell's vireos in other parts of their range (Barlow 1962, Bent 1965, Brown and Trosset 1989, Olson and Gray 1989, Brown 1993).

One possibility explaining this shift by blue grosbeaks is that they may have been competitively excluded from their typical nesting habitat (e.g., Williams and Batzli 1979, Robinson 1981). However, competition for nest-sites and food, predation, and aspects of other bird species in the community such as behavior, physiology, and habitat selection shape breeding bird communities, and the relative contributions of these factors change spatially and temporally. Therefore, identification of factors that ultimately explain why birds nest in an area is problematic.

### Nest predation

Overall, reproductive success for phainopeplas, Bell's vireos, and northern cardinals was low (~24%) and represents some of the lowest reported reproductive success for birds in the southwest. Most nest failures were caused by predation. The most abundant diurnal nest predators in the study area (Appendix C) were probably Sonoran whipsnakes (*Masticophis bilineatus*) and Mexican jays (*Aphelocoma ultramarina*). We observed two predation events by each species during the study.

Nest predation is an important factor influencing breeding bird communities because nesting has such important fitness consequences (Martin 1998). Therefore, birds will likely select nest-sites to reduce chances of predation. Nest concealment (the amount and dispersion of vegetation around nests) is important 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 8 studies that correlated nest success with concealment in passerines; in 6 studies predation was lower at nests with more concealment. We found no association between nest predation or failure and concealment, suggesting this micro-site habitat characteristic may not have been important in the predation process in this area. Instead, features of the nest-patch (within 5 m of nests) or larger-scale habitat features seemed more important. For example, we found an inverse relationship between nest success for Bell's vireos and the amount of netleaf hackberry in the nest-patch.

### Cowbird parasitism

Cowbirds were uncommon in 1997 and 1998 with an estimated 10 females throughout the study area during both breeding seasons (B. Powell, unpublished data). Bell's vireos, however, were impacted strongly by cowbird parasitism. Parasitism rates of Bell's vireos in Arizona range from 90% (116 of 129 nests) in the Lower Colorado River Valley (Averill 1996) to 7% (4 of 57 nests) in the Grand Canyon (Brown 1994), though 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 had similar nesting habitats (Figs. 1-3) and were equally abundant (B. Powell, unpublished data), only one northern cardinal nest was parasitized. Northern cardinals are heavily parasitized in some parts of their range (Ehrlich et al. 1988, Robinson 1989, Eckerle and Breitwisch 1997) but may not be impacted seriously by parasitism because they can mitigate the effects of parasitism by raising their own young along with cowbirds or through re-nesting (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; rather cardinals, the most abundant species in their study area, attracted cowbirds to the area, but cowbirds subsequently parasitized vireo nests.

Species in the genus *Vireo* are often heavily or disproportionately parasitized (Marvil and Cruz 1989, Staab 1995, Averill 1996, Hanski et al. 1996, Barber and Martin 1997, Coguen and Mathews 1998). Three factors likely make vireos more susceptible to parasitism: (1) males are loud and conspicuous around nests, (2) males share in nest building and attentiveness, and (3) they are not aggressive toward cowbirds (Barber and Martin 1997). Bell's vireos were conspicuous near at nest sites in our study area; males sang incessantly when near the nest but stopped when on the nest (personal observation). 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.

Birds can mitigate effects of parasitism by abandoning then re-nesting. Averill (1996) found that 57% of Bell's vireo nests in the lower Colorado River valley with cowbird eggs or nestlings were abandoned. We found no evidence of abandonment in relation to brood parasitism in this study. Although we did not mark individuals, Bell's vireos and northern cardinals likely re-nested as many as three times following unsuccessful nesting attempts based on the presence of new nests in the vicinity and immediately after failed or successful attempts. In contrast, Bell's vireos in the lower Colorado River nested no more than two times (Averill 1996). Low frequency of nesting attempts, coupled with high parasitism rates, may partially explain the precipitous population declines of Bell's vireos in that area (Rosenberg et al. 1991).

## CONCLUSIONS

Information about nesting habitat for many of the species we studied is vital, as many have undergone significant population declines in some areas. In the lower Colorado River valley, numbers of Bell's vireos and summer tanagers declined 57% and 36%, respectively, from 1976 to 1986 (Rosenberg et al. 1991). Although summer tanagers are more common in parts of central and southern Arizona, loss or degradation of large riparian trees in these areas may adversely affect this species. The high rate of brood parasitism of Bell's vireos may precipitate its decline in some areas.

Riparian vegetation, especially structurally important species such as sycamore and netleaf hackberry, are components required by many songbird species in riparian areas of the southwest. In particular, sycamore trees provide nest-sites and enhance vertical vegetation structure that is important for many birds, even species that nest in the lower strata. Throughout southern Arizona, however, sycamore regeneration is low or nonexistent due to a variety of factors including reduced water tables, fewer flooding events, and cattle grazing (Glinski 1977). Managers interested in maintaining this vital component should consider promoting regeneration of this important species.

The lack of apparent habitat features associated with nest predation and parasitism suggests that processes determining these phenomenon can be difficult to identify or that they are incidental (e.g., Vickery et al. 1992). Despite these difficulties, successful conservation of songbirds will require identification and promotion of resources that favor high reproductive success.

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## NEST-SITE SELECTION

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### INTRODUCTION

The area and resources that an individual selects to carry out life-history functions depends on a variety of genetic and learned responses to both biotic and abiotic environmental stimuli (Hutto 1985b). Although many environmental features influence patterns of avian community structure and habitat selection, vegetation characteristics are believed to influence the selection process most. Important vegetation characteristics for birds include both vegetation structure (MacArthur and MacArthur 1961, James 1971, Roth 1976, Cody 1981, Mills et al. 1991) and floristic resources (Bock and Bock 1984, Rice et al. 1984, Strong and Bock 1990).

Measuring characteristics used by birds, rather than correlating measures of abundance and diversity to environmental features, is more appropriate because the scale of measurement better reflects the actual scale of resource use. This approach, along with comparisons to characteristics available at random locations, increases the precision with which resources required for nesting can be identified.

The need to identify these critical habitat resources has been heightened by the decline of many bird species in North America in the last few decades (Robbins et al. 1989). In the arid southwestern United States, birds that rely on riparian and associated vegetation may be particularly susceptible to population declines because riparian areas comprise < 0.5% of the landscape, yet support a large proportion of bird diversity in the region (Johnson et al. 1977). Furthermore, in some parts of Arizona and neighboring Sonora, Mexico riparian areas are decreasing in both size and quality (Rosenberg et al. 1991, Russell and Monson 1998).

We investigated characteristics influencing selection of nest-site habitat at two spatial scales for seven songbird species that co-occurred along a riparian area in southern Arizona. Specifically, we identified environmental characteristics that differed between sites used and not used for nesting and determined if patterns of selection changed between spatial scales. Finally, we sought to identify habitat characteristics that were most important for members of the bird community.

### METHODS

#### Nest searching

In 1997 and 1998 we searched for nests of Bell's vireos, verdins, phainopeplas, summer tanagers, northern cardinals, blue grosbeaks, and hooded orioles. Collectively, these species nest in a wide variety of vegetation types in the southwest but co-occurred throughout the study area. We searched all accessible areas within 75 m of the creek channel with approximately equal effort to avoid biasing nest locations by vegetation type and distance from creek.

#### Measuring habitat selection

After completion of each nesting attempt, we measured characteristics associated with each nest and a nearby paired-random plot. Additionally, we measured characteristics at plots located at random throughout the study area.

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To assess habitat selection at the scale of the nest-patch, we measured vegetation characteristics in a 5-m radius plot, centered on nests. We sampled vegetation at each nest and an associated paired-random (PR) plot placed 10-60 m and in a random compass direction from the nest. We randomly assigned a branch at the same height as the original nest upon which an "imaginary" nest lay, then sampled vegetation exactly as we did for nests (see *Nest-site Characteristics and Reproductive Success* for vegetation sampling protocol). We restricted PR plots to locations having vegetation at the same height as nests, regardless of plant species, assuming that species with similar physical structure had equal chances of being selected for nest-sites and that nest height is an important characteristic of nesting habitat (see discussion in *Nest-site Characteristics and Reproductive Success*).

To assess habitat selection on a larger, within-canyon scale, we quantified the range of vegetation characteristics available to birds throughout the study area. We sampled vegetation at 50 completely-random (CR) plots placed randomly within 75 m of the primary stream channel. We sampled vegetation at CR plots as for nest and PR plots, but excluded nest-specific information such as nest-tree characteristics (species, dbh, and height) and nest concealment and diameter of nest branch.

## Data analysis

We used all nests for analysis ( $n = 162$ ), including those that were abandoned or depredated before we observed any evidence of egg laying because selection of nest location had occurred. Nests from 1997 and 1998 were combined for analyses as nest-site characteristics between years were similar. Data were transformed with natural log, natural log+1, or square-root when necessary to meet assumptions of parametric tests.

We compared nest-site characteristics of each bird species to available (random) vegetation for both PR and CR plots. To determine factors affecting habitat selection at the nest-patch, we used paired  $t$ -tests to compare nests to PR plots for each species and for all environmental characteristics. We used case-controlled logistic regression to determine characteristics that best distinguished nest from PR plots. Because of the large number of explanatory variables, we first used stepwise logistic regression on several small subsets of variables, then ran the final analysis including all variables where  $P < 0.10$  (Ramsey and Schafer 1997). We tested for selectivity of common plant species using Chi-squared tests of independence using a 2 X 2 table by comparing the number of times a plant species was used versus the number of times it was available randomly.

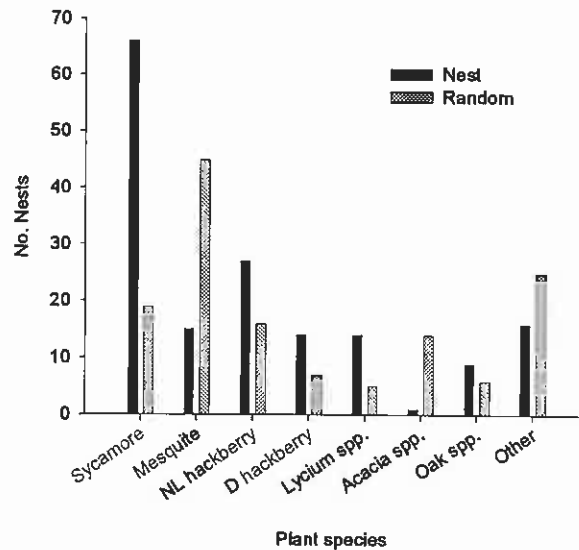
To determine factors affecting habitat selection at the within-canyon scale, we used two sample  $t$ -tests to compare nest plots to CR plots. We also used canonical discriminant function analysis (DFA) to identify environmental characteristics that best distinguished among species and CR plots. We used variables selected by stepwise DFA ( $P < 0.20$  to enter,  $P < 0.05$  to stay) to find a linear combination of characteristics that best differentiated nests of each species and CR plots (SAS 1985). We used canonical coefficients to determine the influence of environmental characteristics on each discriminant function. We used mean squared (Mahalanobis) distances from the mean of CR plots to determine the degree of selection by each species, where greater distance from zero indicated greater selectivity. Finally, we plotted standard deviation (SD) of canonical scores for each species to display intraspecific habitat breadth for characteristics influencing each discriminant axis.

## RESULTS

We quantified vegetation characteristics at 162 nests of seven species in 1997 and 1998: Bell's vireo ( $n = 44$  nests), verdin ( $n = 13$ ), phainopepla ( $n = 15$ ), summer tanager ( $n = 18$ ), northern cardinal ( $n = 23$ ), blue grosbeak ( $n = 18$ ), and hooded oriole ( $n = 31$ ).

### Nest-patch habitat selection

Selection of nesting substrate ranged considerably among species (Table 4). Hooded orioles and blue grosbeaks both were highly selective, using sycamores as nesting substrate for all but one of their nests ( $\chi^2 = 28.2$  and  $12.5$ , respectively,  $P < 0.001$ ). Bell's vireos used 11 plant species as nesting substrates but were most selective for netleaf hackberries ( $\chi^2 = 15.1$ ,  $P < 0.001$ ). Phainopeplas used mesquite



**Figure 4.** Plant species used for nesting by all bird species and those available randomly at nest-patches (PR plots). See Appendix A for scientific names of plants.

**Table 4.** Plant species used for nests (N) and those available randomly at the nest-patches (R), Brown Canyon, Baboquivari Mountains, Arizona, 1997 and 1998. Bird species: BV = Bell's vireo, VE = verdin, PH = phainopepla, ST = summer tanager, NC = northern cardinal, BG = blue grosbeak, HO = hooded oriole.

Plant Species <sup>a</sup>	Bird Species													
	BV		VE		PH		ST		NC		BG		HO	
	N	R	N	R	N	R	N	R	N	R	N	R	N	R
Sycamore	6	3			1		10	7	3	1	17	7	30	10
Velvet mesquite	1	9		5	12	11	1	3		7	1	5		5
Netleaf hackberry	17	2	1	2		3		2	9	3		4		7
Desert hackberry	5	6	3						6	2				
Lycium spp.	7	3	6	1					2	1				
Acacia spp.	1	7		2						4		1		
Oak spp.					2	1	6	4	1			1		9
Other species <sup>b</sup>	8	16	4	3			1	2	2	6				1

<sup>a</sup> See Appendix A for scientific names.

<sup>b</sup> See Powell (1999) for complete list.



for most nests, though mesquite was common ( $\chi^2 = 0.19$ ,  $P = 0.67$ ). For all bird species combined, sycamores were highly selected ( $\chi^2 = 15.1$ ,  $P < 0.001$ ; Fig. 4).

Every environmental characteristic measured at the nest-patch, except percent herbaceous ground cover, differed between nest and PR plots for at least one species ( $P < 0.05$ , for all paired  $t$ -tests; Fig. 5). In general, most species nested in areas closer to the creek with less slope, and in microsites with higher nest concealment ( $P < 0.05$ , for all paired  $t$ -tests; Fig. 5). In particular, characteristics at nests of Bell's vireos, northern cardinals, hooded orioles, and blue grosbeaks differed most from PR plots, and nests of verdins, phainopeplas, and summer tanagers differed less (Fig. 5). Blue grosbeaks and hooded orioles nested in areas with less vegetation (total coverage and volume) in the under- and midstory with fewer trees and shrubs in nest-patches (Fig. 5). In contrast, Bell's vireos and northern cardinals generally nested in areas with more vegetation in all height categories.

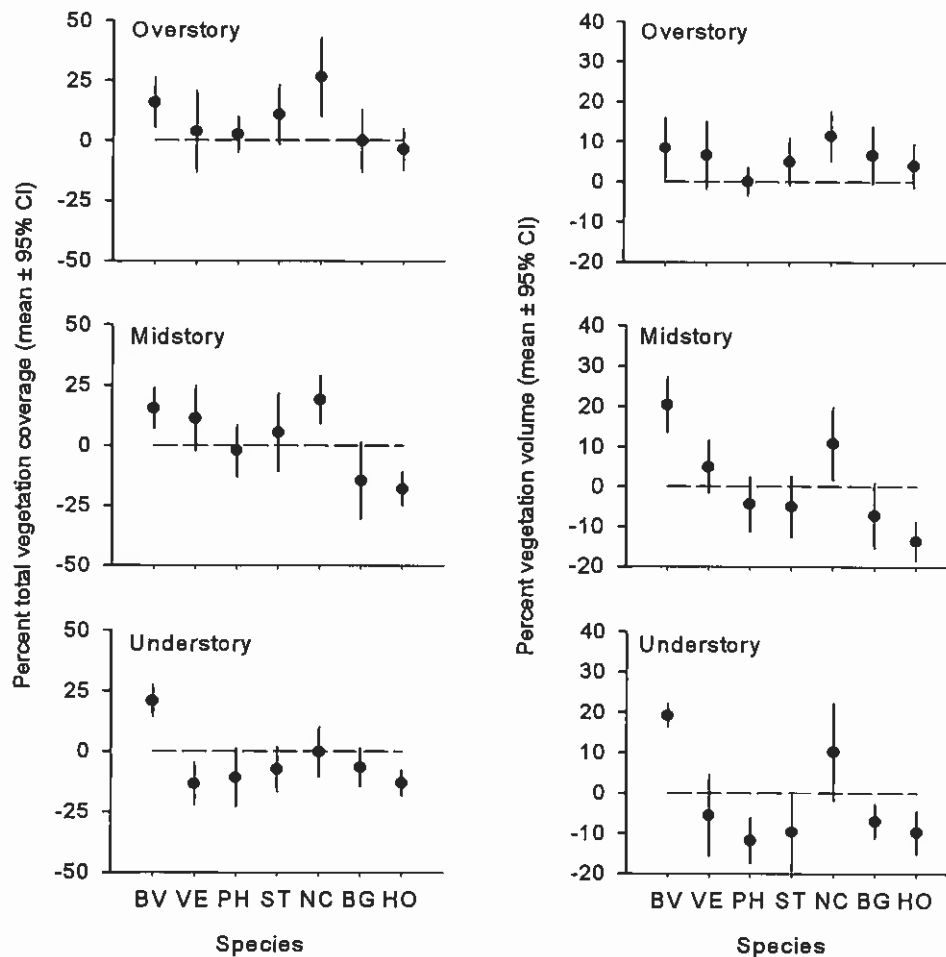


Figure 5. Difference between characteristics at nest-sites and those at nearby random (PR) plots. Mean  $\pm$  95 % confidence interval above or below zero indicate value for nest was greater or lesser than random ( $P < 0.05$ , paired  $t$ -tests), respectively. Species codes as in Table 5.

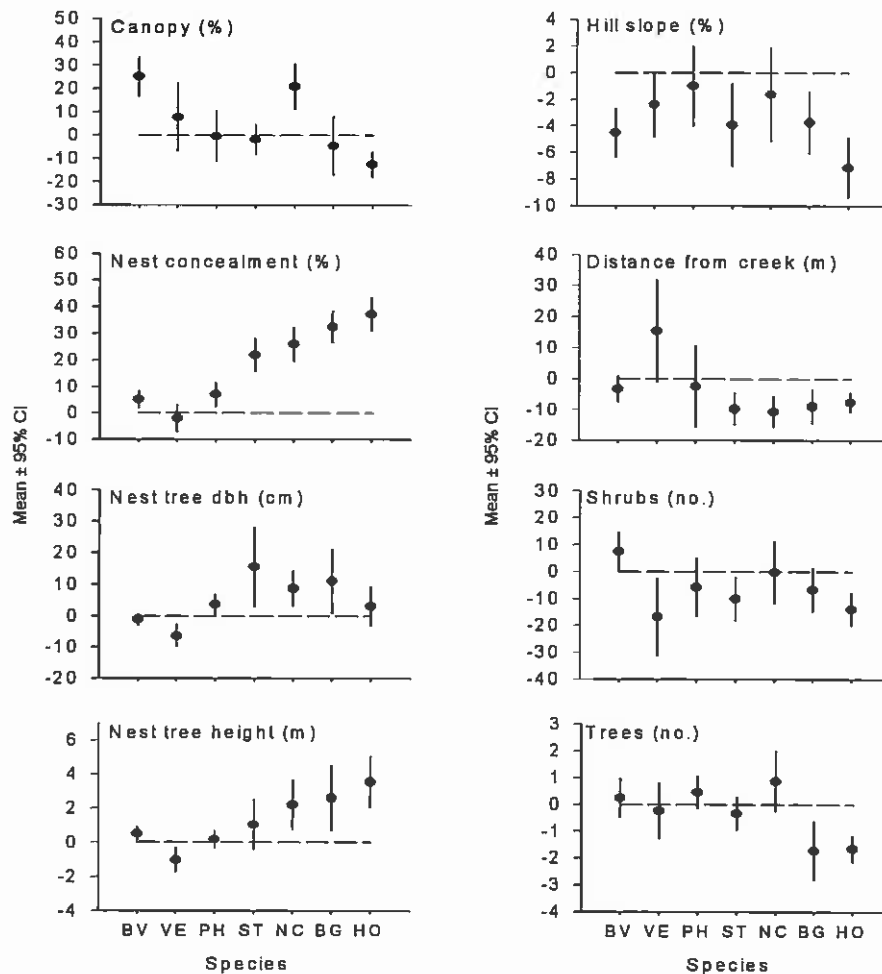


Figure 5. Continued.

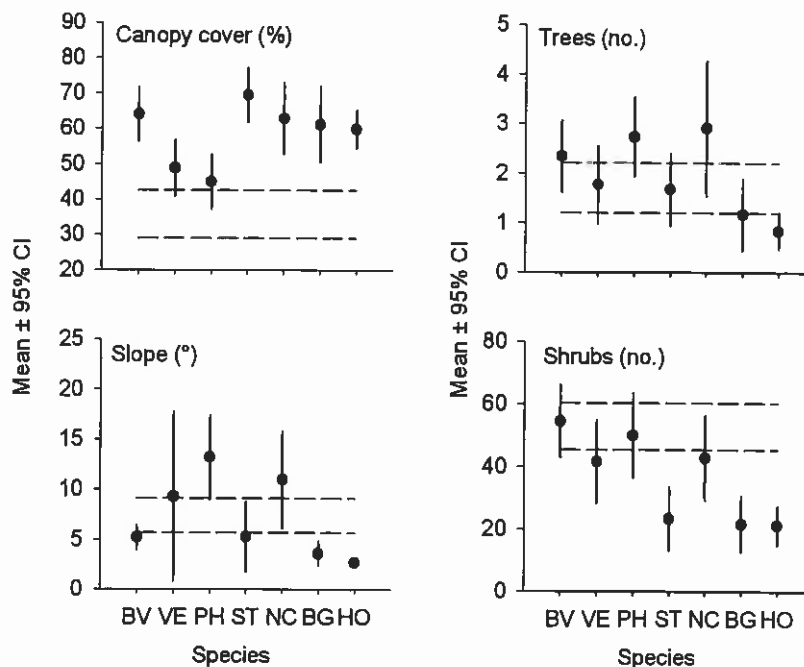
Because many characteristics at nest-patches differed from random for most species ( $P < 0.05$ , paired  $t$ -tests), identifying the most important environmental characteristics was difficult. However, when all characteristics were considered simultaneously, to reduce the effects of intercorrelation, the number of seemingly influential characteristics decreased (Table 5). Both blue grosbeaks and hooded orioles nested in areas with more sycamore coverage in the overstory, and Bell's vireos nested in areas with more netleaf hackberry coverage and vegetation volume in the understory. For example, the odds of a Bell's vireo nesting in an area approximately doubled for every 15% increase in vegetation volume in the understory.

### Within-canyon habitat selection

Every environmental characteristic measured within-canyon, except the number of trees, percent herbaceous ground cover, and total vegetation coverage in the midstory, differed from random ( $P < 0.05$ , two-sample  $t$ -tests) for at least one species (Fig. 6). The largest and most consistent differences between nests and CR plots were for percent canopy cover and vegetation volume in the overstory, where all species except

**Table 5.** Habitat characteristics that distinguished between nest and nearby random (PR) plots, using case-controlled logistic regression.

Species	Habitat Characteristic	Parameter estimate	SE	$\chi^2$	P	Odds ratio
Bell's vireo	Netleaf hackberry coverage in the understory (log)	0.014	0.0061	5.2	0.022	1.014
	Vegetation volume in the understory	0.140	0.0524	7.1	0.008	1.150
Summer tanager	Distance from creek	-0.128	0.0668	3.7	0.055	0.880
Northern cardinal	Distance from creek	-0.102	0.0442	5.3	0.022	0.903
Blue grosbeak	Sycamore coverage in the overstory (log)	0.003	0.0013	4.3	0.039	1.003
Hooded oriole	Sycamore coverage in the overstory (log)	0.005	0.0020	5.1	0.024	1.005
	No. trees within 5 m of nest	-1.785	0.8693	4.2	0.040	0.168



**Figure 6.** Comparison of nest-sites characteristics to those available within-canyon (CR plots). Nest means  $\pm$  95% confidence intervals. Area between dashed lines indicate 95% confidence interval for CR plots. Species codes as in Table 4.

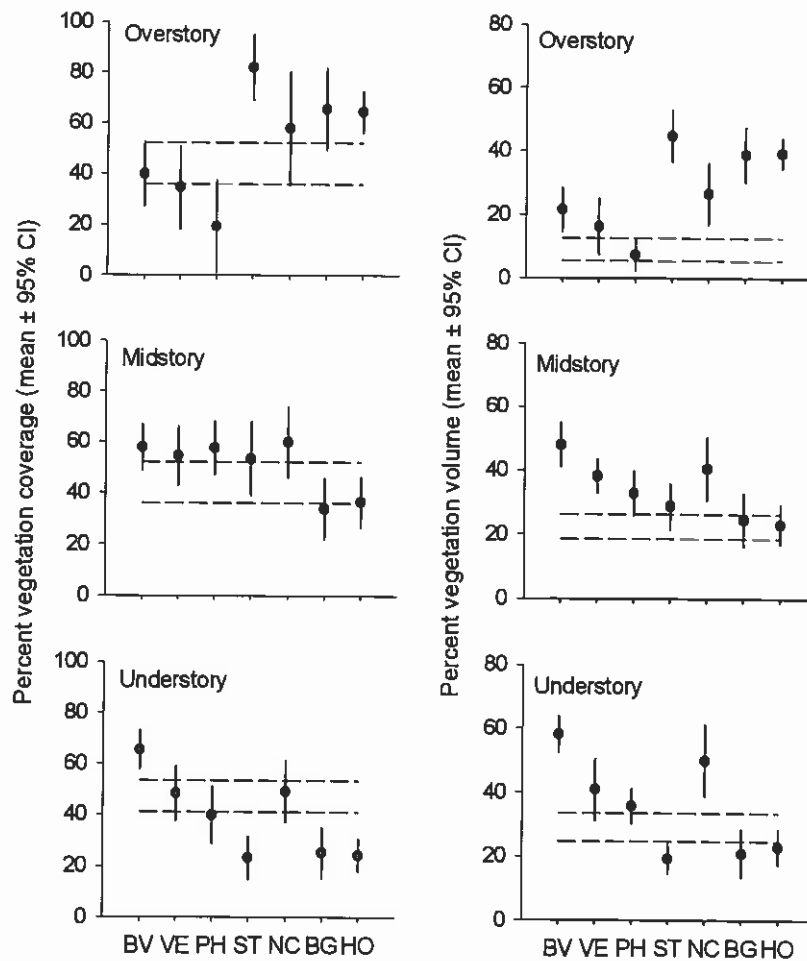


Figure 6. Continued.

verdins and phainopeplas selected areas with considerably more canopy cover and vegetation volume in the overstory than was available randomly (Fig. 6).

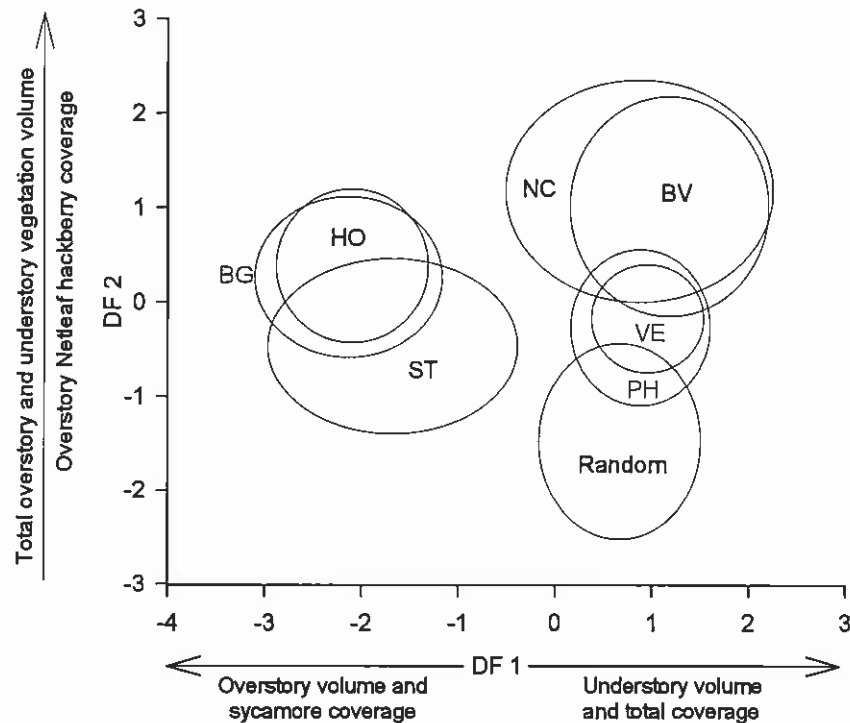
Sycamore coverage and vegetation volume in the overstory as well as vegetation volume and total coverage in the understory explained approximately 50% of the variation among species and CR plots along the first discriminant axis (Table 6). This axis represented a gradient from dense vegetation in the understory to large sycamore trees and greater vegetation in the overstory (Fig. 7). Characteristics used by Bell's vireos, verdins, phainopeplas, and northern cardinals differed little from those available randomly along this axis, whereas those used by summer tanagers, blue grosbeaks, and hooded orioles differed strongly from those available along this axis.

Vegetation volume in both the understory and overstory, and netleaf hackberry coverage and total coverage in the overstory explained approximately 25% of the variation among species and CR plots along the second discriminant axis (Table 6). This axis represented a gradient from more complex to less complex vertical vegetation structure. Characteristics at Bell's vireo and northern cardinal nests departed most strongly from vegetation characteristics available along this axis (Fig. 7).

**Table 6.** Characteristics that differentiated nest and within-canyon random (CR) plots, using canonical discriminant function analysis.

Habitat Characteristic <sup>a</sup>	Discriminant Function		
	1	2	3
Hill slope	0.36	0.01	-0.44
Vegetation volume			
Understory	0.63	0.67	0.18
Overstory	-0.62	0.41	-0.09
Vegetation coverage -			
Total	0.64	0.19	0.34
Succulents	0.25	-0.30	-0.40
Vegetation coverage -			
Total	-0.47	0.36	-0.18
Netleaf hackberry	0.20	0.40	0.16
Sycamore	-0.83	0.32	0.11
Mesquite	0.37	0.21	-0.43
Percent variance explained	49.6	25.3	11.7

<sup>a</sup> See Appendix A for scientific names of plants and groups.



**Figure 7.** Distribution of nest and random (CR) plot scores for first two discriminant functions (DF1 and DF2). Ellipsoids are SD of scores along each axis. Species codes as in Table 4. Arrows indicate direction of increasing values for vegetation characteristics influencing axes strongly (Table 6).

Coverage of succulents in the understory, coverage of mesquites in the overstory, and percent hill slope explained approximately 12% of the variation among species and CR plots along the third discriminant axis (Table 6). This axis represented a gradient from riparian to upland vegetation associations. Characteristics used by phainopeplas, that nested primarily in the desert-scrub vegetation association, were furthest from available along this axis, and those used by verdins and summer tanagers also differed considerably from random.

Habitat selection, as measured by Mahalanobis distances from CR plots, ranged from 4.4 for verdins to 11.0 and 11.2 for blue grosbeaks and hooded orioles, respectively, and was intermediate for phainopeplas (6.4), Bell's vireos (6.6), northern cardinals (8.2), and summer tanagers (9.9).

## DISCUSSION

We found considerable interspecific differences in the degree of selection of nesting habitat at both the nest-patch and within-canyon scales. At the nest-patch, characteristics of phainopepla nests differed little from available characteristics whereas those at Bell's vireo nests differed considerably compared to the degree of selection within-canyon (Figs. 5, 6). At both spatial scales, verdins nested in areas that were most similar to those available whereas hooded orioles and blue grosbeaks nested in areas that were most dissimilar (Figs. 5, 6).

Riparian vegetation, particularly sycamore and netleaf hackberry, was uncommon and selected heavily by most species, particularly Bell's vireos, northern cardinals, blue grosbeaks, hooded orioles, and summer tanagers (Tables 4, 5, Fig. 4). Riparian vegetation is preferred nesting habitat by a disproportionate number of species in many ecotonal vegetation communities containing both riparian and adjacent vegetation types (e.g., Carothers et al. 1974, Bock and Bock 1984, Knopf 1985, Szaro and Jakle 1985, Finch 1989, McGarigal and McComb 1992). Riparian vegetation often has greater volume and structure than upslope areas and therefore provides an abundance of well concealed nest-sites that offer protection from weather and predators (Bock and Bock 1984). In the southwestern U.S., riparian vegetation is distributed sparsely and patchily along narrow corridors and these highly heterogeneous areas provide the majority of nesting sites.

We found that several structural characteristics, including vegetation volume and coverage, were consistently selected by most species. At both spatial scales, Bell's vireos and northern cardinals nested in areas with higher vegetation volume (Figs. 5, 6), and summer tanagers, blue grosbeaks, and hooded orioles nested in areas with less vegetation volume in the under- and midstory, but higher vegetation volume in the overstory (Figs. 5, 6). These consistent patterns suggest that vegetation structure is a most important characteristic of nesting habitat, and increased amounts of vegetation at varying heights increases bird species diversity in an area.

Within a species' geographic range, structural characteristics of vegetation are good predictors of that species' presence (Pitelka 1941, Weins 1985), suggesting that vegetation structure is an important cue for selecting nesting habitat. For example, throughout its geographic range, Bell's vireos nest consistently in dense, patchy riparian vegetation, but the plant species used as nesting substrate varies considerably (e.g., Barlow 1962, Bent 1965, Brown and Trosset 1989, Olson and Gray 1989, Brown 1993). Consequently, nest placement is explained proximally by presence of specific structural characteristics of the environment such as vegetative cover and volume.

Blue grosbeaks typically nest close to the ground in riparian areas with dense understory vegetation and little canopy cover, often in dense thickets or hedgerows (Bent 1968, Whitmore 1975, Ehrlich et al. 1988, Rosenberg et al. 1991, Staab 1995, Averill 1996). A previous study of canyon bird communities in southern

Arizona found that blue grosbeaks were more abundant in areas without sycamores than in those with sycamores (Bock and Bock 1984). In my study, by contrast, blue grosbeaks nested high in large sycamores (see *Nest-site Selection and Reproductive Success*) in areas with less vegetation in the understory (Fig. 5).

Vertical nest placement is thought to have evolved through competition and nest predation, thus systematic differences in vertical nest placement (and by extension vegetation structure) are rare (Martin 1988). Deviations from what we believe to be static and evolutionarily refined characteristics suggest that habitat selection “programs” (Mayr 1974) for nest-sites by some passerines may be more dynamic than thought previously. Consequently, a species with the ability to change nest location will be able to occupy a broader range of vegetation types. For example, the consistent nest-site characteristics of Bell's vireos across their geographic range noted earlier implies that they have a narrow range of nesting conditions, however, species such as the blue grosbeak may be considerably more flexible. This may help explain why blue grosbeak populations are stable or increasing while Bell's vireo populations are declining precipitously in the lower Colorado River valley (Rosenberg et al. 1991).

Ambient air temperature probably has an important influence on the nest-site selection process in extreme environments as in the desert southwest. Birds have evolved physiological and behavioral adaptations to cope with these challenges (e.g., Walsberg 1993) that would likely be manifested in nest type and placement. For example, verdins build a dome-shaped nest (Ehrlich et al. 1988), which may allow them to nest in areas exposed to solar radiation (Ricklefs and Hainsworth 1969, Austin 1976). Accordingly, we found verdins to be the species least selective of vegetation and the only species that did not select areas with greater nest concealment (Fig. 5). Further, all species except verdins and phainopeplas selected areas with greater vegetation volume within the height category in which they placed their nests, suggesting that, although verdins (and perhaps phainopeplas) can ameliorate the negative effects of solar radiation, other species in this study are likely choosing dense areas of vegetation for shade. The influence of predators on nest placement, however, may produce similar patterns.

Nest-site selection is, in part, a function of what investigators chose to measure and therefore believe to be important to animals. A myriad of other factors may influence individual choices, however, such as predator trails, past nesting attempts, and availability of food resources within foraging distance.

Understanding the habitat-selection process and proximate cues that attract species to an area is essential information for land managers, particularly for managing species in decline. By determining critical resources, managers may be able to identify and manipulate these vegetation components to enable species to settle and reproduce. Ultimately, the value of management efforts should be judged on the contribution of areas to both elicit a settling response in individuals and provide conditions necessary for reproductive success (see *Nest-site Characteristics and Reproductive Success*).

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## CANYON-LEVEL HABITAT ASSOCIATIONS

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### INTRODUCTION

Although many environmental factors influence bird communities, vegetation characteristics are one of the most important predictors of avian community structure (James 1971). Important vegetation characteristics include vertical structure (MacArthur and MacArthur 1961, James 1971, Cody 1981, Mills et al. 1991), horizontal patchiness (Roth 1976, Kotliar and Weins 1990), and floristics (Rice et al. 1984, Strong and Bock 1990).

In southern Arizona, riparian areas comprise <0.5% of the landscape, yet support much of Arizona's bird species diversity (Johnson et al. 1977). Past research on birds in these riparian areas focused on communities dominated by cottonwood (*Populus fremontia*), willow (*Salix* sp.), and exotic saltcedar (*Tamarix chinensis*) along the Colorado River and other major river courses (Carothers et al. 1974, Anderson and Ohmart. 1977, Stamp 1978, Szaro 1980, Rice et al. 1984). Little research has focused on mid-elevation (1200 to 1700 m) riparian areas where Sonoran desert-scrub grades into Madrean evergreen woodland (see Strong and Bock 1990). Hence, little information exists about the diversity, vegetation associations, and breeding habitat of birds in this biologically rich zone.

We examined vegetation associations of breeding bird communities in three canyons in southern Arizona. Our objectives were to assess the contribution of vegetation characteristics to bird abundance and diversity, and assess patterns evident in the local bird communities and local vegetation features.

### METHODS

#### Bird-counts

In 1997 and 1998, we censused birds at 45 count points (hereafter referred to as points),  $\geq 200$  m apart along the creeks of each canyon (27 in Brown, 9 in Ramonote, and 9 in Lone Dog). We counted birds at points using a form of the variable-circular plot method (Reynolds et al. 1980), identified each bird to species and sex, and assigned each to a distance category. Distances were recorded in 5-m increments for the first 100 m and 10-m increments from 100 to 150 m. Counts were 10 minutes in duration at each point and began 20 minutes before sunrise and ended no later than three hours after sunrise or when bird activity declined. In both 1997 and 1998 we performed four counts at each point between 15 April and 15 July, peak breeding season for most birds in these areas.

#### Vegetation sampling at points

We measured 14 variables at 10 sample points located randomly within 100 m of each point. We measured percent canopy cover using a spherical densiometer. We estimated percent herbaceous cover (in 5% increments) within a 1-m radius and recorded total number of shrub species within a 5-m radius. We used the point quarter method (Cottam and Curtis 1956) to estimate density of trees  $>8$  cm diameter at breast height (dbh); at each sample point we recorded distance and dbh of all trees.

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To estimate vegetation volume, we used a method similar to that of McGarigal and McComb (1992). Within a 5-m radius circle centered on the sample point, we estimated the volume of vegetation within three height strata: 0-1.5 m (understory), 1.5-4.0 m (midstory), and >4 m (overstory). We estimated percent vegetation volume of leaves and branches (excluding tree trunks) by extending an imaginary cylinder from the bottom to top of each strata, then we estimated the percentage of this volume that was filled with vegetation.

## Data Analysis

We characterized birds at each point using three community measures: total number of species (richness), Shannon's diversity index (diversity), and total number of individuals (overall abundance). We included all birds detected within 150 m of each point. We estimated tree density (no. stems / ha) using program QUARTER (Krebs 1989). We used minimum-variance cluster analysis (Ward's method) on the abundance of each species at each point to organize points into homogeneous groups. We used analysis of variance (ANOVA) to compare bird measures among groups and used the Tukey-Kramer procedure to separate means. To identify vegetation characteristics that best explained each community measure, we used stepwise multiple linear regression ( $P < 0.10$  for entry). For each vegetation characteristic included in the model, we calculated an estimate (and standard error) of the regression coefficient and  $R^2$  to evaluate the explanatory power of each variable in predicting bird measures.

We used principal components analysis to summarize species relationships. We used cumulative abundance of each bird species at each point and used the correlation matrix for the analysis. To assess associations among species and vegetation, we correlated principal component scores with vegetation measures from each point.

## RESULTS

### Bird communities and habitat associations

Four ecologically distinct groups of bird census points emerged based on similarities of bird species at those points (Table 7). Group 1 consisted of upper-elevation points in Brown Canyon, an area with a high density of oak with some juniper and sycamore. Group 2 consisted of all points in Lone Dog and Ramonote Canyons combined. These canyons had high densities of oak, juniper, and mesquite, and low shrub diversity. Group 3 consisted primarily of intermediate-elevation sample points in Brown Canyon, areas with low to moderate vegetation densities and little overstory vegetation resulting from relatively low tree density. The most common trees here were oak and mesquite with some netleaf hackberry and sycamore. Group 4 consisted of lower-elevation points in Brown Canyon, areas with high vegetation volume in all three height strata and corresponding high density of mesquite, netleaf hackberry, and sycamore. All three community measures differed among groups (Table 8). Group 3 differed most from other groups and had highest species richness and second highest overall abundance (Table 8). Groups 1 and 2 were similar for all measures, and Groups 3 and 4 differed only with regards to diversity.

**Table 7.** Vegetation characteristics averaged for all bird-count points within Groups. Groups identified using cluster analysis on abundance of each bird species at each point. Brown, Lone Dog, and Ramonote Canyons, Arizona, 1997 and 1998

Vegetation Characteristic	Group							
	1		2		3		4	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Herbaceous cover	22.1	1.8	26.0	1.9	23.0	2.6	26.6	1.9
Understory vegetation volume	11.3	1.2	11.4	0.6	15.8	1.3	19.8	0.7
Midstory vegetation volume	12.8	0.5	13.1	0.6	10.6	1.4	17.3	0.7
Overstory vegetation volume	8.1	1.2	6.6	0.6	6.3	1.3	8.5	0.8
Canopy cover	59.1	2.9	51.1	3.3	39.7	5.4	57.5	2.9
Shrub species	6.6	0.3	4.0	0.2	5.8	0.20	6.7	0.18
Tree density (per hectare)								
Juniper	2.9	0.8	11.0	2.7	1.1	0.7	0	0
Walnut	15.0	3.4	0	0	3.9	2.0	1.5	0.6
Mesquite	8.1	6.0	32.3	7.1	48.4	6.4	90.9	8.4
Hackberry	0.7	0.7	0	0	14.1	6.5	34.0	4.1
Oak spp.	91.1	14.5	99.6	14.2	34.0	9.4	7.0	1.5
Pine	0.7	0.3	0.3	0.3	0	0	0	0
Sycamore	5.4	2.3	0	0	16.1	3.5	20.9	3.7
Manzanita	0	0	6.0	1.4	0	0	0	0
Other	12.6	3.9	6.5	2.1	1.9	1.9	13.1	2.0
Total	136.5	14.5	155.6	14.6	119.5	14.2	167.7	11.8

**Table 8.** Bird measures per bird-count point, averaged within groups of points and compared using ANOVA. Groups formed using cluster analysis based on abundance of each bird species at each point. Groups with same superscripted letter for each bird measure do not differ (using Tukey-Kramer multiple pairwise procedure).

Bird measure	Group								F	P
	1		2		3		4			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE		
Species richness	24.1 <sup>a</sup>	1.22	23.8 <sup>a</sup>	0.61	29.0	0.90	26.3	0.90	7.5	0.0004
Overall abundance	71.0 <sup>a</sup>	3.81	75.5 <sup>a</sup>	1.45	84.2 <sup>b</sup>	3.04	87.7 <sup>b</sup>	2.64	9.3	<0.0001
Species diversity	18.9 <sup>a</sup>	1.29	18.2 <sup>a</sup>	0.55	23.3	0.77	18.0 <sup>a</sup>	0.80	8.9	0.0001

## Vegetation characteristics and bird community measures

Vegetation volume in the understory had a strong positive influence and density of mesquite had a weak but consistent negative influence on all bird community measures (Table 9). Density of netleaf hackberry also had a strong positive influence on overall abundance. Density of pine (*Pinus spp.*) trees had a strong negative influence on species richness, and density of walnut trees had a strong negative influence on overall abundance. Vegetation volume in the midstory had a strong negative influence on diversity.

## Bird species-habitat gradients

Vegetation volume in the understory and density of mesquite, hackberry, sycamore, and oaks influenced the ordination of birds along the first principal component axis (Table 10). This axis represented an elevational and vegetation gradient; species commonly found in riparian and desert-scrub vegetation loaded positively on this axis and species commonly associated with oak woodlands loaded negatively on this axis (Fig. 8). For example, Bell's vireos, blue grosbeaks, and yellow-breasted chats are riparian obligate species and were loaded positively. Conversely, species such as bridled titmouse, black-headed grosbeak, and acorn woodpecker are associated with oak woodlands and were loaded negatively on this axis.

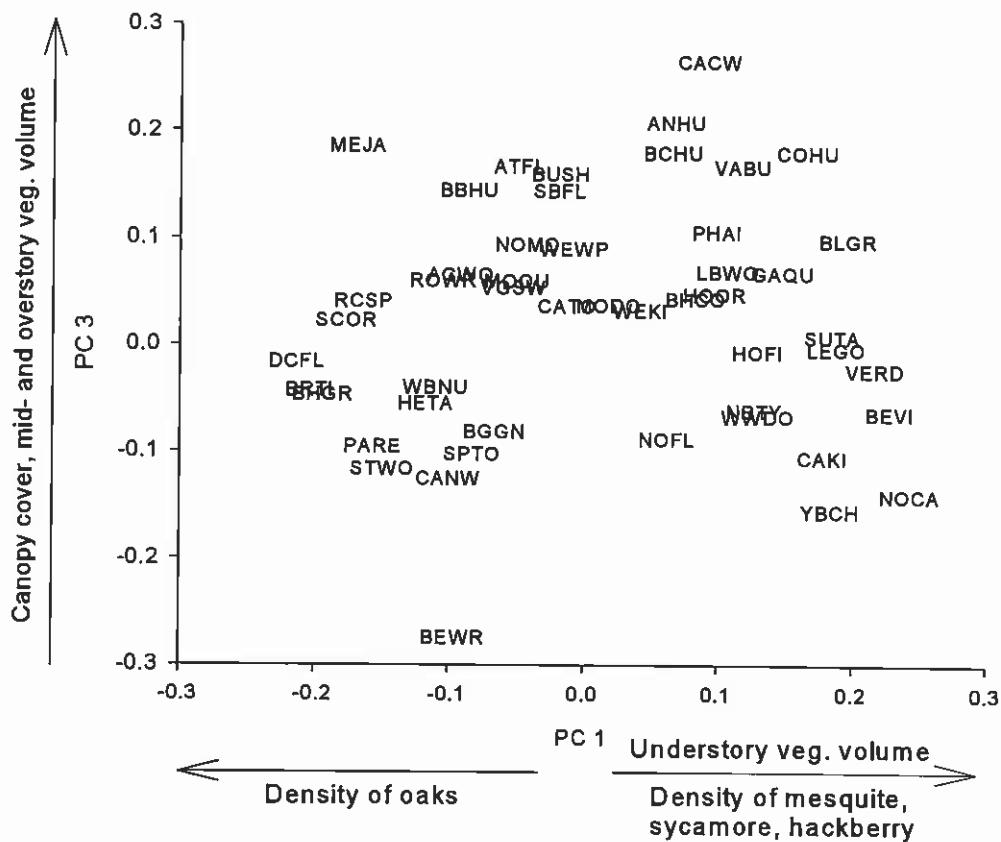
The amount of canopy cover and vegetation volume in the mid- and overstory most influenced the ordination of bird species along the third principal component axis (Table 10). This axis represented a structural gradient from an open to dense mid- and overstory. Species associated with an open canopy, such as cactus wrens and Abert's towhees, were loaded positively on this axis and species associated with a more closed canopy, such as Bewick's wren and painted redstart were loaded negatively along the third axis.

**Table 9.** Vegetation characteristics that predicted bird community measures, using multiple linear regression. Models made using bird measures from all bird-count points.

Bird measure	Explanatory variables	Coefficient	SE	R <sup>2</sup>
Species richness	Understory vegetation volume	0.526	0.110	0.620
	Density of mesquite trees	-0.060	0.012	
	Density of pine trees	-1.009	0.447	
	Density of oak trees	-0.020	0.008	
	Density of other trees	-0.158	0.040	
Overall abundance	Understory vegetation volume	1.329	0.296	0.671
	Density of mesquite trees	-0.097	0.034	
	Density of hackberry trees	0.279	0.076	
	Density of walnut trees	-0.388	0.148	
	Density of other trees	-0.242	0.113	
Species diversity	Understory vegetation volume	0.472	0.116	0.434
	Midstory vegetation volume	-0.371	0.139	
	Density of mesquite trees	-0.036	0.013	

**Table 10.** Correlation of vegetation variables with first three principal components from correlation matrix using bird species.

Variable	Principal Component		
	1	2	3
<b>Mean</b>			
Canopy cover	-0.08	0.07	-0.68
No. shrub species	0.49	0.45	0.11
Understory vegetation volume	0.83	0.01	0.02
Midstory vegetation volume	0.40	-0.20	-0.59
Overstory vegetation volume	0.11	0.15	-0.60
<b>Density</b>			
Velvet mesquite	0.74	-0.26	0.00
Arizona sycamore	0.69	0.18	-0.18
Netleaf hackberry	0.82	0.06	-0.38
Arizona walnut	-0.23	0.55	-0.16
Manzanita	-0.35	-0.49	0.14
Oaks	-0.78	0.01	-0.08
<b>Variance explained (%)</b>	<b>19.7</b>	<b>8.8</b>	<b>6.7</b>



**Figure 8.** Ordination of bird species along first and third principle components (PC 1 and PC 3) from PCA, based on the correlation matrix. See Table 10 for correlation scores and Appendix D for key to species abbreviations.

## DISCUSSION

We found that complex sets of environmental characteristics influenced avian communities in canyons of the desert southwest. In general, dense vegetation in the understory, often found in riparian areas, was an important predictor of bird diversity (Table 9). Increased vertical vegetation structure plays an important role in increasing avian diversity because areas with high vegetation structure provide more sites for foraging, nesting, and protection from predators (MacArthur & MacArthur 1961, Whitmore 1975).

Heterogeneous distribution of structural and floristic resources may also promote high levels of bird diversity (Weins 1985), which may explain the high diversity and abundance of birds at points that comprised Group 3. This area in Brown Canyon is ecotonal between Sonoran desert-scrub and Madrean evergreen woodland, and may reflect the occurrence of bird species common to both vegetation types.

In addition to structural attributes of an environment, birds are influenced by plant species composition (Rice et al. 1983), and we found strong support for the influence of floristics on bird communities. For example, there appeared to be gradients (i.e. axes) that were largely determined by the dominant plant species or vegetation type (i.e., oak woodland vs. desert scrub) and bird species were distributed along these axes according to their general habitat associations (Table 10, Fig. 8).

Riparian trees are important for many bird species in arid and semi-arid environments (e.g., Carothers et al. 1974, Anderson & Ohmart 1977, Johnson et al. 1977, Bock & Bock 1984). These trees, with their large volume and structure, provide more places for foraging and nesting, as well as support for prey (Bock & Bock 1984). Brown Canyon was the only canyon with typical riparian trees (sycamore and desert hackberry). Surprisingly, sycamore did not predict bird diversity or abundance (Table 9) and was not correlated strongly with any principal component axis (Table 10). Sycamore were used heavily as a nesting substrate, however, by hooded orioles, blue grosbeaks, and summer tanagers (see *Nest-site Characteristics and Reproductive Success* and *Nest-site Selection*). These findings demonstrate the need to isolate specific resources used by vertebrates in habitat studies rather than simply correlating community measures with characteristics of the environment.

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## RECOMMENDATIONS

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We found that riparian vegetation of Brown Canyon was a vital component for the breeding bird community that distinguished it from nearby canyons in the Atascosa Mountains. In particular, sycamore trees were important for many species. Unfortunately, sycamore regeneration in Brown Canyon is poor and this may be cause for concern. Also, reproductive success was extremely low, though factors explaining this phenomenon were difficult to identify. Finally, although brown-headed cowbird parasitism did not appear to be a problem for the community as a whole, it was for Bell's vireos. Bell's vireo populations in parts of southern Arizona are declining, due in part to high rates of parasitism. To maintain or promote the health of the bird community in Brown Canyon, we recommend the following management practices:

- Foster sycamore regeneration and consider replanting sycamore trees where appropriate. The floodplain area upstream from the Harm House may be an ideal place to test the efficacy of this endeavor because there is potential for supplemental irrigation from the nearby water pump and storage unit.
- Do not maintain bird feeding stations in the canyon during the prime breeding season - April thru July. The only place we observed cowbirds foraging was at these stations and reducing the food supply may reduce the impacts of cowbirds on songbirds in Brown Canyon.

In addition, we recommend the following research and monitoring activities:

- Establish permanent bird-count stations to monitor the bird community. This effort, along with vegetation monitoring, will allow for a better understanding of species and population trends over a longer and more appropriate time period. Also, other characteristics of the community such as nest success and rates of brood parasitism should be monitored concurrently to determine their long-term trends.
  - Initiate a study of the predator community in the canyon. In our study we could determine only reproductive success and could not properly identify the most important nest predators. As such, our understanding of the actual predator community is speculative.
  - Designate the canyon as a long-term ecological research station and begin to define long-term objectives for the understanding, monitoring, and protecting of its biological resources. The faunal and floristic diversity of Brown Canyon are high and somewhat unique in southern Arizona. As such, the area could be an important center from which researchers could study its diversity and ecological processes.
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**LITERATURE CITED**


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**APPENDIX A. Plant species and groups associated with nests and random plots. Groups formed by life-form, floristic, and habitat similarities.**

Group	Plant Species	
	Common Name	Scientific Name
OAKS	Arizona white oak	<i>Quercus arizonica</i>
	Emory oak	<i>Quercus emoryi</i>
	Mexican blue oak	<i>Quercus oblongifolia</i>
	Silverleaf oak	<i>Quercus hypoleucoides</i>
MESQUITE	Velvet mesquite	<i>Prosopis velutina</i>
NL HACK.	Netleaf hackberry	<i>Celtis reticulata</i>
SYCAMORE	Arizona sycamore	<i>Platanus wrightii</i>
AZ WALNUT	Arizona walnut	<i>Juglans major</i>
PINES	Alligator juniper	<i>Juniperus deppean</i>
	Mexican pine	<i>Pinus cembroides</i>
OTHER TREES	Rosewood	<i>Vauquelinia californica</i>
	Soapberry	<i>Sapindus saponaria</i>
LEGUMES	Calclaw acacia	<i>Acacia greggii</i>
	White-thorn acacia	<i>Acacia constricta</i>
	Wait-a-minute bush	<i>Mimosa bluncifera</i>
MISC. HACKBERRY	California buckthorn	<i>Rhamnus californica</i>
	Desert hackberry	<i>Celtis pallida</i>
	Texas mulberry	<i>Morus microphylla</i>
MISC. SHRUBS	Narrowleaf hoptree	<i>Ptelea angustifolia</i>
	Quinine bush	<i>Garrya flavescens</i>
	Skunk bush	<i>Rhus trilobata</i>
	Wright silk tassel	<i>Garrya wrightii</i>
SUCCULENTS	Barrel cactus	<i>Ferocactus wislizenii</i>
	Cholla sp.	<i>Opuntia sp.</i>
	Ocotillo	<i>Fouquieria splendens</i>
	Desert prickly pear	<i>Opuntia phaeacantha</i>
THORNY SHRUBS	Desert olive	<i>Forestiera shrevei</i>
	Grey thorn	<i>Zizyphus obtusifolia</i>
	Berlandier wolfberry	<i>Lycium berlandieri</i>
	Anderson thornbush	<i>Lycium andersonii</i>
BUSHY SHRUBS	Desert broom	<i>Baccharis sarothroides</i>
	Four-wing saltbush	<i>Atriplex canescens</i>
	Hopbush	<i>Dodonaea viscosa</i>

## APPENDIX A. Continued.

BACCHARIS	Arizona baccharis	<i>Baccharis neglecta</i>
	Seep willow	<i>Baccharis salicifolia</i>
CLIMB SHRUBS	Canyon grape	<i>Vitis arizonica</i>
	Clematis	<i>Clematis ligusticifolia</i>
	Poison ivy	<i>Rhus radicans</i>
ASTERS	Brickellia	<i>Brickellia sp.</i>
	Burroweed	<i>Isocoma tenuisecta</i>
	Snakeweed	<i>Gutierrezia sarothrae</i>
	Tetramerium	<i>Tetramerium nervosum</i>
CORAL + COTTON	Turpentine bush	<i>Ericameria laricifolia</i>
	Coral been	<i>Erythrina flabelliformis</i>
	Wild cotton	<i>Gossypium thurberi</i>
AGAVES	Desert Agave	<i>Agave parryi</i>
	Shindagger agave	<i>Agave schottii</i>
	Sotol	<i>Dasylirion wheeleri</i>
HONYSUCKLES	Desert honeysuckle	<i>Anisacanthus thurberi</i>
	Smooth bouvardia	<i>Bouvardia glaberrima</i>
	Long-flowered snowberry	<i>Symphoricarpos longiflorus</i>
	Utah honeysuckle	<i>Lonicera utahensis</i>

APPENDIX B. Number of insects caught in sticky traps (30 cm X 20 cm) at three elevation sites in Brown Canyon, May and June 1998. All sites were sampled during the same three, 24-hour periods with *n* sticky traps per tree species per trap session. Traps were set three per tree. High elevation site was in oak/riparian woodland, Medium and Low elevation sites were in desert scrub/riparian.

Tree species	Elevation								
	High			Medium			Low		
	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE
Arizona walnut	18	139	13						
Velvet mesquite	18	160	16	27	216	20	27	250	21
Netleaf hackberry	18	100	8	27	110	9	27	136	10
Oak spp.	27	98	11	18	112	11	18	108	9
Sycamore	18	211	26	27	251	22	27	166	9

## APPENDIX C. List of known (or potential) nest predators, Brown Canyon, Arizona, 1996-1998.

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**Mammals**

Opossum	<i>Didelphis marsupialis</i>
Coyote	<i>Canis latrans</i>
Grey fox	<i>Urocyon cinereoargenteus</i>
Coati	<i>Nasua nasua</i>
Ringtail	<i>Bassariscus astutus</i>
Spotted skunk	<i>Spilogale putorius</i>
Hooded skunk	<i>Mephitis macroura</i>
Hognose skunk	<i>Conepatus leuconotus</i>
Striped skunk	<i>Mephitis mephitis</i>
Mountain lion	<i>Felis concolor</i>
Bobcat	<i>Felis rufus</i>
Rock squirrel	<i>Citellus variegatus</i>

**Birds**

Cooper's Hawk	<i>Accipiter cooperii</i>
Greater Roadrunner	<i>Geococcyx californianus</i>
Mexican Jay	<i>Aphelocoma ultramarina</i>

**Reptiles**

Clark's spiny lizard	<i>Sceloporus clarki</i>
Mountain spiny lizard	<i>Sceloporus jarrovi</i>
Sonoran whipsnake	<i>Masticophis bilineatus</i>
Western patch-nosed snake	<i>Salvadora hexalepis</i>
Green rat snake	<i>Elaphe triaspis</i>
Gopher snake	<i>Pituophis melanoleucus</i>
Sonoran mountain kingsnake	<i>Lampropeltis pyromelana</i>
Black-necked garter snake	<i>Thamnophis cyrtopsis</i>
Western diamondback	<i>Crotalus atrox</i>
Black-tailed rattlesnake	<i>Crotalus molossus</i>

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**APPENDIX D.** List of bird species recorded during point counts and used in principal components analysis. Brown, Lone Dog and Ramonote Canyons, Arizona, 1997 and 1998.

Code	Species	Scientific Name
GAQU	Gambel's Quail	<i>Callipepla gambelli</i>
MOQU	Montezuma quail	<i>Cyrtonyx montezumae</i>
COHA	Cooper's hawk	<i>Accipiter cooperii</i>
ELTR	Elegant trogon	<i>Trogon elegans</i>
MODO	Mourning dove	<i>Zenaida macroura</i>
WWDO	White-winged dove	<i>Zenaida asiatica</i>
COGD	Common ground-dove	<i>Columbina passerina</i>
GRRO	Greater roadrunner	<i>Geococcyx californianus</i>
YBCU	Yellow-billed cuckoo	<i>Coccyzus americanus</i>
ANHU	Anna's hummingbird	<i>Calypte anna</i>
COHU	Costa's hummingbird	<i>Calypte costae</i>
BBHU	Broad-billed hummingbird	<i>Cyanthus latirostris</i>
BCHU	Black-chinned hummingbird	<i>Archilochus alexandri</i>
VCHU	Violet-crowned hummingbird	<i>Amazilia violiceps</i>
ACWO	Acorn woodpecker	<i>Melanerpes formicivorus</i>
GIWO	Gila woodpecker	<i>Malanerpes uropygialis</i>
LBWO	Ladder-backed woodpecker	<i>Picoides scalaris</i>
STWO	Strickland's woodpecker	<i>Picoides stricklandii</i>
CAKI	Cassin's kingbird	<i>Tyrannus vociferans</i>
WEKI	Western kingbird	<i>Tyrannus verticalis</i>
BCFL	Brown-crested flycatcher	<i>Myiarchus tyrannulus</i>
ATFL	Ash-throated flycatcher	<i>Myiarchus cinerascens</i>
DCFL	Dusky-capped flycatcher	<i>Myiarchus tuberculifer</i>
SBFL	Sulphur-bellied flycatcher	<i>Myiodynastes luteiventris</i>
WEWP	Western-wood pewee	<i>Contopus sordidulus</i>
BLPH	Black phoebe	<i>Sayornis nigricans</i>
SAPH	Say's phoebe	<i>Sayornis saya</i>
WEFL	Western flycatcher	<i>Empidonax occidentalis</i>
COFL	Cordilleran flycatcher	<i>Empidonax minimus</i>
NBTY	Northern beardless-tyrannulet	<i>Camptostoma imberbe</i>
WTSW	White-throated swift	<i>Aeronautes saxatilis</i>
VGSW	Violet-green swallow	<i>Tachycineta thalassina</i>
SCJA	Scrub jay	<i>Aphelocoma coerulescens</i>
MEJA	Mexican jay	<i>Aphelocoma ultramarina</i>
BRTI	Bridled titmouse	<i>Parus wolweberi</i>
BUSH	Bushtit	<i>Psaltriparus minimus</i>
VERD	Verdin	<i>Auriparus flaviceps</i>
WBNU	White-breasted nuthatch	<i>Sitta carolinensis</i>
BEWR	Bewick's wren	<i>Thryomanes bewickii</i>
CANW	Canyon wren	<i>Catherpes mexicanus</i>

Code	Species	Scientific Name
ROWR	Rock wren	<i>Salpinctes obsoletus</i>
CACW	Cactus wren	<i>Campylorhynchus brunneicapillus</i>
BGGN	Blue-gray gnatcatcher	<i>Polioptila caerulea</i>
BTGN	Black-tailed gnatcatcher	<i>Polioptila melanura</i>
NOMO	Northern mockingbird	<i>Mimus polyglottos</i>
CRTH	Crissal thrasher	<i>Toxostoma crissale</i>
CBTH	Curve-billed thrasher	<i>Toxostoma curvirostre</i>
PHAI	Phainopepla	<i>Phainopepla nitens</i>
SOVI	Solitary vireo	<i>Vireo solitarius</i>
BEVI	Bell's vireo	<i>Vireo bellii</i>
BTGW	Black-throated gray warbler	<i>Dendroica nigrescens</i>
PARE	Painted redstart	<i>Myioborus picta</i>
LUWA	Lucy's warbler	<i>Vermivora luciae</i>
YBCH	Yellow-breasted chat	<i>Geothlypis trichas</i>
GTGR	Great-tailed grackle	<i>Quiscalus mexicanus</i>
BHCO	Brown-headed cowbird	<i>Molothrus ater</i>
BRCO	Bronzed cowbird	<i>Molothrus aeneus</i>
HOOR	Hooded oriole	<i>Icterus cucullatus</i>
SCOR	Scott's oriole	<i>Icterus parisorum</i>
SUTA	Summer tanager	<i>Piranga rubra</i>
HETA	Hepatic tanager	<i>Piranga flava</i>
BTSP	Black-throated sparrow	<i>Amphispiza bilineata</i>
RCSP	Rufous-crowned sparrow	<i>Aimophila ruficeps</i>
SPTO	Spotted towhee	<i>Pipilo erythrophthalmus</i>
CATO	Canyon towhee	<i>Pipilo fuscus</i>
ABTO	Abert's towhee	<i>Pipilo aberti</i>
BHGR	Black-headed grosbeak	<i>Pheucticus melanocephalus</i>
BLGR	Blue grosbeak	<i>Gulraca caerulea</i>
INBU	Indigo bunting	<i>Passerina cyanea</i>
LABU	Lazuli bunting	<i>Passerina amoena</i>
VABU	Varied bunting	<i>Passerina versicolor</i>
NOCA	Northern cardinal	<i>Cardinalis cardinalis</i>
HOFI	House finch	<i>Carpodacus mexicanus</i>
LEGO	Lesser goldfinch	<i>Carduelis psaltria</i>