

NEST-SITE CHARACTERISTICS OF OPEN-NESTING BIRDS IN RIPARIAN HABITATS IN IOWA

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ABSTRACT.—We analyzed interrelationships among nest sites of 13 open-nesting bird species of riparian communities in Iowa. Cluster analysis of a Euclidean distance matrix, based on the nesting substrate and mean values of nest-site measurements, identified three nesting assemblages comprising species nesting primarily in trees (six species), shrubs (four), or herbaceous cover (three). Discriminant canonical analyses were used to elucidate relationships among species within each nesting group. Two canonical axes separated most species nesting in trees along gradients of (I) nest and support-structure height and (II) support-limb diameter, distance to periphery of substrate, and nest height. Nest sites of American Robins (*Turdus migratorius*) were not different ($P > 0.05$) from those of Blue Jays (*Cyanocitta cristata*) and Mourning Doves (*Zenaida macroura*), which did differ from each other. Two canonical axes, representing (I) nest and support-structure height and (II) support-limb diameter and cover at the nest, separated all shrub-nesting species except Gray Catbirds (*Dumetella carolinensis*) and Brown Thrashers (*Toxostoma rufum*). One significant ($P < 0.05$) canonical axis, representing nest and relative nest height and cover at the nest, separated Red-winged Blackbirds (*Agelaius phoeniceus*) from Common Yellowthroats (*Geothlypis trichas*) and Song Sparrows (*Melospiza melodia*), which did not differ from each other. Species with similar nest sites tended to have different habitat use patterns. Nest-site analysis should be considered when investigating intra-community relationships among birds. Received 17 Aug. 1985, accepted 26 Dec. 1985.

Considerable effort has been devoted to investigating interspecies relationships within avian communities, but little research has focused on differences in nest-site use at the community level. Nest-site selection is an integral component of habitat selection and may be influenced by interrelationships among species in avian communities. Beecher (1942) provided the first general description of nest-site characteristics within a community. The heights at which birds nest in various habitats have been reported by several authors (Preston 1946, Preston and Norris 1947, Cruickshank 1956, Taylor 1965, DeGraff et al. 1975), but additional nest-site measurements were not provided. More recently, McCrimmon (1978), Collins (1981), Titus and Mosher (1981), MacKenzie et al. (1982), and Clark et al. (1983) have used multivariate methods to investigate relationships among nest sites.

Our objective was to describe the interrelationships among nest sites used by open-nesting species of riparian communities (herein defined as

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TABLE 1
 MEANS (SE) OF VARIABLES MEASURED AT 517 OPEN NESTS OF BIRD SPECIES NESTING IN
 RIPARIAN HABITATS IN IOWA

	Abbreviated name	N	Nest height (m)	Support-structure height (m)	Relative nest height (%)
Tree-nesting species					
Mourning Dove (<i>Zenaida macroura</i>)	MD	58	2.4 (0.2) A ^a	6.0 (0.6) A	47.6 (3.1) A
Eastern Wood-Pewee (<i>Contopus virens</i>)	EWP	20	8.6 (0.6) B	17.5 (0.9) B	49.6 (3.1) AB
Blue Jay (<i>Cyanocitta cristata</i>)	BJ	34	6.1 (0.7) C	13.8 (1.1) BC	44.4 (2.9) A
American Robin (<i>Turdus migratorius</i>)	AR	17	4.7 (0.9) C	9.8 (1.3) AC	49.8 (4.9) AC
Northern Oriole (<i>Icterus galbula</i>)	NO	13	11.0 (0.9) B	20.6 (1.9) B	60.0 (7.0) AD
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	RBG	47	4.2 (0.4) C	7.3 (0.7) A	64.3 (2.9) BCD
Shrub-nesting species					
Gray Catbird (<i>Dumetella carolinensis</i>)	GC	92	1.4 (0.1) A	2.5 (0.1) A	56.9 (1.6) A
Brown Thrasher (<i>Toxostoma rufum</i>)	BT	31	1.2 (0.1) A	2.7 (0.4) A	52.7 (2.6) A
Northern Cardinal (<i>Cardinalis cardinalis</i>)	NC	74	1.4 (0.1) A	2.7 (0.2) A	55.1 (2.1) A
Indigo Bunting (<i>Passerina cyanea</i>)	IB	41	0.6 (0.1) B	1.2 (0.1) B	51.0 (2.2) A
Herbaceous-nesting species					
Common Yellowthroat (<i>Geothlypis trichas</i>)	CY	12	0.1 (0.0) A	1.2 (0.1) A	11.3 (1.7) A
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	RWB	31	0.6 (0.1) B	1.2 (0.2) A	51.7 (2.6) B
Song Sparrow (<i>Melospiza melodia</i>)	SS	12	0.1 (0.1) A	0.8 (0.1) A	11.2 (3.6) A

^a Bonferroni *t*-tests; values within each species assemblage with the same capital letter are not significantly different ($P > 0.05$).

^b Value in brackets indicates sample size if different from that first presented.

TABLE 1
EXTENDED

Cover		Support-limb diameter (cm)	Distance to support (m)	
Above	Below		Trunk	Periphery
2.5 (0.1) A	2.0 (0.1) A	5.7 (0.9) A	0.8 (0.1) [48] ^b A	1.7 (0.1) [54] A
2.4 (0.1) A	1.1 (0.1) A	3.6 (0.2) A	3.8 (0.4) B	1.9 (0.2) A
2.8 (0.1) AB	1.9 (0.1) A	8.5 (0.7) B	1.9 (0.5) [32] A	2.7 (0.2) A
2.8 (0.2) AC	2.0 (0.2) A	7.3 (1.0) AB	1.6 (0.6) [16] A	1.8 (0.3) [16] A
3.5 (0.2) BC	2.3 (0.3) A	0.7 (0.2) C	5.0 (0.9) B	0.8 (0.3) B
3.1 (0.1) BC	2.1 (0.1) A	1.6 (0.1) D	1.2 (0.2) [40] A	0.9 (0.1) [45] B
3.2 (0.1) A	3.1 (0.1) A	1.3 (0.2) A		
3.4 (0.1) AB	3.1 (0.1) AB	1.8 (0.7) A		
3.1 (0.1) A	2.8 (0.1) B	1.0 (0.1) A		
3.9 (0.1) B	3.5 (0.1) B	0.4 (0.1) [24] B		
3.9 (0.1) A	4.0 (0.0) A	—		
2.9 (0.1) B	3.2 (0.2) [28] B	1.0 (0.3) [10]		
3.6 (0.2) A	4.0 (0.0) A	—		

uncultivated land within 250 m of a stream edge). Previously, we have reported on the interrelationships among nest sites of cavity-nesting species (Stauffer and Best 1982).

STUDY AREA AND METHODS

Twenty-eight sites were selected for study in southeastern Guthrie County, Iowa, along Brushy Creek, Beaver Creek, and the Middle and South Raccoon rivers. In choosing study sites, we attempted to sample a broad spectrum of riparian habitats from open hayfields and pasture to closed-canopy woodlands. Characteristics of the study area and the habitats sampled (142 total ha) are detailed in Stauffer and Best (1980).

Field work was conducted from mid-April through mid-July in 1976 and 1977 as part of a study of the avian community (Stauffer and Best 1980). Some nests were found during early morning bird counts on the study sites, but most were located in the morning after counts and during the evening, when we watched nesting behavior and systematically searched suitable areas. We attempted to locate nests of every open-nesting species on each study site. The sample is biased, however, because less well concealed nests and those located in more open sites, where birds could be followed more easily, were probably represented disproportionately.

For each nest, we recorded nest height and height of the supporting substrate, relative nest height (nest height/support height), diameter of supporting limb(s), cover above and below the nest (1 = poor, 2 = fair, 3 = good, 4 = excellent), distance from nest to trunk and substrate periphery (for nests in trees), and life form of nesting substrate (forb, grass, shrub, deciduous sapling or tree, evergreen tree).

Mean values of the variables for each species were calculated. A matrix of Euclidean distances (Pielou 1984:14) between each species pair was calculated using nest, support-structure, and relative nest heights; support-limb diameter; cover above and below the nest; and percentage of nests in substrates of each life form. (Life-form data are presented in Stauffer and Best 1980.) The Common Yellowthroat (scientific names of species are in Table 1) and Song Sparrow were assigned a support-limb diameter value of 0.3 cm, which is approximately the diameter of herbaceous vegetation typically supporting their nests (diameter measurements were not made on herbaceous vegetation). We then conducted a cluster analysis (BMDP1M, Dixon 1983) on the matrix of pair-wise distance values to develop a dendrogram illustrating the relationships among species on the basis of nest-site characteristics.

For each of the three nesting assemblages identified through cluster analysis, we conducted analyses of variance (ANOVA) to test the null hypothesis of no difference among species for each variable. Bonferroni *t*-tests (Ray 1982) were used for multiple comparisons of differences between pairs of species within each assemblage. Canonical discriminant analyses also were conducted to further determine relationships among the species within each nesting group. Only species represented by at least 12 nests were analyzed. Before statistical analyses, data were checked for normality and, when necessary, were transformed to achieve a more normal distribution.

RESULTS AND DISCUSSION

Cluster analysis delineated three assemblages of species, represented by those nesting predominantly in tree, shrub, or herbaceous substrates (Fig. 1). Relationships among species within each of these three groups are addressed below.

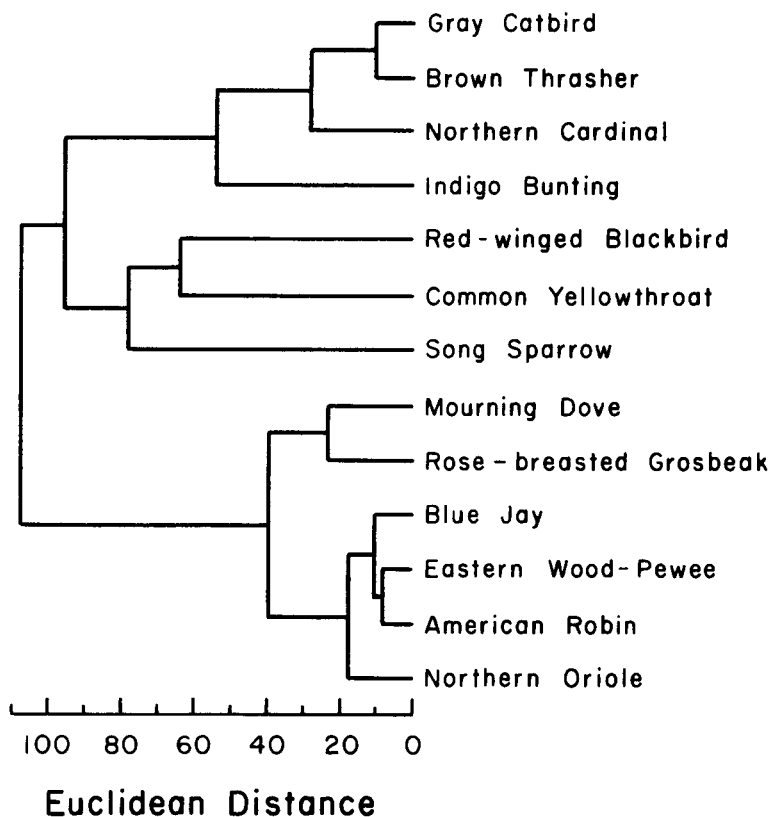


FIG. 1. Dendrogram depicting the relationships among nest sites of 13 open-nesting bird species. Results are based on a cluster analysis of a Euclidean-distance matrix derived from nest-site characteristics.

Univariate analyses.—Nest heights differed ($P < 0.05$) among species within each nesting assemblage (Table 2). Nests of tree-nesting species were distributed in three strata, with the Northern Oriole and Eastern Wood-Pewee nesting at the highest level and the Mourning Dove nesting at the lowest level (Table 1) (see also DeGraff et al. 1975). Indigo Buntings nested lower than other species in the shrub-nesting group, and among the herbaceous-nesting species, Red-winged Blackbirds had nests in the highest locations. Nest height was positively related to support-structure height and relative nest height for all nesting groups but negatively correlated with cover above and below the nest; higher nests were less well concealed (Table 3). For shrub- and herbaceous-nesting species, nest height also was correlated with support-limb diameter.

TABLE 2

F STATISTICS FROM ONE-WAY ANOVA'S TO TEST THE NULL HYPOTHESES OF NO DIFFERENCE IN NEST-SITE CHARACTERISTICS AMONG SPECIES WITHIN EACH NESTING GROUP

Variable	Tree-nesting species (df = 5,158)	Shrub-nesting species (df = 3,234)	Herbaceous-nesting species (df = 2,52)
Nest height	25.87 ^a	27.30 ^a	33.12 ^a
Support-structure height	20.81 ^a	20.68 ^a	3.02
Relative nest height	6.13 ^a	1.57	67.34 ^a
Cover above nest	5.57 ^a	8.63 ^a	10.89 ^a
Cover below nest	5.98 ^a	8.78 ^a	7.23 ^b
Support-limb diameter	36.21 ^a	16.78 ^a	
Distance to trunk	8.44 ^a		
Distance to periphery	14.69 ^a		

^a Indicates $P < 0.001$.

^b Indicates $P < 0.01$.

Support-structure height followed trends similar to those for nest height (Table 1), and differed among tree-nesting species and among shrub-nesting species (Table 2). The negative correlation of support-structure height with relative nest height for tree and shrub nesters (Table 3) implies that nests were placed relatively lower in taller plants. Within each nesting group, support-limb diameter was positively correlated with support-structure height, indicating that nests were supported by larger limbs in taller substrates (Table 3).

Relative nest height differed for tree- and herbaceous-nesting species but not for shrub nesters (Table 2). Northern Orioles and Rose-breasted Grosbeaks nested relatively higher than some of the other species in the tree-nesting assemblage; Red-winged Blackbirds nested relatively higher than the other two species using herbaceous cover (Table 1). Nests placed relatively higher in trees and shrubs were supported by smaller limbs (Table 3).

Cover above and below the nest differed within all nesting assemblages (Table 2); these two measures were significantly correlated (Table 3). For tree and shrub nesters, cover above the nest was greater than cover below the nest; the opposite was true for species nesting in dense herbaceous vegetation (Table 1). Cover above the nest was negatively related to support-structure height for shrub nesters, and cover below the nest correlated negatively with support-structure height for both shrub- and tree-nesting species (Table 3). Thus, nests placed in taller woody substrates tended to be less well concealed, primarily because nests were placed relatively lower in taller substrates. In contrast, as height of herbaceous substrates in-

TABLE 3

SIGNIFICANT ($P < 0.05$) CORRELATIONS BETWEEN VARIABLES MEASURED AT NEST SITES OF SPECIES IN THE TREE- ($N = 189$), SHRUB- ($N = 238$), AND HERBACEOUS- ($N = 55$) NESTING GROUPS

	Nesting group	NH ^a	SSH	RNH	CAN	CBN	SLD	DT
Support-structure height	Tree	0.83 ^b						
	Shrub	0.80 ^b						
	Herbaceous	0.37 ^b						
Relative nest height	Tree	0.21 ^b	-0.34 ^b					
	Shrub	0.40 ^b	-0.21 ^b					
	Herbaceous	0.81 ^b						
Cover above nest	Tree	-0.16 ^c		0.26 ^b				
	Shrub	-0.19 ^c	-0.24 ^c					
	Herbaceous	-0.35 ^c		-0.38 ^b				
Cover below nest	Tree	-0.19 ^c	-0.36 ^b	0.33 ^c	0.48 ^b			
	Shrub	-0.27 ^b	-0.22 ^b		0.56 ^b			
	Herbaceous	-0.55 ^b	0.50 ^b	-0.43 ^b	0.58 ^b			
Support-limb diameter	Tree		0.23 ^b	-0.22 ^b	-0.24 ^b	-0.22 ^b		
	Shrub	0.57 ^b	0.68 ^b	-0.13 ^c	-0.21 ^b	-0.16 ^c		
	Herbaceous	0.62 ^b	0.49 ^b					
Distance to trunk	Tree	0.55 ^b	0.61 ^b			-0.28 ^b		
Distance to periphery	Tree	0.26 ^b	0.33 ^b	-0.25 ^b		-0.21 ^b	0.60 ^b	0.30 ^b

^a Nest height.^b Indicates $P < 0.01$.^c Indicates $P < 0.05$.

creased, cover below nests increased (Table 3). For tree nesters, cover both above and below the nest increased with greater relative nest height (Table 3), probably because relatively higher nests tended to be in the foliage zone of the canopy and thus were concealed better. The opposite relationship was found in herbaceous-nesting species; nests placed relatively higher in the nesting substrate had less cover (Table 3). Cover both above and below nests in trees and shrubs was negatively correlated with support-limb diameter. Generally, larger limbs had fewer small twigs and less foliage than did smaller limbs; thus, nests placed on larger limbs were less concealed.

The diameter of supporting limbs differed within the shrub- and tree-nesting assemblages (Table 2). The greatest variation in support-limb diameter occurred among the tree nesters, for which mean support diameter ranged from 0.7 cm for the Northern Oriole to 8.5 cm for the Blue

TABLE 4
CORRELATIONS OF NEST-SITE VARIABLES WITH THE FIRST TWO CANONICAL FUNCTIONS
DERIVED FOR EACH SPECIES GROUP

Variable	Canonical function					
	Tree-nesting species		Shrub-nesting species		Herbaceous-nesting species	
	I	II	I	II	I	II
Nest height	-0.56	0.74	0.90	0.09	0.85	0.49
Support-structure height	-0.36	0.86	0.81	-0.05	0.03	0.68
Relative nest height	-0.37	-0.23	0.21	0.18	0.97	-0.01
Cover above nest	-0.31	-0.14	-0.53	0.37	-0.61	0.34
Cover below nest	-0.11	-0.26	-0.43	0.79	-0.53	0.04
Support-limb diameter	0.76	0.56	0.73	0.32		
Distance to trunk	-0.32	0.38				
Distance to periphery	0.54	0.49				
Cumulative variance accounted for	68.5	87.6	84.5	97.5	92.2	100.0
Significance of canonical function ^a	<0.001	<0.001	<0.001	<0.01	<0.001	0.19

^a Based upon minimizing Wilk's lambda.

Jay (Table 1). The Indigo Bunting had a smaller support-limb diameter than did other shrub-nesting species.

The distance of the nest from the trunk and periphery of the support differed among species nesting in trees (Table 2). These two measures were positively correlated with each other and with nest and support-structure height (Table 3). This suggests that species responded to variation in substrate width and were consistent in positioning the nest relative to the distance between tree trunk and periphery. Cover below the nest was negatively correlated (Table 3) with the latter two, suggesting that nests nearer the trunk or periphery were better concealed.

Multivariate analyses.—The first two canonical functions derived for tree-nesting species accounted for 88% of the variance in the data (Table 4). On the basis of correlations of these functions with the original variables, we interpreted the first function to represent a gradient of decreasing nest height and increasing support-limb diameter and distance to support periphery (Fig. 2). The second function was defined as a gradient of increasing nest and support-structure height. The Northern Oriole was well-separated from the other species on the first axis; this species had the greatest nest height and smallest support-limb diameter and distance to periphery (Table 1). The Eastern Wood-Pewee and Rose-breasted Grosbeak occupied an intermediate position on the first axis, and Blue Jays, American Robins, and Mourning Doves were located where the function

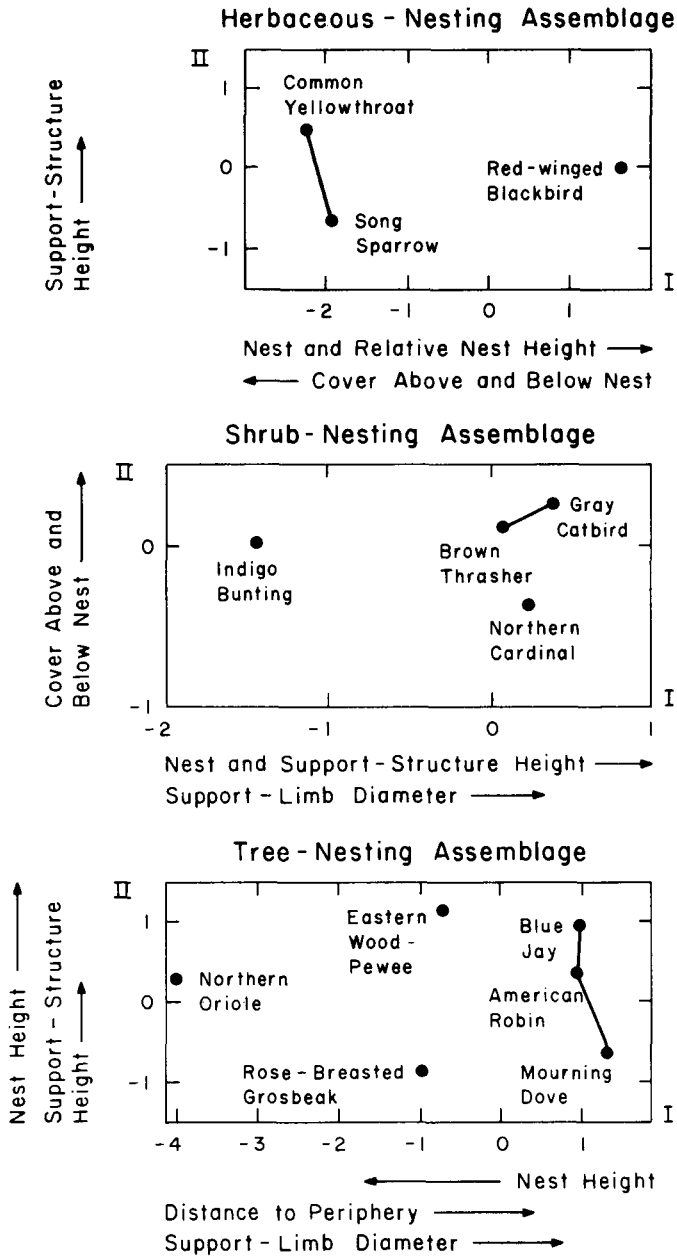


FIG. 2. Distribution of mean canonical scores along the first two canonical axes (I and II) of species nesting predominantly in trees, shrubs, and herbaceous cover. Species' means connected by a line do not differ ($P > 0.05$) in canonical space, as determined by Mahalanobis' distance.

represented the lowest nest height and the greatest distance to periphery and support-limb diameter (Fig. 2). The second axis separated the Eastern Wood-Pewee from the Rose-breasted Grosbeak and the Blue Jay from the Mourning Dove, primarily on the basis of support-structure and nest height. We conclude that all tree nesters we considered, except the American Robin, have nest sites distinctive from one another. On the basis of the variables used in the analysis, nest sites of American Robins did not differ significantly from those of Blue Jays and Mourning Doves, as determined by the significance of Mahalanobis' distance (Fig. 2).

From analysis of five nest-site characteristics, MacKenzie et al. (1982) also found that Northern Oriole nest sites were distinct from those of the other species. In contrast with our results, however, they reported significant differences between nest sites of Mourning Doves and American Robins. Although, in our study, nest sites of American Robins were similar to those of Mourning Doves and Blue Jays, their habitat-use patterns differed (Stauffer and Best 1980). Robins were most common in the savannah habitat, with wooded edge and floodplain woodland habitats also being used frequently. Blue Jays and Mourning Doves were most commonly encountered in upland woodlands; floodplain woodlands received the second most intensive use. Thus, even though some nest-site characteristics were similar, these species had different habitat-use patterns.

The first canonical function derived for the shrub-nesting assemblage was interpreted as a gradient of increasing nest and support-structure height and support-limb diameter (Fig. 2). On the first canonical axis, only the Indigo Bunting was distinct from the other species. The second canonical function, representing a gradient of cover above and below the nest, distinguished the Northern Cardinal from the Brown Thrasher and Gray Catbird, the latter two species having nest sites with greater cover (Fig. 2). These two functions represented 98% of the information contained in the original data (Table 4). Nest sites of Gray Catbirds and Brown Thrashers were not different in canonical space (Fig. 2), but habitat-use patterns differed between the two species. The upland woodland and scrub habitats were used most frequently by Brown Thrashers, whereas floodplain woodland and scrub habitats had the greatest use by Gray Catbirds (Stauffer and Best 1980). Thus, the potential for competition for nest sites between these two species may have been alleviated somewhat by their differential use of habitat.

Only the first canonical function was significant for herbaceous-nesting species (Table 4). This function represented a gradient of increasing nest and relative nest height and decreasing cover at the nest (Fig. 2). The Red-winged Blackbird was well separated from the other two species along this axis, tending to nest higher and at locations with less cover. The

second axis represented a gradient of increasing support-structure height and did not provide additional significant separation of the species (Fig. 2). On the basis of the nest-site variables that we used, nest sites of Song Sparrows and Common Yellowthroats were not different. Both Common Yellowthroats and Song Sparrows used wooded edge habitat most commonly, but yellowthroats also showed substantial use of floodplain woodlands, whereas Song Sparrows also frequently used herbaceous and scrub habitats (Stauffer and Best 1980).

Our results confirmed that, in many instances, substantial differences exist among the nest sites used by open-nesting (and cavity-nesting, see Stauffer and Best 1982) bird species breeding in riparian habitats. Most multivariate studies of avian community structure and composition have relied heavily on describing bird distributions along resource axes. These gradients usually are defined either by habitat characteristics recorded at locations where the birds were observed (e.g., James 1971, Anderson and Shugart 1974, Whitmore 1975, Smith 1977) or by foraging behavior (e.g., Rabenold 1978, Landres and MacMahon 1983, Sabo and Holmes 1983). Nest-site use is an important component of habitat selection in birds (Hildén 1965); presumably, habitats lacking suitable potential nesting substrates for a particular species will not be used as breeding sites by that species. Thus, when assessing species' interrelationships within a community, nest-site use should be considered (Collins 1981, Titus and Mosher 1981, Clark et al. 1983).

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