

AVIAN SPECIES DIVERSITY IN DESERT SCRUB¹

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Abstract. Along a gradient of habitat complexity in desert scrub communities of the Sonoran Desert in southern Arizona, nest sites and food niches become more diverse, and breeding bird population density and species diversity increase. Birds are highly specific in their selection of plants for nest placement; densities of most species are strongly related to densities of nest plants. The MacArthur foliage-height diversity model does not yield consistently accurate predictions of breeding bird species diversities in desert scrub communities.

A significant relationship is found between physiognomic coverage diversity and breeding bird species diversity. This index, based on a system of plant life forms, quantifies critical environmental features used by birds in habitat selection. A model that combines aspects of foliage-height diversity and physiognomic coverage diversity may provide greater accuracy and wider applicability for predicting breeding bird species diversity.

Key words: Bird diversity; creosotebush; desert scrub; diversity, bird.

INTRODUCTION

The number of species in biotic communities generally increases from high to low latitudes and from high to low elevations. An Arctic tundra supports fewer species than does a deciduous forest, an alpine meadow less than a succulent desert. Yet, under the same macroclimatic conditions, community diversities can vary markedly at any latitude. MacArthur (1965), Pianka (1966), Orians (1969), Karr (1971), and Recher (1971) discuss and summarize factors that may affect general and/or local patterns of species diversity.

Analysis of species diversity of birds in desert scrub communities in the Sonoran Desert reveals that on gradients of habitat complexity extending from valley bottom *Larrea* communities upslope through bajada and rockslope *Cercidium* communities, nest sites and food niches become more diverse and breeding population density and species diversity increase upslope with gradient complexity. In desert scrub communities, forest foliage-height diversity of MacArthur and MacArthur (1961) does not yield consistently accurate predictions of breeding bird diversities in the Sonoran Desert.

Investigation of the problem reported here was conducted in the Tucson Basin and the Avra Valley-Silverbell Mountain system in the Sonoran Desert in southern Arizona. The Arizona model should be tested in analog environments and communities, as in the Monte of Argentina.

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STUDY SITES

The creosotebush (*Larrea divaricata*) occurs commonly throughout the southwestern desert scrub (Lowe 1964), often dominating extensive areas in the Chihuahuan, Sonoran, and Mohave Deserts. In the Sonoran Desert of southwestern Arizona, creosotebush (alone or with other species) forms one of two major climax associations, broadly meeting and intermingling with the palo-verde/sahuaro (*Cercidium microphyllum/Carnegiea gigantea*) association.

Three study sites were selected to represent a gradient of structural complexity of the vegetation in creosotebush habitats. At each site a 20-ha rectangular plot was gridded with stakes or flagging tape every 100 m and halved into subplots (300 m × 400 m). The 20-ha plots (10-ha subplots in parentheses) were designated: Avra (A1, A2), Houghton (H2, H3), and Silverbell (S1, S2). Additional 10-ha plots established at the Avra and Houghton sites were designated A3 and H1 respectively.

Avra

The site is south of Silverbell Road, about 9 miles west of Marana, Avra Valley, Pima County, Arizona (Sections 19 and 20, T. 11 S., R. 10 E., Silverbell Peak Quadrangle) at an elevation of 585 m. Rainfall on the plots totaled less than 114 mm during 1970. The soil consists of fine sand overlaid with fine gravel. Except in widely separated dry runoffs, the vegetation is homogeneous throughout, composed of evenly spaced creosotebushes. The runoffs are lined and creosotebushes and varying densities of spinescent, microphyllous shrubs and short trees. The ground between shrubs is bare pavement most of the year, with annuals associated only with sufficient winter rains. Herbaceous plants, present only from

March to early May, consisted of several species of annual forbs and grasses.

Houghton

The site is west of Houghton Road, 0.8 km south of Interstate-10, about 32 km southeast of Tucson, Pima County, Arizona (Section 11, T. 16 S., R. 15 E., Tucson Quadrangle) at an elevation of 930 m. Rainfall measured at Tucson International Airport, 18 km northwest of the study site, totaled 304 mm for 1970. The soil is mixed sand and gravel. The vegetation is relatively homogeneous, with spinescent shrubs scattered throughout. Clusters of cholla (*Opuntia* sp.) provide a significant structural component of the habitat. In addition, ground cover of various suffrutescents, forbs, and annuals, present throughout the study period, flowered in March and April, August and September.

Silverbell

The site is about 11 km east of Silverbell, Avra Valley, Pima County, Arizona (Section 24, T. 12 S., R. 9 E., Silverbell Peak Quadrangle) at an elevation of 640 m. Rainfall measured at Silverbell Mine totaled 248 mm for 1970. The soil is mixed sand and gravel, overlaid with coarse gravel, typical of lower bajada slopes. The vegetation contains rather evenly spaced creosotebushes, spinescent shrubs, and a few sahuaros and chollas. The ground between shrubs is mostly bare, with scattered bursage (*Franseria deltoidea*); a few other perennials and some annuals flower during the rainy season.

METHODS

I studied breeding bird populations from March 10 through August 31, 1970, spending parts of 24 or more days on each plot and making observations throughout the day, but mostly during the morning or late afternoon and early evening. For each species, I recorded nest locations, foraging movements, song perches, and intraspecific encounters on a grid map. Data for nests included the date found, species and height of plant selected, height and position of nest, number of eggs and/or young, and fate of the nesting attempt. The total breeding density per species was expressed as the maximum number of active nests or territories held during the breeding season. Many pairs were resident throughout the study.

I put each species of bird in an ecologic foraging category based on its primary food type (seeds, insects, or larger prey) and the foraging substrate (ground, foliage, bark, or air) on the study plots. I used the categories (ground seed, ground insect, foliage insect, bark insect, mixed ground and foliage insect, aerial insect, and predator) with bird densities

and species composition to compute the foraging diversity (FD) for each plot.

I assigned each plant species on the plots to one of the following life form or physiognomic categories adapted from Whittaker (1970): (1) evergreen sclerophyll (with small evergreen leaves), (2) spinescent (armed with spines, usually with deciduous compound leaves), (3) stem succulent (cactus), (4) perennial—including suffrutescents (semi-shrub with upper parts of stems and branches dying back in unfavorable seasons) and forb (plants without perennial above-ground woody stems), or (5) annual. Plant coverage was measured with the line-intercept method described by Canfield (1941), on twenty-four 30-m lines established on each plot. Plant densities were measured within belt transects (30 m × 2 m) defined by the intercept lines and expressed as total number per 1440 m². I recorded only plants with emergent stems 50% or more within the belt. Spinescents were recorded in height classes (0–1 m, 1–2 m, > 2 m) and succulents as (0–0.3 m, 0.3–1 m, > 1 m). I listed perennials as suffrutescents or forbs and did not count annuals.

ANALYSIS

I calculated breeding bird species diversity (BSD) for each plot using the Shannon (1948) formula with the tables of Lloyd et al. (1968), and natural logarithms. Diversity (H) increases with a rise in the total number of species (S) and/or with an increase in the "evenness" with which individuals are distributed among species (Lloyd and Ghelardi 1964).

The J index (Pielou 1966), the proportion of maximum possible diversity for a community ($J = H/H_{\max}$), is a measure of the relative abundance component of diversity ranging from 0 to 1.0.

I calculated foraging diversity (FD) for each plot using (1) the number of species in each ecologic foraging category and (2) the number of pairs in each category.

The physiognomic complexity of each plot was expressed as (1) physiognomic coverage diversity (PCD), computed with H and relative coverage of life forms, and (2) number of equally important physiognomic dimensions (E_p), calculated as e^{PCD} .

I used foliage measurements, following the method of MacArthur et al. (1966), to construct foliage density profiles. The profiles were divided into horizontal layers (0–1 m, 1–2 m, > 2 m) and the proportion of the total profile in each layer was used to compute foliage-height diversity (FHD) with H . The regression

$$\text{BSD} = 0.46 + 2.01 \text{ FHD} \quad (\text{MacArthur and MacArthur 1961})$$

was used to predict breeding bird diversities, and

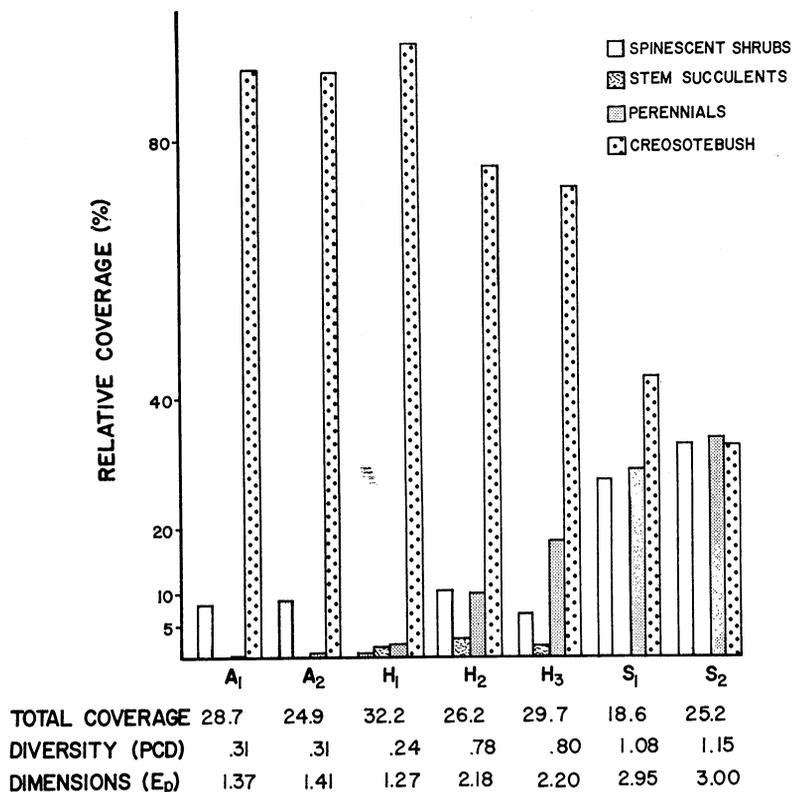


FIG. 1. Plant coverage, physiognomic coverage diversity (PCD), and number of equally important physiognomic dimensions (E_p) on 10-ha plots in desert scrub in southern Arizona 1970.

these were compared with the diversities observed. FHD's calculated with the foliage layers used by MacArthur (0–0.6 m, 0.6–7.6 m, > 7.6 m) as well as layers (0–0.9 m, 0.9–7.6 m, > 7.6 m) and (0–0.6 m, 0.6–1.5 m, > 1.5 m) yielded predicted bird diversities much poorer than those obtained with layers (0–1 m, 1–2 m, > 2 m).

RESULTS

The differences in physiognomic complexity of the three study sites are illustrated in Fig. 1. Total plant coverage is approximately equivalent at each site, but the different coverage values of spinescent shrubs and perennials indicate their increasing importance as structural elements. Habitat complexity, expressed as physiognomic coverage diversity (PCD) and as equally important physiognomic dimensions (E_p) values, correspond well with the over-all visual appearance of each site. Cacti, even in trace amounts by analytical standards, add another important dimension to habitat structure.

Breeding birds and nest site selection

Table 1 presents the breeding bird densities, species compositions, and diversity indices for one 20-ha

plot at each study site during 1970. Note that, with increasing habitat complexity, there is increase in total density, total species, and species diversity indices H and J . In addition, combined densities of four species common to each site (Verdin, Cactus Wren, Blacktailed Gnatcatcher, Black-throated Sparrow) rise from 11 pairs at Avra to 19.5 pairs at Houghton to 25 pairs at Silverbell. The high J indices at Houghton and Silverbell indicate an unusually high "evenness" of the relative abundance of species in these communities (Tramer 1969).

The high degree of specificity with which birds selected plants for nest placement is demonstrated in Fig. 2. No nests were found in creosotebush or suffrutescents in this study or by other investigators (Anderson and Anderson 1946, Hensley 1954, Austin 1970) working in creosotebush habitats. However, Black-throated Sparrows do construct nests in the bases of creosotebush (Raitt and Maze 1968, Tomoff *unpublished data*), especially in relatively pure *Larrea* stands. All nests found were either (1) in succulents—chollas (*Opuntia fulgida*) higher than 1 m, or sahuaros (*Carnegiea gigantea*) higher than 4 m, or (2) in spinescent shrubs or trees taller than 2 m—acacias (*Acacia constricta*, *A. greggii*), con-

TABLE 1. Foraging categories and breeding bird densities, expressed as max no. of active nests or territories, on 10-ha plots in desert scrub in southern Arizona 1970

Species	Study Plot							
	A1	A2	A3	H1	H2	H3	S1	S2
White-winged Dove (GS) ^a							1	1
Mourning Dove (GS)			1	1	2	2	1	1
Roadrunner (P)						0.5		
Screech Owl (P)			1				1	1
Gilded Flicker (GI)							1	1
Gila Woodpecker (BI)							1	1
Ash-throated Flycatcher (AI)			1		1	1	2	3
Verdin (FI)	0.5	1	1.5	0.5	1.5	1.5	2	3.5
Cactus Wren (GFI)	1		1.5	1	2.5	4	2.5	4
Bendire's Thrasher (GI)					0.5	0.5		
Curve-billed Thrasher (GI)				0.5	1.5	2.5	2	2
Crissal Thrasher (GI)		1	1					
Black-tailed Gnatcatcher (FI)	0.5	1	1	0.5	1	1	1	2
House Finch (GS)				1	2	3		
Brown Towhee (GS)						1		1
Black-throated Sparrow (GS)	3	4	4	3	4	4	4	6
Rufous-winged Sparrow (GFI)								1
10-ha plots								
Total density	5	7	12	7	16	21	18.5	28.5
Total species (S)	4	4	8	7	9	11	11	13
Diversity (H)	1.09	1.17	1.92	1.71	2.13	2.19	2.27	2.36
% Maximum diversity (J)	.78	.86	.93	.88	.97	.91	.95	.92
Combined 20-ha plots								
Total density		12			37		47	
Total species		5			11		13	
Diversity (H)		1.25			2.16		2.35	
% Maximum diversity (J)		0.78			0.90		0.92	

^a GS = Ground Seed, GI = Ground Insect, FI = Foliage Insect, BI = Bark Insect, GFI = Ground and Foliage Insect, AI = Aerial Insect, P = Predator.

dalia (*Condalia spathulata*), mesquite (*Prosopis juliflora*), or paloverdes (*Cercidium microphyllum*, *C. floridum*).

Local variation in the densities of nest site plants, i.e., cacti and spinescents, significantly modify the occurrence and densities of breeding birds. Table 1 gives the 1970 breeding bird populations on 10-ha plots. At the least diverse Avra site, densities varied from 5 to 7 to 12 pairs with 4, 4, and 8 species on the A1, A2, and A3 plots respectively. The smaller Verdins, gnatcatchers, and sparrows occurred on all plots; the larger wrens and thrashers were present on

two plots. All nests were located within or immediately adjacent to the acacia- and mesquite-lined shallow runoffs. Cholla was absent from the general area.

The striking rise in density and diversity on the A3 plot was due in part to the presence of a single sahuaro and adjacent riparian vegetation. The sahuaro was used by two hole-nesting species: Screech Owl during April and May and Ash-throated Flycatcher in May and June. There were more large shrubs, and the acacia-mesquite thickets along the wash passing through the plot were denser. The spinescent-nesting doves, Verdins, wrens, and thrashers all nested in the wash within 50 m of the sahuaro. I noted this tendency toward clumped nesting throughout the general creosotebush habitat and also in the mature riparian woodland adjacent to the study area.

At the Houghton site, densities ranged from 7.5 to 16 to 21 pairs with 7, 9, and 11 species on the H1, H2, and H3 plots respectively. Seven species, including the Verdin, gnatcatcher, and sparrow, occurred on all plots. Only two species did not select cholla: the hole-nesting flycatcher and the mesquite-nesting gnatcatcher. Black-throated Sparrow nests were found in cholla in adjoining habitat.

Spinescents were virtually absent from H1; all

TABLE 2. Shrub densities (no. per 1440 m²) on 10-ha plots in desert scrub in southern Arizona with densities (no. of pairs) of spinescent shrub-nesting birds 1970

Plot	A1	A2	H1	H2	H3	S1	S2
Creosote-bush	163	201	256	238	217	63	60
Spinescent shrubs	6	12	5	34	34	10	30
Relative per cent spinescent shrubs	3.6	5.6	1.9	12.5	13.5	13.6	33.3
Spinescent shrub-nesting birds	2.0	3.0	1.0	3.5	3.5	6.5	12.5

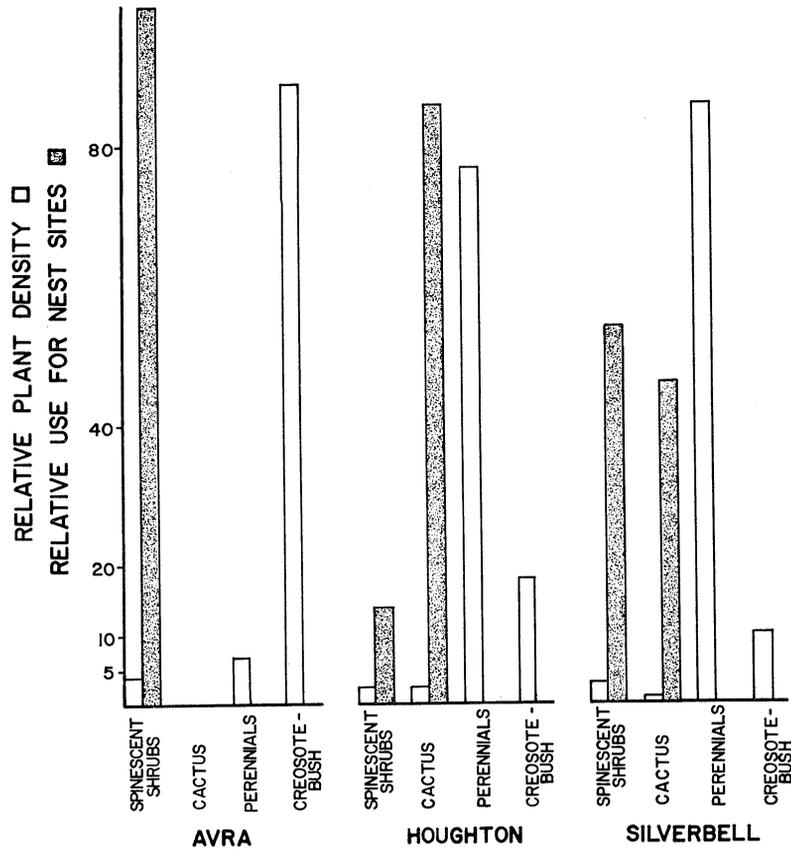


FIG. 2. Relative plant densities and relative use of plants for nest sites on 20-ha plots in desert scrub in southern Arizona 1970.

nesses were in jumping cholla. On plots H2 and H3 spinescents were essentially equally available (Table 2), as were the densities of spinescent-nesting birds. The higher total density of H3 was due to the presence of 6 more pairs of cholla-nesting birds.

At the Silverbell site, densities were 18.5 and 28.5 pairs with 11 and 13 species on S1 and S2 respectively. These differences were due primarily to the presence of 6 more pairs of shrub-nesting species, including doves, Verdins, gnatcatchers, wrens, and Rufous-winged Sparrows. On both plots nest site succulent densities were nearly identical, as were the densities of succulent-nesting birds. Eleven pairs (28%) nested in sahuaro cavities, 7 pairs (18%) in jumping cholla.

In review, on study plots with the same dimensions, breeding bird population densities and species compositions vary with differences in habitat complexity. To me these differences appear either obvious or subtle. Obvious differences are demonstrated by the presence of cholla or the absence of sahuaro cacti at the Houghton site. Subtle differences are shown by the variable spinescent densities between different sites (Table 2, Fig. 3) and by the variable

densities of cholla within the Houghton site (Fig. 4). This highly specific nest site selection is a response to both subtle and gross habitat features.

Foraging diversity

A classification of breeding birds according to foraging behavior is included in Table 1. Most species were relatively consistent in their foraging activities throughout the study period, occasionally exploiting food sources or substrates other than those indicated by their assigned category. For example, the ground-insect-foraging thrashers and seed-eating doves fed upon succulent fruits at the Silverbell site, and Crissal Thrashers gulped moth larvae from creosotebush foliage during a brief emergence at the Avra site. However, Black-throated Sparrows, feeding almost exclusively on annual grass and forb seeds throughout most of the study, expanded their foraging repertoire to include insect-gleaning in creosotebush foliage with the emergence of insects during the rainy months of July and August. Cactus Wrens and Rufous-winged Sparrows, which generally exploited both ground and foliage during the study, likewise

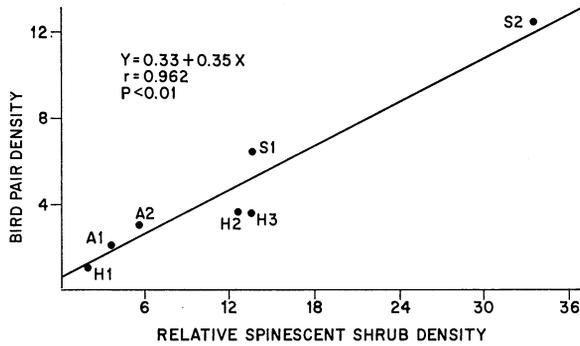


FIG. 3. Regression of density of spinescent shrub-nesting birds on relative spinescent shrub density of 10-ha plots in desert scrub in southern Arizona 1970. Shrub densities = percentage of total shrub density per 1440 m².

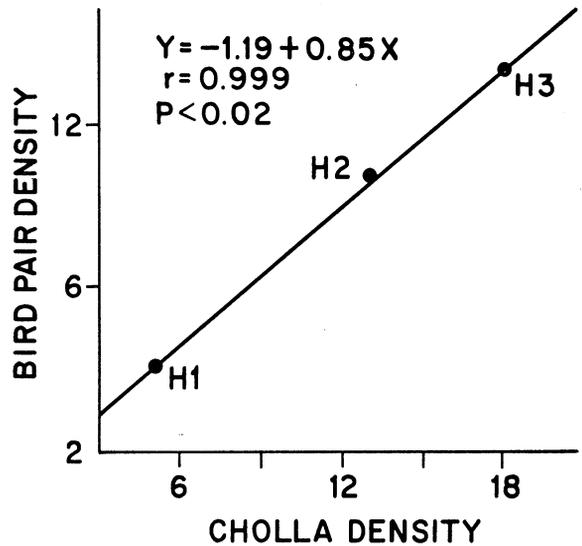


FIG. 4. Regression of densities of cholla-nesting birds on cholla density at the Houghton site 1970. Cholla densities = no. of *Opuntia fulgida* > 1 m per 1440 m², bird densities = as no. of pairs per 10 ha.

increased their intensity of foliage-gleaning during periods of greater insect abundance.

Habitats with greater physiognomic diversity support a higher number of avian foraging patterns than do simpler ones, and yield higher foraging diversity indices (FD). As shown in Table 3, Avra (the simplest site) has four foraging categories represented; Houghton has six with the addition of the aerial insectivore and predator; and the most diverse, Silverbell, has seven foraging categories including the bark forager. In addition the densities of the more common types tend to increase. For example, the foliage-gleaners (Verdin and gnatcatcher) occur at each site, but their combined densities rise from 3 pairs at Avra to 5 pairs at Houghton to 8.5 pairs at Silverbell. This is probably partially due to the increasing foliage density with its probable concomitant increase in insect food resources. The sharp increase in ground-feeding seed-eaters at the Houghton and Silverbell sites is related to the greater den-

TABLE 3. Foraging diversity of breeding bird species on 20-ha study plots. Numerals = total no. of species in each foraging category at three study sites in desert scrub in southern Arizona 1970, no. of pairs in parentheses

Foraging category	Study plot		
	Avra	Houghton	Silverbell
Ground seed	1 (7)	4 (18)	4 (16)
Ground insect	1 (1)	2 (5)	2 (6)
Foliage insect	2 (3)	2 (5)	2 (8.5)
Bark insect			1 (2)
Ground and foliage	1 (1)	1 (6.5)	2 (7.5)
Aerial insect		1 (2)	1 (5)
Predator		1 (0.5)	1 (2)
Total species (pairs)	5 (12)	11 (37)	13 (47)
Foraging diversity for species	1.33	1.64	1.82
Foraging diversity (pairs)	(0.98)	(1.41)	(1.74)

sities of annuals and perennials (Fig. 2) which provided most of the food of these species.

The trend toward increased foraging diversity with increased vegetative diversity, seen in the comparisons between sites, can also be demonstrated locally within sites as well. Table 4 presents analyses of the foraging patterns and diversities for the populations on 10-ha plots.

Habitat diversity

Foliage density profiles that depict horizontal and vertical distribution of foliage are useful in making comparisons between habitats. Although total foliage density increases along the gradient of habitat complexity in this study, the numbers of equally important foliage layers (E_f) on the 20-ha plots are nearly the same (Fig. 5): for example, 2.12 layers at Avra, 2.28 layers at Houghton, and 2.34 layers at Silverbell. Thus differences in foliage distribution at each site do not account for the striking differences in breeding bird population densities and species diversities.

Foliage-height diversities (FHD's) were calculated from each profile. The observed BSD's vary from values far below those predicted (i.e., A1 and A2) to some considerably higher than expected (i.e., S1). The model fails to predict consistently in desert scrub communities. MacArthur (1964), working in succulent desert scrub and montane communities in southeastern Arizona, speculated that birds here were using more than foliage layers for habitat selection in these structurally more complex habitats.

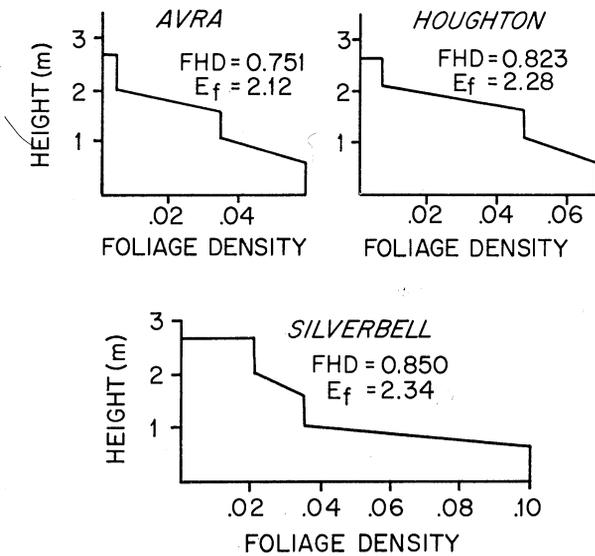


FIG. 5. Foliage density profiles of 20-ha study plots. Leaf silhouette, cm² per cm² of space at various heights above ground, foliage-height diversities (FHD's), no. of equally important foliage layers (E_f) in desert scrub in southern Arizona, 1970, during the summer rains; FHD's calculated using foliage layers 0-1 m, 1-2 m, > 2 m and natural logs; $E_f = e^{FHD}$.

To quantify habitat diversity with the physiognomic coverage diversity index (PCD), I used a simplified scheme of plant life forms. Fig. 6 illustrates a significant relationship between PCD and BSD. An advantage of this kind of system is that unusual structural entities can be weighted more evenly, thus

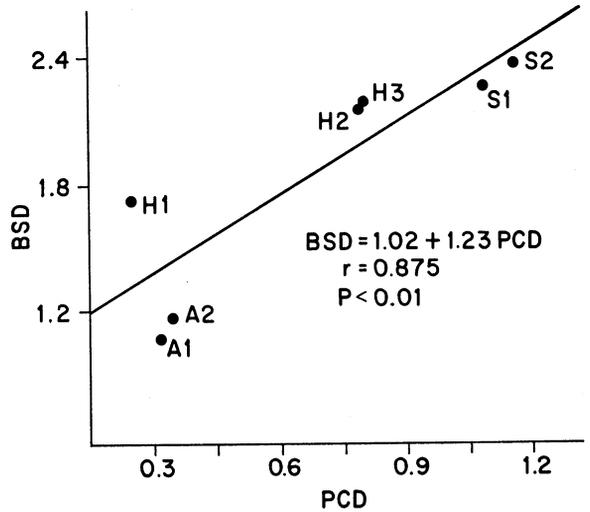


FIG. 6. Regression of breeding bird species diversity on physiognomic coverage diversity for 10-ha study plots in desert scrub in southern Arizona 1970.

minimizing the masking effect of dominant vegetational features, such as creosotebush or deciduous tree foliage. For example, the FHD model describes the habitats in this study as having 2.12, 2.28, and 2.34 equally important dimensions, giving the impression that the environments are practically identical structurally. The PCD model, on the other hand, describes them as having 1.4, 2.1, and 3.0 equally important dimensions, which is much more appropriate for the habitat as seen and occupied by breeding birds.

TABLE 4. Foraging diversity of breeding bird species on 10-ha study plots. Numerals = total no. of species in each foraging category on study plots in desert scrub in southern Arizona 1970, no. of pairs in parentheses

Foraging category	Study plots							
	A1	A2	A3	H1	H2	H3	S1	S2
Ground seed	1 (3)	1 (4)	2 (5)	3 (5)	3 (8)	4 (10)	3 (6)	4 (10)
Ground insect		1 (1)	1 (1)	1 (0.5)	2 (2)	2 (3)	2 (3)	2 (3)
Foliage insect	2 (1)	2 (2)	2 (2.5)	2 (1)	2 (2.5)	2 (2.5)	2 (3)	2 (5.5)
Bark insect							1 (1)	1 (1)
Ground/foliage	1 (1)		1 (1.5)	1 (1)	1 (2.5)	1 (4)	1 (2.5)	2 (5)
Aerial insect			1 (1)		1 (1)	1 (1)	1 (2)	1 (3)
Predator			1 (1)			1 (0.5)	1 (1)	1 (1)
Total species	4 (5)	4 (7)	8 (12)	7 (7.5)	9 (16)	11 (21)	11 (18.5)	13 (28.5)
Foraging diversity species	1.04	1.04	1.73	1.28	1.52	1.64	1.84	1.82
Foraging diversity (pairs)	(0.95)	(0.96)	(1.57)	(0.99)	(1.37)	(1.43)	(1.78)	(1.70)

DISCUSSION

An assumption implicit in the foliage-height model is that nest site selection by birds is random (MacArthur *personal communication*). This assumption is reasonable when applied to deciduous forests or woodlands, habitats that have less physiognomic diversity than do succulent deserts. For the eastern Wood Pewee (*Contopus virens*), which usually saddles its nest on a horizontal branch of a deciduous tree, the species of tree is not as important as is the structural quality of the branch on which the nest is built. Hence MacArthur's (1961) conclusion that plant species composition is not directly related to breeding bird species diversity applies to this type of habitat.

This assumption of randomness, however, does not apply to birds in desert scrub communities, for these breeding birds are highly responsive to particular life forms. At Silverbell over 50% of all species and almost 50% of the total number of pairs selected either jumping cholla or holes in sahuaros for nest sites, and these plants were present in trace amounts. At Houghton, which had no sahuaros, 86% of all nests found were located in jumping cholla. This is a wide departure from random nest site selection.

Thus, plant species composition is highly significant in regulating breeding bird communities in desert scrub. In this case, the particular plants have distinctive growth forms which meet specific needs of birds for nest sites. One major difference between deciduous forest and desert scrub is the occurrence of specific structural elements in the vegetation present in trace amounts but critical to birds for nest sites.

Although life form diversity may be directly and closely correlated with foliage-height diversity in eastern deciduous forests, it is not in desert scrub habitats. Not only does the dominant life form in the forests usually determine the quantity of foliage, it also provides nest sites for the preponderance of breeding bird species there. Thus, in eastern deciduous forests, as one measures FHD, one may also be measuring life form diversity.

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