

# THE COMPOSITION OF FOUR BIRD COMMUNITIES IN SOUTH TEXAS BRUSH-GRASSLANDS

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Avian community diversity is related to vegetational complexity (e.g., MacArthur and MacArthur 1961, Karr and Roth 1971, Willson 1974, Roth 1976). This prompts the prediction that communities in similar habitats should be similar with respect to species richness and composition, population density, standing crop, community energy requirements, and feeding guilds. Several avian studies in recent years tested aspects of the above prediction in various ways. Some compared habitats of the same type from different continents (e.g., Cody 1968, 1974, Karr 1971, 1975) or from different localities on the same continent (Cody 1968, 1974, Orians 1969, Wiens 1973, 1974a, b, Willson 1974, Pearson 1975). Willson (1974), Karr (1975) and, especially, Pearson (1975) compared habitats of the greatest apparent similarity in profile.

I tested the prediction in a study of avian community composition and habitat selection and usage during the 1969 breeding season at four localities in the south Texas brush-grasslands. The Coastal Bend region of south Texas was appropriate for my study because vegetation of one type extended over a well-known faunal transition zone (Webb 1950) and, therefore, included the range limits of a number of species. In addition, the study areas could be separated geographically yet be near enough to one another to be studied alternately during a single breeding season. Some of my results concerning species diversity and vegetation complexity have been reported (Karr and Roth 1971, Roth 1976). In this paper I describe and discuss species richness, composition, and abundance and total population density with respect to the prediction. Coincidentally, I describe quantitatively the bird communities of localities and a habitat-type from which such information is almost totally lacking.

## METHODS

### BIRD POPULATIONS

I visited the study areas for 1 or 2 days biweekly from mid-March through July 1969. Using a modified spot-map method (Kendeigh 1944, Enemar 1959), I made one morning count and usually one late afternoon count daily. Because of time spent on other observations, only about half an area was

covered during a count. Alternation of starting points insured that all parts of the area were censused twice during each visit and that one count was in the morning. Each area was visited for 120–160 h distributed over 32–48 counts on 22–48 days (Roth 1976).

Multiple locations of individual birds often were recorded during a count. Consequently, records of a species made close to one another but at different times could be confused, especially for very abundant or mobile species. I resolved such questions of identity by: (1) mapping the movements of a bird flushed repeatedly (Wiens 1969); (2) observing a bird's behavior with respect to a nest or to another bird flushed from a nest; (3) noting as many conspecifics singing or visible simultaneously as possible; (4) noting non-singing birds and their behavior toward other individuals and vice versa; (5) interpreting chronologies of ca. 450 nests.

### VEGETATION

I modified the point-contact methods of Emlen (1967) and Karr (1968) to determine vegetation profiles between 28 May and 5 June. Sample points were at 7.6 m intervals along grid lines 54.3 m apart. I classified vegetation cover as grass, forb, cactus, shrub foliage, shrub bark, litter, dead vegetation, or absent at heights of 0, 0.15 m, 0.3 m, 0.6 m, and, thereafter, at 0.3 m intervals upward through all vegetation. Any vegetation that lay within 2.5 cm horizontally of an erect rod (1.3 cm × 4 m) and ±2.5 cm vertically of the height being considered was a contact. Because of the size of the sample point, more than one plant form could occur at a given height. This method differs from the usual point-contact sampling method because theoretically the point should be non-dimensional. A point 6.3 cm in diameter causes an upward bias in percent cover measurements. The method was acceptable, however, for the comparative purposes of this study as it was used on all four areas. Percent cover at the different heights was calculated from these measurements. I identified the contacts along alternate transects (280–300 of the 630–700 points sampled on each of the areas) to species.

I used the point-quarter method (Cottam and Curtis 1956) to determine density, height, and species composition of the shrubs. At each grid intersection and midway between each intersection I identified the nearest shrub ≥1.5 m tall in each quarter. I recorded point-to-plant distance, height, and height of the foliage base of each shrub ( $N \approx 550$ ). I considered a shrub to be any unit of vegetation equivalent functionally or in form to the usual concept of a single shrub. Thus, tight clumps of shrubs of several species and vine-covered cacti or small shrubs were shrubs, operationally, just as were single plants or single species clumps. The shrubs were sampled 4–14 August.

Botanical nomenclature follows Jones et al. (1961) and Gould (1969).

TABLE 1. Non-shrub plant taxa or categories and relative frequencies on each study area. (Rel. freq. = percent of sample points with vegetation at which the taxon occurred.) Total percentages exceed 100 because several species could be counted at any one point.

Taxon	Seadrift	Welder	Kingsville	Raymondville
Grasses and sedges:				
<i>Aristida</i> sp.	—	5.1	5.0	*
<i>Bouteloua rigidiseta</i>	7.0	7.8	*	—
<i>Brachiaria ciliatissima</i>	—	—	*	5.5
<i>Buchloe dactyloides</i>	—	12.6	*	*
<i>Cenchrus incertus</i>	—	*	*	6.2
<i>Chloris</i> sp.	5.4	*	21.0	*
<i>Eragrostis oxylepis</i>	*	*	16.1	*
<i>Hilaria belangeri</i>	—	16.3	*	—
<i>Panicum capillarioides</i>	—	—	5.7	7.3
<i>P. filipes</i>	—	5.1	*	—
<i>Schedonardus paniculatus</i>	9.9	—	7.1	—
<i>Setaria geniculata</i>	*	15.0	—	—
<i>S. leucopila</i>	—	5.1	*	*
<i>Spartina spartinae</i>	7.0	—	—	—
<i>Sporobolus asper</i>	—	23.5	—	—
<i>S. pyramidatus</i>	27.6	*	*	—
<i>Stipa leucotricha</i>	*	39.8	—	—
<i>Tridens congestus</i>	—	6.8	—	—
<i>Vaseyochloa multinervosa</i>	—	—	—	14.3
Unidentified spp.	2.5	10.2	7.9	1.5
Other taxa**	14.8(13)	19.7(15)	34.6(21)	20.9(12)
Forbs and forb-like plants:				
<i>Ambrosia psilostachya</i>	*	16.0	27.1	—
<i>Clematis drummondii</i>	—	—	*	57.1
<i>Coreopsis cardaminaefolia</i>	—	10.9	*	—
<i>Prosopis glandulosa</i>	*	12.6	*	—
<i>Ratibida columnaris</i>	—	11.9	*	—
<i>Thurovia triflora</i>	23.1	—	—	—
<i>Xanthisma texanum</i>	*	14.6	—	—
<i>Ximenesia encelioides</i>	—	—	—	13.6
Unidentified spp.	7.0	10.5	8.9	0.4
Other taxa	24.7(17)	22.8(17)	24.6(25)	13.9(10)
Cactus:				
<i>Opuntia lindheimeri</i>	*	—	6.8	—
Other taxa	3.3(2)	1.7(1)	—	—
Dead vegetation	8.2	51.0	6.8	8.4
Total sample points	300	294	288	295

\* Present but &lt;5% relative frequency.

\*\* Taxa with relative frequencies &lt;5% which are not listed for another area. Numbers in parentheses are number of taxa included.

## STUDY AREAS

### DESCRIPTION

The study region is described variously as the "Rio Grande Plain," Texas "brush country" (Inglis 1964), and "South Texas Plains" (Gould 1969). Human-related activities such as restriction of fire and overgrazing by livestock (Johnston 1963, Inglis 1964, Box et al. 1967) have facilitated the spread of many shrub species into the grasslands of the region in the recent past. As a result, shrubs of varying densities and heights dominate former grasslands. Hence, I call the vegetation "brush-grassland."

Four study areas 80–95 km apart in the eastern part of this region (Fig. 1), were

chosen as study areas on the basis of apparent similarity, primarily in density and height of shrubs and secondarily in development of the grass and forb layer. The geographic spacing of the areas was intended to span as much of the brush-grassland and faunal transition zone as possible.

*Seadrift* (96°41'50"W, 28°22'44"N). 12.2 ha located on the Jay Welder Ranch, 2.2 km SE Seadrift, Calhoun Co., within 200 m of San Antonio Bay between Swan Point and Mosquito Point. The "fine-textured saline area" (Gould and Box 1965) was characterized by heavy clay; halophytic plants, e.g. *Spartina spartinae* (Table 1); short, sparse grass; and a paucity of shrub species. The shrubs (Table 2), predominantly mesquite (*Prosopis glandulosa*) and lotebush (*Condalia obtusifolia*), had recently spread into the grassland. One clump of large mes-

TABLE 2. Relative frequency of shrubs or species comprising shrub-like forms from point-quarter sampling.

Species	Seadrift	Welder	Kingsville	Raymondville
<i>Acacia farnesiana</i>	*	7.0	15.5	*
<i>A. rigidula</i>	—	11.4	—	—
<i>Berberis trifoliolata</i>	—	6.4	—	—
<i>Celtis spinosa</i>	*	8.6	50.4	38.3
<i>Clematis drummondi</i>	—	—	*	34.3
<i>Condalia obovata</i>	—	5.9	*	*
<i>C. obtusifolia</i>	23.1	*	*	*
<i>Diospyros texana</i>	—	6.0	—	*
<i>Prosopis glandulosa</i>	60.7	33.7	26.9	9.4
<i>Zanthoxylum fagara</i>	—	8.4	—	11.6
Others**	16.3(8)	12.6(9)	7.2(7)	5.8(7)
No. of Species	10	17	10	11

\* As in Table 1.

\*\* As in Table 1.

quite and some live oak (*Quercus virginiana*) were the only brush present in the vicinity "twenty years ago" (Wesley Vivion, pers. comm.).

**Welder** (97°24'12"W, 28°6'9"N). 11.3 km NE Sinton, San Patricio Co., in Section 20, Lots 1 and 2 on the Welder Wildlife Refuge. The 11.5 ha were a combination of Box and Chamrad's (1966) mesquite-buffalograss and chaparral-bristlegrass communities. Emlen (1972) termed it "open brushland." The site was of the "fine-textured upland" type of Gould and Box (1965). A well-developed grass-forb layer and the presence of the dense clumps of various mixtures of shrubs—"the chaparral complex" (Box and Chamrad 1966)—characterized the area structurally and floristically (Tables 1 and 2). Brush control by chopping occurred on the site in the mid-to-late 1940's (O. W. Maley, pers. comm.).

**Kingsville** (97°51'2"W, 27°22'54"N). 12.6 ha located 4.4 km S Ricardo, Kleberg Co., on the J. K. Northway Ranch. It lay in the "loamy-soiled peripheral zone of the eolian plain"—historically a 'mesquite prairie' with mesquite and granjeno (*Celtis spinosa*) predominant. The region is covered now mostly with brush, but some grass remains (Johnston 1963). Granjeno, mesquite, prickly pear (*Opuntia lindheimeri*) and short and mid-grasses characterized the vegetation on my area (Tables 1 and 2). The brush had been chained (a method of brush control) about twenty years earlier (Ralph Northway, pers. comm.).

**Raymondville** (97°48'58"W, 26°32'33"N). 12.6 ha located 7.6 km NW Raymondville, Willacy Co., on the Esperanza Ranch. The study area lay in the loamy peripheral zone of the eolian plain where it meets the eolian sands in this vicinity according to Johnston's (1963) map. The soil on the ranch, however, was much sandier than at Kingsville. Large, dense mesquite with an understory of other shrubs covered much of this region. Such was the study area prior to being root-plowed and raked (brush control methods) in 1953 and 1954 (W. E. Bakke, Sr., pers. comm.). *Clematis drummondi*, the most frequently encountered plant species, was present both as ground cover and in shrubs (Tables 1 and 2); it often added considerably to the foliage density of shrubs. Granjeno was the predominant shrub (Table 2).

#### COMPARISON OF AREAS

Vegetation profiles (Fig. 2) were similar among the areas except in the herbaceous layer (0–0.6 m). Those

differences were due to short, sparse grass and forbs at Seadrift; tall, dense herbaceous and dead vegetation components at Welder; a prominent herb component less than 0.15 m tall at Kingsville; and tall annual forbs and a dense *Clematis* ground cover at Raymondville.

Other characteristics of the vegetation which may be important to birds are the size and dispersion of the shrubs. Mean height and height of the foliage base of shrubs differed little among the areas (Table 3). There were some differences in density. Differences in plant species composition also existed (Tables 1 and 2). The taxonomic differences probably affect birds only insofar as they affect structure. For example, the *Clematis* at Raymondville added foliage to low shrubs by overgrowing them.

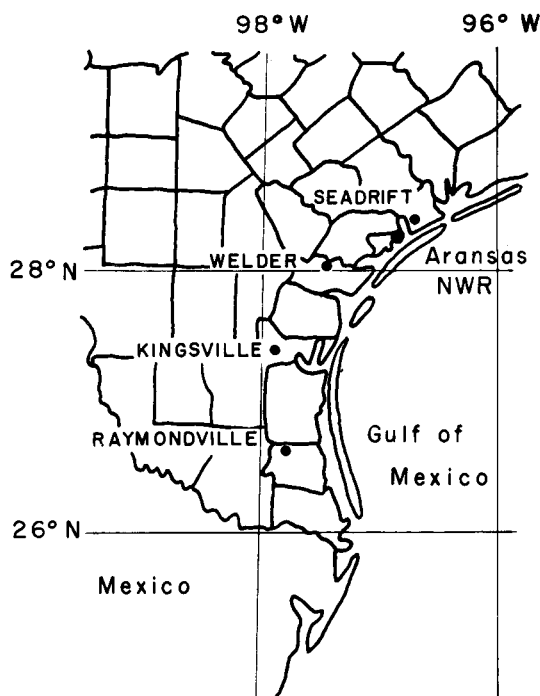


FIGURE 1. Map of south Texas showing locations of study areas and other selected localities. Scale: 1 cm = 50 km.

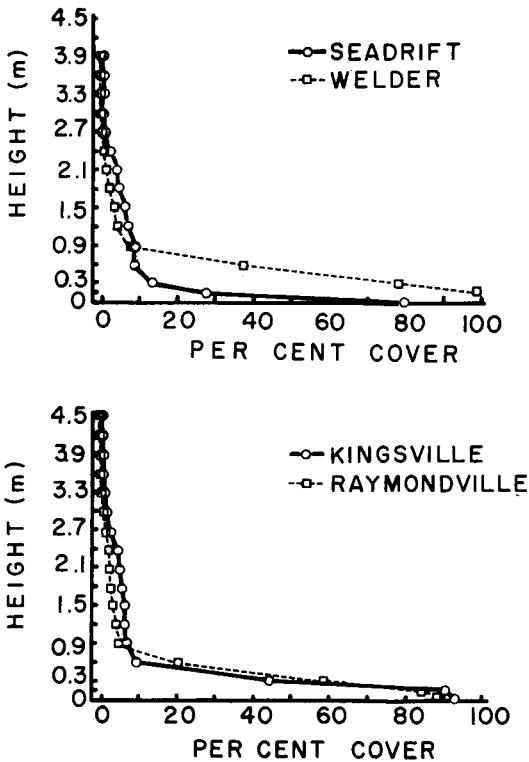


FIGURE 2. Vegetation profiles on the four study areas plotted as percent cover at the various heights.

These comparisons and my general impressions of other brush-grassland sites indicated that my areas had essentially similar vegetation configurations. Of course, some differences existed, and their importance to certain species will be seen.

## RESULTS AND DISCUSSION

### THE AVIAN COMMUNITIES

*Species richness.* Species richness was almost equal among the areas (Table 4). Similar results have been obtained from grasslands and Mediterranean shrub (Cody 1966, 1968, 1974, Wiens 1974b), from some Illinois forests (Willson 1974), and from Liberian and Panamanian forests (Karr 1975). My results do not agree with Pearson's (1975) and some of Willson's data.

*Species composition and abundance.* Despite similarities in richness, taxonomic differences were large. Only 6 of the 24 species were resident on all four areas. Only 8–10 were held in common by any two areas with one exception; Kingsville and Raymondville shared 12 (Table 4). Such species replacement among similar habitats also was reported by Cody (1966) and Wiens (1973).

In view of such replacement, it is not surprising that several abundance patterns of individual species existed (Table 4). Only

TABLE 3. Mean and standard deviation of height, foliage base height (FBH), and density of shrubs ( $\geq 1.5$  m) on the four areas.

	Height (m)	FBH (m)	Density (No./ha)
Seadrift	2.4 $\pm$ 0.7	0.5 $\pm$ 0.3	143
Welder	2.3 $\pm$ 0.6	0.6 $\pm$ 0.3	185
Kingsville	2.5 $\pm$ 0.8	0.6 $\pm$ 0.9	212
Raymondville	2.7 $\pm$ 0.9	0.5 $\pm$ 0.3	146

2 species, Bobwhite (*Colinus virginianus*) and Yellow-billed Cuckoo (*Coccyzus americanus*), approached equal abundance on the four areas. A second pattern reflected geographical trends in abundance largely unmodified by local habitat differences, e.g., the southwardly increasing populations of Ground Dove (*Columbina passerina*), Groove-billed Ani (*Crotophaga sulcirostris*), Bronzed Cowbird (*Molothrus aeneus*), and Pyrrhuloxia (*Cardinalis sinuatus*). Other species of south-western affinity (see below, Population Density) generally reflected the above pattern but showed that local habitat features could interrupt such gradients; examples were Cactus Wren (*Campylorhynchus brunneicapillus*), Curve-billed Thrasher (*Toxostoma curvirostre*), and Black-throated Sparrow (*Amphispiza bilineata*). A fourth and larger group were distributed over the entire region in such numbers that one could expect them to occur on all four areas in about equal numbers. Instead, some were absent from one or more areas while others were present unevenly among the areas. Common Nighthawk (*Chordeiles minor*), Eastern Meadowlark (*Sturnella magna*), Dickcissel (*Spiza americana*), and Mockingbird (*Mimus polyglottos*) exemplified species that responded to a characteristic of an area. Finally, certain abundance patterns appeared to have been influenced by interspecific competition; two possible cases were Brown-headed (*Molothrus ater*) and Bronzed cowbirds and Cardinal (*Cardinalis cardinalis*) and Pyrrhuloxia. Detailed discussion of the species' distribution in terms of habitat selection and usage appears in Roth (1971). Those data and the patterns described above make two points about species composition and replacement. (1) One habitat type is not uniformly attractive to the same collection of species nor to a single species throughout a region. (2) Habitats that appear to be similar may differ subtly thereby affecting exploitation patterns and abundance of birds.

TABLE 4. Bird species and their abundances (stationary males per 40 ha) on the four study areas.

Species	Seadrift	Welder	Kingsville	Raymondville
<i>Colinus virginianus</i> (U) <sup>1</sup>	3	6	5	6
<i>Zenaida macroura</i> (U)	8	1	3	10
<i>Columbina passerina</i> (S)	—	—	6	25
<i>Coccyzus americanus</i> (U)	6	10	10	8
<i>Geococcyx californianus</i> (S)	5	1	—	—
<i>Crotophaga sulcirostris</i> (S)	—	—	—	6
<i>Nyctidromus albicollis</i> (S)	—	1	—	3
<i>Chordeiles minor</i> (U)	5	—	—	—
<i>Muscivora forficata</i> (S)	—	—	—	6
<i>Myiarchus</i> sp. (S)	—	—	1	—
<i>Auriparus flaviceps</i> (S)	—	3	—	—
<i>Thryomanes bewickii</i> (U)	5	5	6	—
<i>Campylorhynchus brunneicapillus</i> (S)	7	—	32	37
<i>Mimus polyglottos</i> (U)	55	13	22	59
<i>Toxostoma curvirostre</i> (S)	10	—	36	29
<i>Sturnella magna</i> (U)	—	3	—	—
<i>Molothrus ater</i> (U)	4	7	13	6
<i>Molothrus aeneus</i> (S)	—	—	6	10
<i>Cardinalis cardinalis</i> (E)	24	26	—	—
<i>Cardinalis sinuatus</i> (S)	—	13	39	57
<i>Passerina ciris</i> (U)	2	26	7	6
<i>Spiza americana</i> (E)	—	48	—	—
<i>Chondestes grammacus</i> (U)	13	—	1	—
<i>Amphispiza bilineata</i> (S)	—	—	11	3
Males per 40 ha	147	163	198	271
Number of species	13	14	15	15
Individuals (males) per species	11.3	11.6	13.2	18.1

<sup>1</sup> Denotes affinity group. U = ubiquitous, S = southwestern, E = eastern.

**Population density.** The total population of the community, the net effect of the abundance patterns just described, increased greatly in the two southernmost areas with only minor concomitant increases in species richness. Consequently, number of individuals per species also increased in southern areas (Table 4).

I found that several species became progressively more abundant toward the centers of their ranges usually from north to south (e.g., Ground Dove, Cactus Wren, Pyrrhuloxia). To relate this to population density of the community, I assigned each species to one of three affinity groups: (1) Eastern—species with ranges predominately in northern or eastern United States which approach their range limits or inhabit only a narrow range of habitats in the region under study; (2) Southwestern—those with ranges largely west and south of the Coastal Bend and which approach their limits or have a restricted habitat breadth in the region of study; (3) Ubiquitous—those spread over the entire region connecting eastern North America and the Southwest or Mexico (Table 4). Decisions were based on range information from the A.O.U. Checklist (1957), Robbins et al. (1966), Oberholser and Kincaid (1974), and Hubbard (1974).

The number of species, total population, and population per species increased southward for the southwestern group while the minor eastern component disappeared and the ubiquitous component changed only slightly and inconsistently (Fig. 3). Thus, the higher population density to the south resulted not from more southwestern species but from their greater abundance per species. The dearth of species which typically inhabit shrubby situations in the eastern deciduous forest, as well as of southwestern species, on the two northern areas further enlarged the differences.

We should expect this pattern. A species should be more abundant toward the center of its range than at its periphery because factors critical to existence are more favorable for more individuals near the center (e.g., Kendeigh 1974:12–13). A corollary is that a species should occupy a broader range of habitats at the center of its range than at the periphery. Dow (1969) found both predictions to be true for Cardinals in eastern North America. The suitability, then, of one habitat-type (vegetational configuration) recurring through an environmental gradient or through the range of a species is likely to change for that species from one place to

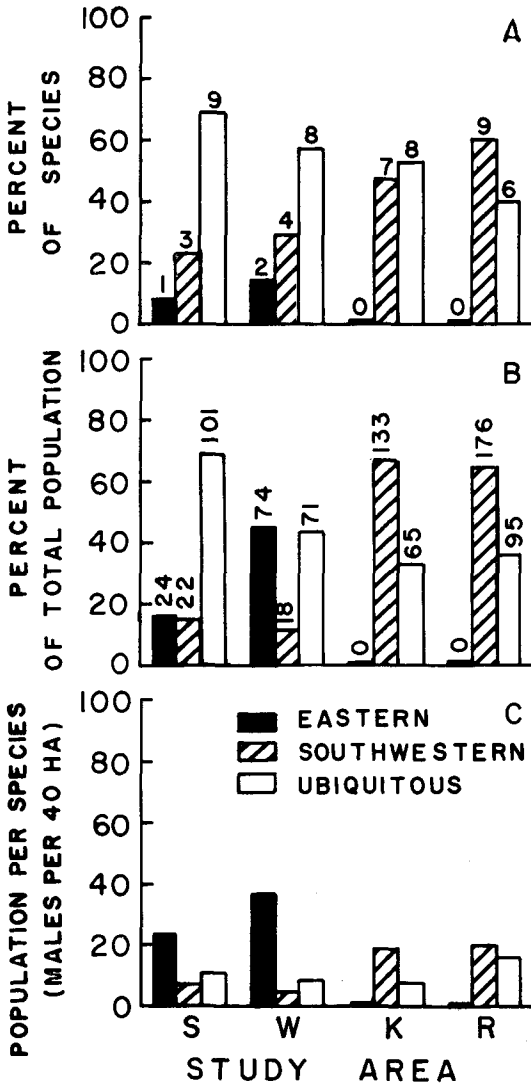


FIGURE 3. Composition of the communities on the four areas (S = Seadrift, W = Welder, K = Kingsville, R = Raymondville) by regional affinity groups as percent of total species (A) and population (males per 40 ha) (B) and as population (males) per species (C). Numbers indicate the size of each category. The northernmost areas are to the left.

another. That notion was demonstrated by the specific abundance patterns and the total density patterns in south Texas.

A gradient in rainfall probably underlies the population and faunistic changes. Both annual and breeding season rainfall generally decline to the south (Table 5), which favor xerophyllic southwestern species in the same direction. Species less tolerant of the xeric conditions, the eastern component, should drop out, at least from the open type of habitat I studied. Their disappearance does not mean that no eastern species occurred in the drier regions but only that they were not in

TABLE 5. Total annual and April-July precipitation  $\pm$  standard deviation at four stations near the respective study areas (in parentheses). Values are means of U.S. Weather Bureau data for 1951-1966, 1968-1969.

Location	Precipitation (cm)	
	Annual	April-July
Port O'Connor (Seadrift)	93.5 $\pm$ 28.2	28.1 $\pm$ 15.3
Sinton (Welder)	79.0 $\pm$ 24.5	25.0 $\pm$ 12.3
Ricardo (Kingsville)	52.1 $\pm$ 16.0	18.0 $\pm$ 9.5
Raymondville (Raymondville)	62.7 $\pm$ 16.3	23.3 $\pm$ 10.6

my habitat-type. Cardinals exemplified this pattern. Likewise White-eyed Vireos (*Vireo griseus*) occupied the adjacent taller, denser vegetation at Kingsville and Raymondville (pers. observ.) and wooded streamside vegetation at Welder (Lemon and Herzog 1969) but were absent from my study areas. The rainfall gradient alone does not account for the population differences, but it helps to explain an overall pattern which is apparent despite the variety of individual abundance patterns.

COMMUNITY SIMILARITY AND ECOLOGICAL SATURATION

The prediction that similar habitats hold similarly organized avian communities was partially supported by my data. Although species richness was similar, total population, species composition and abundance were not. Cody (1974) reported similar results for such comparisons. His analyses also suggest that guilds or niche-types should be similar despite different species combinations. Since species richness was about equal, one might expect replacements to have been one-for-one ecologically, but that did not seem to occur. Possible exceptions were Cardinal-Pyrrhuloxia, the two cowbirds, and Black-throated Sparrow and Lark Sparrow (*Chondestes grammacus*). Perhaps the competition which may have helped shape the communities was largely diffuse (MacArthur 1972:29, Cody 1974:131), and the particular collection of species depended as much on subtle habitat features as on direct competitive replacement.

The question of community similarity and saturation has been addressed in quantitative, theoretical fashion by several workers (e.g., MacArthur 1969, 1972:170-173, 237-238; Cody 1974). In several tests of the theory, the final evaluations of similarity or saturation

have been largely subjective (e.g., Cody 1966, Wiens 1974b, Pearson 1975). This subjectivity is important to arguments about the reality of saturation or equilibrium communities.

Should we expect close agreement in structure among avian communities in similar habitats? The correlations between foliage diversity and avian diversity suggest that communities are packed with species according to each habitat's foliage complexity and that exclusion of one species is a prerequisite to the addition of another (Pearson 1975). (Proportional population reductions of resident species seem more likely, however, than total exclusion.) Consequently, habitats of similar profile have similar packing limits. However, the diversity correlations have often contained considerable variance (Roth 1976) because factors other than vertical foliage complexity can modify avian community diversity: e.g., area (Galli et al. 1976), presence of non-avian competitors and paleoecological history (Pearson 1975), unique resources (Karr 1971, 1975), climate and food availability (Wiens 1974b), and horizontal complexity (Roth 1976). Consequently, we should expect some communities of similar habitats, even of similar profiles, to differ considerably in species richness and other aspects of community structure. To expect this does not mean that some are not saturated but that the saturation limits are different.

Ecologists perhaps can approximate the variation to be expected in a series of similar communities. The coefficient of variation for collections of similar habitats may be a useful index for such an effort. My calculations suggest that there is often as much as 15–20% variation in species richness (Table 6). Wiens (1974b) concluded that individual packing may be limited. If a limit exists, it apparently has a much wider neighborhood than does species richness. My survey suggests that variation of 30–40% can be expected (Table 6).

The ecological relevance of faunistic differences to community organization is pertinent to this discussion. Species are abstractions of resource spaces. Each species does not represent a single, unique resource but several resources shared to varying degrees with other organisms. Likewise, total populations are abstractions of a collection of generalized birds of equal sizes and physiologies. Both species and populations are approximations to characteristics that more accurately relate to community organization—viz., niche-types and caloric requirements.

TABLE 6. Coefficients of variation of species richness and community population density for several series of similar habitats.

Habitat and source	Coefficient of variation (%)	
	Species richness	Population density
Illinois forests (Areas 17–21, Willson 1974)	15	40
Liberia and Panama forests (Karr 1975)	8	4
Texas brush-grasslands (This study)	7	28
North American grasslands (Wiens 1974b)		
Tallgrass	15	12
Mixed-grass	33	37
Shortgrass	38	25
Palouse	18	34
Shrubsteppe	13	65

We should expect less variation among similar habitats, in number of foraging types and existence energy, than in species richness and population density. This is substantiated by Pearson's (1975) and Karr's (1975) data, respectively. A better approach, then, to studies of saturation may be in terms of energy requirements, foraging guilds, body sizes and food availability (e.g., Salt 1957, Cody 1968, 1974, Karr 1971, 1975, Wiens 1974b, Pearson 1975).

Are the Texas brush-grasslands saturated, based on the approximations of species and population density? Despite the high species replacement and large species pool, the similar values for species richness argue for the existence of a limit to species packing and for ecological saturation. Has there been enough time to achieve equilibrium and saturation? Arid brushlands probably existed before the Pleistocene and were pushed to refugia in Mexico during glacial periods (Hubbard 1974). The brush species returned to south Texas in post-Pleistocene times and have been known for at least 200 years in the southern part of my study region. They increased in density and spread north and east into the coastal grasslands during the last 100 years (Price and Gunter 1942, Johnston 1963, Inglis 1964, Box et al. 1967). The northern edge of this expansion is not far beyond the Seadrift area. Thus, the brushland habitat, especially the brush-grasslands of the Texas coast, are relatively young. Some of the xerophyllic elements of the brush-grassland avifauna may date to Miocene-Pliocene aridlands, but others probably differentiated in aridland refugia in the Pleistocene (Hubbard 1974).

In post-Pleistocene times these elements probably spread into the expanding brushlands of Mexico and Texas. This may have been a time of mixing of aridland species with refugees returning northward and eastward. The avian species are not necessarily young, but the combinations of species may be.

I judge that the communities in the Raymondville and Kingsville areas probably are saturated, while those at Seadrift and Welder may not be. One or two southwestern species may be added with time and northward expansion. However, the avifauna may never stabilize in the northern region because of the great climatic variability in southern Texas. My study transcended a zone where xerophilic species advance and retreat in response to rainfall (C. Cottam, pers. comm.). They may have difficulty becoming established at this climatic border as did the brush-grasslands (Price and Gunter 1942). Interspecific competition also may retard northward expansion. Several pairs of possibly competitive species meet in the region: e.g., Brown Thrasher (*Toxostoma rufum*) and Curve-billed Thrasher, Pauraque (*Nyctidromus albicollis*) and Chuck-will's-widow (*Caprimulgus carolinensis*), Pyrrhuloxia and Cardinal, and the two cowbirds. Eastern species do not seem to be invading southward. Hamilton (1962) found a similar pattern in the mesquite plains of northern Texas. I conclude that the brush-grasslands of the type I studied have a saturation limit of about 15 species. Fluctuations around that value are to be expected depending on climatic conditions, location and subtle vegetation features. Limits on population densities are not so predictable.

My discussion and conclusions should be viewed with caution. First, in such a climate, variation between years at a site may be as great as variation between sites within a year. I have attempted to explain the patterns observed during one semi-dry year. Wet years and very dry years also should be studied to understand fully the dynamics and organization of the brush-grassland system. Wiens (1976) warned against overgeneralization from short-term data. Second, several factors affect species diversity and community organization. Some of these (area, geological age, general habitat configuration) were relatively constant in this study, while others (rainfall, subtle vegetation patterns) varied. Comparisons of very similar habitats in close proximity where all of these variables are controlled will be necessary to answer ques-

tions about similarity of habitats and the avian communities inhabiting them.

## SUMMARY

I tested the prediction that habitats of similar vegetational configuration support similarly organized avian communities in the breeding season. Communities occupying four Texas brush-grassland sites were compared taxonomically. Species richness was quite similar, but total population density, individual species abundances, and species composition differed considerably among the areas.

Some species were equally abundant on all areas. Others reflected general regional abundance patterns or responded to local habitat features. Interspecific competition may have affected some species. Total population density increased along a gradient of decreasing rainfall as the proportion of species with southwestern affinities and their average abundances increased.

Ecological saturation and the degree of similarity to be expected among communities in similar habitats were discussed. A coefficient of variation of 15–20% for species richness and 30–40% for total density may be expected in such cases as a first approximation. Taxonomic features are only approximations to more ecologically significant features of communities such as niche-types and community existence energy and should vary more than the latter. In turn, the latter should be more useful in answering questions about community saturation. The packing limit for the habitat under study is about 15 species.

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