ECOLOGICAL AND DISTRIBUTIONAL RELATIONS OF DESERT SCRUB BIRDS OF WESTERN TEXAS

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In the deserts of North America, as in other areas remote from centers of population, initial studies of the avifauna were directed principally along taxonomic and distributional lines. In recent years, interest in desert birds has broadened, and studies of breeding bird populations, life histories of individual species, and physiological ecology have been undertaken. The principal focus of the investigations reported here was determination of habitat preferences and population density of birds breeding in desert scrub vegetation in southern Brewster County, Texas, as a part of a long term study of community relations of vertebrates of the Big Bend area. Field work involved parts of four nesting seasons, 1955 to 1958 inclusive. Studies were conducted in the Big Bend National Park and on the Texas Game and Fish Commission's Black Gap Wildlife Management Area, lying east of Big Bend Park and 53 miles southeast of Marathon, since these areas were relatively undisturbed insofar as present economic exploitation is concerned. Taxonomic and distributional background is provided by the writings of Van Tyne and Sutton (1937) and Miller (1955).

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METHODS

The method used was the censusing of singing males as developed by Williams (1936), special reliance being placed upon records of simultaneous singing by two or more individuals. Repeated visits to the study areas were made in the early morning or evening hours, and the positions of individual birds were recorded on maps. Records were transferred later to composite maps for each species. These maps, supplemented by field notes, were used to estimate the number of territories for each species. Kendeigh's (1944:91) recommendation that a minimum of five censuses be spaced through the nesting season was followed insofar as possible.

Some workers, among them Breckenridge (1955), have questioned the validity of results obtained by this method, although Stewart *et al.* (1952:269) estimated the accuracy at "over 90 per cent" in deciduous forest and adjacent habitats in Maryland. Earlier, Hickey (1943:83) had demonstrated some variability in the percentage of known residents of a plot that would be detected on a single trip through the area. Among seven species of warblers the value approximated three-fourths of the individuals. The difficulties involved in enumerating the birds decrease in the open growth in which our censuses were taken, although confusion resulting from intruding individuals sometimes was difficult to resolve.

To circumvent the difficulties of estimating fractions of territories of thinly distributed species in the process of reaching a density figure for a given plot, the number of males judged to include some part of the area in their activity ranges was indicated in parentheses following the "density" value, in addition to the latter figure. Thus, in table 1

we may see that in 1956 two Pyrrhuloxia males were active on the area, although the streambed traversing the 33 acres did not appear to include all of the area occupied and defended by either male. For some species these figures for actual numbers recorded may reflect more accurately the relative abundance of a given species in the area represented by the plot (for year-to-year comparisons) than do territorial equivalence values (sum of territories and fractions thereof) conventionally reported in breeding bird censuses.

Probably greater value will accrue from records of the presence or absence of species on the study plots in subsequent years rather than from interpreted changes in absolute density for a particular species. Data to support the latter type of interpretation are hardly justified on plots of the size censused. On the other hand, larger plots could not have been covered in their entirety before avian activity diminished with increasing warmth of the day.

CENSUS PLOTS

Black Gap area.—In 1956, a 33-acre plot was established at 2200 feet elevation, 2½ miles by road east of the Headquarters, at the top of the hill west of the Dell Tank. The area is one of low limestone hills bisected by a dry streamcourse. The vegetation on dry detrital slopes consists of an open stand of shrubs two to six feet in height (*Larrea*

Table 1

Breeding-bird Populations on a 33-acre Plot, Open Desert Scrub Bisected by a Dry Streamcourse, 2.5 Miles by Road East of Black Gap Headquarters, 2200 Feet, Brewster County, Texas

Species	1956		1957		1958	
	Equiv. terr.[1]	Males active on plot[2]	Equiv. terr.	Males active on plot	Equiv. terr.	Males active on plot
Scaled Quail	V (3 days)		V (7 days)		V (3 days)	
Mourning Dove	2	(3)	1	(1)	3.5	(4)
Elf Owl					V (1 night)	
Trilling Nighthawk	2.5	(3)	1	(2?)	1.5	(2)
Poor-will	V (1 day)		V (2 days)		+	(1)
Ladder-backed Woodpecker			V (2 days)		V (6 days)	
Ash-throated Flycatcher	1+	(2?)	+	(1)	0.5	(1)
Verdin	+	(1)	1	(1)	1	(1)
Cactus Wren	1	(2)	1	(1)	1	(1)
Mockingbird	2+	(4)	1+	(4)	1+	(2)
Curve-billed Thrasher			V (1 day)			
Black-tailed Gnatcatcher	2+	(3)	1	(1)	1	(2)
Scott Oriole	1	(2)	0.5	(1)	+	(1)
Brown-headed Cowbird	V (1 day)				V (1 day)	
Pyrrhuloxia	1.5	(2)	1	(1)	1	(1)
House Finch	2	(3?)	1+	(2)	2	(2)
Black-throated Sparrow	2	(3)	1.5	(3)	1+	(3)
Totals	17+	(29)	10+	(18)	13.5+	(20)
Territorial males per 100 acres	51+		30+		40+	

[1] Equivalent territories; + indicates less than 0.5 territories; V denotes a species apparently nesting nearby, but occurring on the plot irregularly.

[2] Number of males whose territories extended onto the plot; see text.

Coverage: 1956, March 20, 22; April 26, 29; May 3, 19, 20; June 13, 23; total man-hours, about 17.
1957, March 20, 22; April 21, 22, 23, 24; May 10, 11, 12, 14, 15; total man-hours, about 17.
1958, March 24, 27, 28, 29, 30; April 1, 24, 25, 26, 27; May 24, 25, 26, 27, 28; total man-hours, about 17.

tridentata, Acacia constricta, Porlieria angustifolia) grading into a denser scrub growth with a ground layer of the leaf succulent *Agave lechuguilla*. In its densest faciation on limestone rock slopes, this growth includes *Agave* and another leaf succulent (*Hechtia* sp.), a low semi-succulent—the sotol (*Dasylirion leiophyllum*), and shrubs such as *Leucophyllum* sp., *Acacia* spp., and *Forestiera angustifolia*. The streambed supports a more or less continuous growth of rather thin-foliaged shrubs, three to nine feet in height, of which *Acacia constricta, Larrea, Forestiera, Condalia* and *Lippia ligustrina* are prominent (fig. 1). Scattered along this ribbon of shrubbery and extending interruptedly along lateral drainageways are clumps or isolated individuals of the broad-bladed *Yucca torreyi*. Strands of a taller but shorter-leaved yucca (*Y. rostrata*) occur on one of the north-facing slopes (fig. 1). These small stands of either species of yucca may be considered as special habitat features rather than as distinct habitats.

Although the selection of a study plot lacking uniformity of vegetation may seem out of step with current practices in censusing of breeding birds (Pough, 1947), it did serve to emphasize certain points concerning habitat requirements of some breeding species. The activities of at least five species (Mockingbird, Pyrrhuloxia, Verdin, Cactus Wren, Black-tailed Gnatcatcher) were centered in the denser growth of the creekbed, and these would not have been expected in more open areas. Three others (Ash-throated Flycatcher, Scott Oriole, and House Finch) apparently depended upon one of the yucca species for nest sites and/or song perches. (Scientific names of most of the species mentioned in text appear in table 3.) The feathery-leaved shrubs of the creekbed evidently did not provide sufficient shelter and/or foraging sites for several species of thicket-dwelling birds that occurred sparingly elsewhere on the Black Gap area: Bewick Wren, Crissal Thrasher, Phainopepla, Bell Vireo, and Varied Bunting.

The results of three censuses for 1956 to 1958 are presented in table 1. It may be seen that the same 11 species were present and presumably nesting in each of the three years; the twelfth species, the Poor-will was active on the plot in 1958 only. A real decrease in population density from 1956 to 1957 was evident, and it is corroborated by the decreased numbers of males of several species.

The nesting birds of desert scrub vegetation of the Black Gap area as reported by Thompson (1953) are listed in table 3. In addition, I heard the Elf Owl (*Micrathene whitneyi*) at two localities in 1958, and took a male Cassin Sparrow (*Aimophila cassinii*) in a thicket of mesquite (*Prosopis*) and catclaw (*Acacia greggii*) on the bank of Maravillas Creek in June, 1956. The Brown Towhee is found locally on the Black Gap area on lava rock slopes of somewhat denser vegetation, including sotol, and its occurrence in desert scrub vegetation in western Texas is local and marginal, as indicated by Davis (1951:48–49). One male Lark Sparrow, taken in a stand of mesquite in June, 1956, was the only individual of this species seen on the Black Gap area during this investigation.

Big Bend National Park.—A census plot referred to hereafter as the Burnham Flat plot was established in 1957 on the gradually sloping outwash plain north of the Chisos Mountains. This plot, situated at 3400 feet elevation, 3.1 miles by road north of Government Spring, was enlarged from 20 to 33 acres in 1958. The alluvial slope is dissected by shallow drainageways along the eastern and western margins of the 33-acre plot, and by a central creekbed as well. None of these narrow arroyos supports a continuous growth of denser vegetation, although the composition, including scattered individuals of *Yucca torreyi,* is more varied than that of the surrounding slopes. The largest arroyo, along the western margin, is dotted with shrubs of denser foliage, including *Forestiera* and *Diospyros texana*. A prominent feature of the entire plot is the rather dense ground cover of *Agave lechuguilla* (fig. 2). The shrubs (*Larrea, Porlieria, Flourensia cernua, Koeberlinia spinosa, Condalia obtusifolia, Prosopis*) are more scattered and of lower

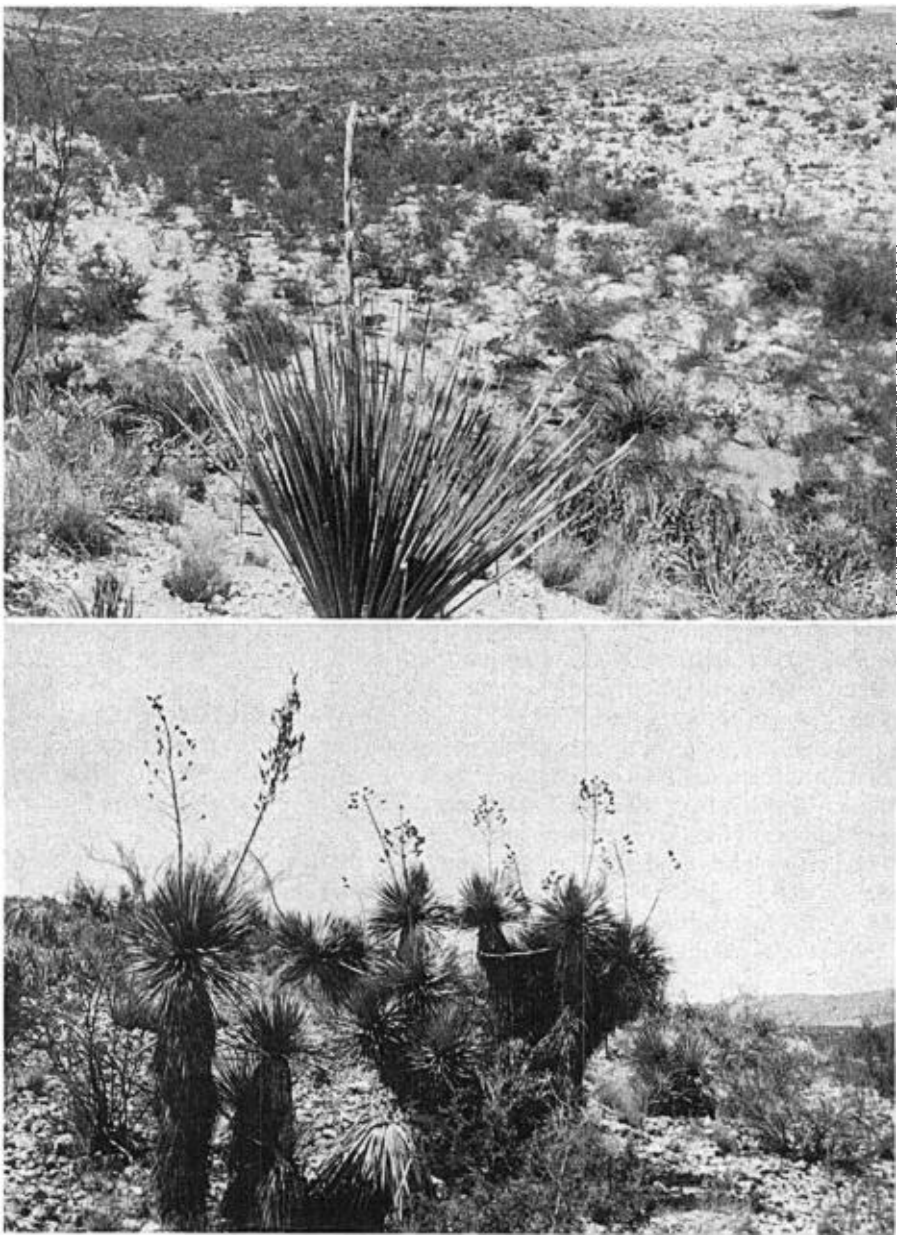

Fig. 1. Upper: view of desert scrub bisected by dry streamcourse on Black Gap census plot, *Dasylirion leiophyllum* in center foreground.
Lower: stand of *Yucca rostrata* on limestone slope.

stature than those on the Black Gap plot. As on the latter area the herbaceous layer consists principally of the perennial bunch grass (*Bouteloua breviseta*), with scattered ephemerals. Bare pebbly or stony ground predominates.

The census data for the two years are presented in table 2. One may note a more

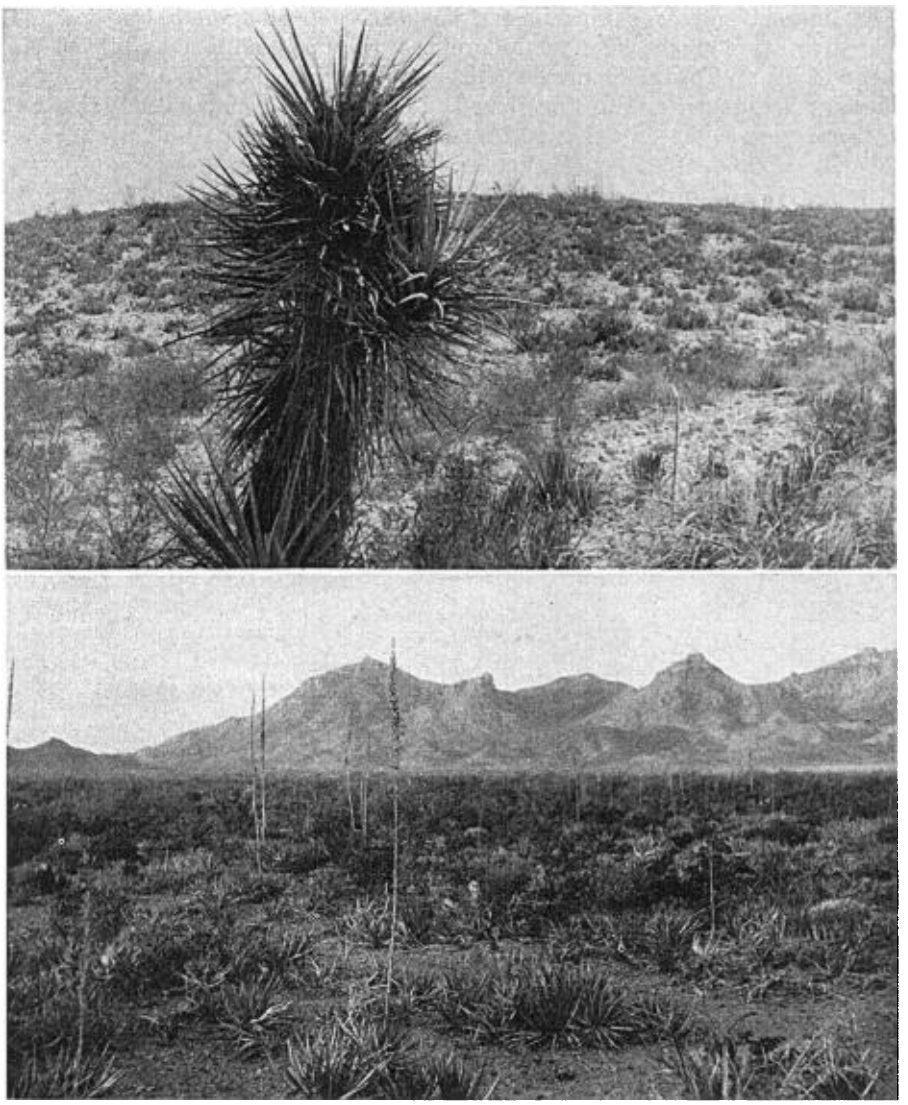

Fig. 2. Upper: desert scrub of Black Gap census plot; *Yucca torreyi* in foreground. Lower: view of Burnham Flat plot showing *Agave lechuguilla* in flower and Chisos Mountains in background.

depauperate fauna and greater variability in composition than that obtaining on the Black Gap census plot. This condition derives from the fact that the vegetation was sparser and less diverse, although it was representative of extensive portions of the outwash plain. Denser stands of shrubs occurred nearby along slightly larger arroyos, and the presence on the plots of Mockingbirds, Pyrrhuloxias, and Cactus Wrens apparently depended upon the population densities of those species in the more desirable stands. This assumption is based on the findings of Kluyver and Tinbergen (1953) in which they reported that certain forest birds in The Netherlands "spilled over" into less desir-

able habitats only in years of higher population density. In addition to those species that appeared on the plot as visitors, the Mourning Dove, Poor-will, Ladder-backed Woodpecker and Brown Towhee occurred sparingly on Burnham Flat. In a rather extensive thicket of taller mesquites with a dense undergrowth of thorny shrubs, such as *Condalia* and *Acacia greggii,* the following additional species were heard: White-winged Dove (1957 only), Elf Owl (1958 only), Verdin, and Bell Vireo.

The presence of surface water within one mile of the Black Gap plot may have accounted for the nesting there of some species, such as the Mourning Dove and House Finch, although possibly the presence of more song perches (for which purpose dead sotol plants were used by Mourning Doves), and the shade provided by denser-foliaged shrubs may also have exerted an influence. Additionally, food patches of Johnson grass (*Sorghastrum*) scattered over the Black Gap area may have favored the granivorous species. The more varied vegetation of the Black Gap plot appears to have attracted more species and more individuals even if those species restricted to the creekbed (Verdin, Pyrrhuloxia) are excluded.

Table 2

Breeding-bird Populations of Open Desert Scrub, 3.1 Miles North of Government Spring, 3400 Feet, Brewster County, Texas

Species	1957 20 acres Equivalent territories[2, 3]	1958[1] 20 acres Equivalent territories	1958[1] 33 acres Equivalent territories
Scaled Quail		+ (1)	+ (1)
California Roadrunner			V (1 day)
Trilling Nighthawk	+ (1)	+ (1)	+ (1)
Poor-will			V (1 night)
Ash-throated Flycatcher	V (1 day)		V (2 days)
Cactus Wren			V (3 days)
Mockingbird	V (2 days)	+ (1)	+ (2)
Black-tailed Gnatcatcher	+ (1)	1 (1)	1 (1)
Loggerhead Shrike			V (1 day)
Scott Oriole	V (2 days)		V (1 day)
Brown-headed Cowbird	*		V (3 days)
Pyrrhuloxia	1 (2)		V (2 days)
House Finch	V (3 days)		V (2 days)
Black-throated Sparrow	2+ (4)	1+ (2)	2 (3)
Totals	3+ (7)	2+ (6)	3+ (8)
Territorial males per 100 acres	15+	10+	(10+)

[1] Plot enlarged from 20 to 33 acres in 1958; values for original plot are presented for comparison to data for 1957.
[2] + indicates less than 0.5 territories; * denotes presence, territory size difficult to assess; V denotes a species apparently nesting nearby, but occurring on the plot only irregularly.
[3] Values in parentheses indicate number of males whose territories extended onto the plot.
Coverage: 1957, April 18, 19, 20, 21; May 12, 24, 28; total man-hours, 13½.
1958, March 23; April 2; May 1, 2, 21, 22, 24; total man-hours, 12.

COMPARISONS TO OTHER AREAS

Both the census plots are fairly representative of the upland desert scrub vegetation of the Big Bend area. Floristically and structurally both may be considered as characteristic of the Chihuahuan Desert as described by Shreve (1942; 1951), and Le Sueur (1945). Shreve (1951:23) characterized the vegetation as ". . . essentially one in which dominance is shared by microphyllous shrubs and low stem succulents or tall semisucculents." The absence of trees is noticeable. The vegetation of the census plot on the Black Gap area fits almost exactly Shreve's (1942:240) description of the ". . . most

distinctive type of vegetation in northern Coahuila," and Le Sueur (1945:56) mentions the occurrence of this complex in eastern Chihuahua. However, the presence of a number of woody plant species listed by Muller (1947) as characteristic of the Tamaulipan thorn shrub of the Gulf coastal plain of northeastern México and southern Texas indicated a transition to that formation. Prominent among the species not listed from eastern Chihuahua by Le Sueur are the shrubs *Porlieria angustifolia, Diospyros texana* and *Lippia ligustrina*. The absence of *Flourensia cernua* from the Black Gap plot is further evidence of this replacement.

The assemblages of birds listed for the Black Gap area and for the Burnham Flat–Grapevine Springs area north of the Chisos Mountains (table 3) compare favorably with those listed for desert scrub at somewhat higher elevations at the base of the Guadalupe Mountains in northern trans-Pecos Texas (Burleigh and Lowery, 1940), and at the eastern base of the nearby Sierra del Carmen of Coahuila (Miller, 1955). With the exceptions listed beyond, no other species of the upland desert scrub was found by Phillips and Thornton (1949:109) for the area between the Sierra Vieja and the Rio Grande in western Presidio County, Texas. This assemblage, then, may be considered a characteristic one for the eastern portion of the Chihuahuan Desert, and I know of no additional species listed in Part 2 of the Mexican Check-list (Pacific Coast Avifauna No. 33, 1957) as occupying Mexican portions of this desert. Excluded from this list are species which range widely and, although foraging in desert scrub, are not attracted to this formation *per se*. Among these are the vultures, diurnal raptors, the Horned Owl (*Bubo virginianus*) and ravens (*Corvus corax* and *C. cryptoleucus*). Excluded also are species, such as the Say Phoebe (*Sayornis saya*) and Rock (*Salpinctes*) and Canyon (*Catherpes*) wrens, which require special features of the geological substrate for nesting, and the oasis inhabitants, such as the Black Phoebe (*Sayornis nigricans*) and Vermilion Flycatcher (*Pyrocephalus rubinus*).

A comparison of the avifauna of the Chihuahuan Desert scrub as here defined to those of the other "creosote bush" deserts (Sonoran and Mojave, as delimited by Shreve, 1942) reveals that the majority of the species are ones that range widely over the deserts of southwestern North America. There are 13 species marked with an asterisk in table 3 that might be considered to comprise a "standard" desert avifauna, occurring in all three of the warm deserts (including the Baja California section of the Sonoran desert, according to Bancroft, 1930). Five of these were detected in Great Basin sagebrush (cold desert) by Fautin (1946), and Behle (1955:10) reported seven from similar habitat. Eight species of more or less regular occurrence in the Chihuahuan Desert also are found in Californian chaparral (four of them represented by populations that are racially distinct from those of the deserts, according to Grinnell and Miller, 1944). Sixteen species of the Chihuahuan Desert are listed from Tamaulipan thorn shrub in Bexar County, Texas, by Quillin and Holleman (1918). Since their writing the House Finch has extended its range into that county. Populations of six of the 16 species differ racially from those of the desert to the west. (For a discussion of the structure of this brushland in relation to the occurrence of certain bird species, see Chapman, 1891:315). To a considerable extent this occurrence of desert species in adjacent formations indicates an attraction to the shrub life form and not to the desert climate *per se*, and in this respect it supports the arguments of Udvardy (1958:62) relative to the derivation of the desert avifauna from that of arboreal formations.

In his discussion of the North American deserts Shreve (1951:25) stated that ". . . the Sonoran Desert is by far the richest in number of life forms and in variety and development of communities . . . and . . . the wealth of life forms . . . is reduced in number and in physiognomic importance on passing north or east into other deserts. Lower rain-

Table 3

Distribution of Birds of Regular Occurrence in Scrub Vegetation of the Chihuahuan Desert

Locality and authority for each of the columns are listed below; asterisk indicates "standard" desert scrub avifauna; values in column 7 are males per 100 acres; V denotes visitor, r indicates infrequent occurrence.

Species	Great Basin	Chaparral	Mojave Desert		Sonoran Desert						Chihuahuan Desert				Tamaulipan thorn shrub
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Scaled Quail (*Callipepla squamata*)											x	x	x	x	x
*Mourning Dove (*Zenaidura macroura*)	x		x	(x)	x		V	x	x	x	x	x	x	x	x
White-winged Dove (*Zenaida asiatica*)							7	x	x	x		x	x	r	
*California Roadrunner (*Geococcyx californianus*)		x	x	x	x	x		x	x	x	x	x	x	x	x
Elf Owl (*Micrathene whitneyi*)						x		x	x				r		
*Trilling Nighthawk (*Chordeiles acutipennis*)			x	x	x	x		x	x	x	x	x	x		
*Poor-will (*Phalaenoptilus nuttallii*)		x	x	x	x	x		x	x	x	x	x	x	x	
Black-chinned Hummingbird (*Archilochus alexandri*)						x					r	x	r	x	
*Ladder-backed Woodpecker (*Dendrocopos scalaris*)			x	x	x	x	V	x	x	x	x	x	x	x	x
*Ash-throated Flycatcher (*Myiarchus cinerascens*)	V	x	x	(x)	x	x	1	x	x	x	x	x	x	x	x
*Verdin (*Auriparus flaviceps*)			x	x	x	x	5	x	x	x		x	x	x	x
Bewick Wren (*Thryomanes bewickii*)		x	x	x							x	x		x	x
*Cactus Wren (*Campylorhynchus brunneicapillus*)			x	x	x	x	8	x	x	x	x	x	x	x	x
*Mockingbird (*Mimus polyglottos*)			x	x			V	x		x	x	x	x	x	x
Curve-billed Thrasher (*Toxostoma curvirostre*)							2	x	x		x	x	x	x	x
Crissal Thrasher (*Toxostoma dorsale*)			x			x		x	x		x	x		x	
*Black-tailed Gnatcatcher (*Polioptila melanura*)		x		x	x	x	6	x	x	x		x	x		
Phainopepla (*Phainopepla nitens*)			x	x		x	1	x	x	x				x	
*Loggerhead Shrike (*Lanius ludovicianus*)	x		x	x	r	x		x	x	x	x	x	x	x	
Bell Vireo (*Vireo bellii*)					x				x			x	x		x
Scott Oriole (*Icterus parisorum*)			x	x					x		r	x	x	x	
Brown-headed Cowbird (*Molothrus ater*)			x	x				x	x		r	x	x		x
Pyrrhuloxia (*Pyrrhuloxia sinuata*)									x	r	x	x	x		x
Varied Bunting (*Passerina versicolor*)									r			r	x	x	
*House Finch (*Carpodacus mexicanus*)	V	x	x	(x)	x	x	2	x	x	x	x	x	x	x	(x)
Brown Towhee (*Pipilo fuscus*)		x		x	r			r	x		r	x	r	x	

Species	Great Basin	Chaparral	Mojave Desert		Sonoran Desert						Chihuahuan Desert				Tamaulipan thorn shrub
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Lark Sparrow (*Chondestes grammacus*)		x		x				r			x			x	x
*Black-throated Sparrow (*Amphispiza bilineata*)	x		x	x	x	x	+	x	x	x	x	x	x	x	x
Other breeding species of desert scrub			9	8	3	5	11	10	14	7	1	0	0	2	
Total species			26	28	17	20	23	31	35	23	22	25	23	24	
Diurnal raptor species			4			3	3	4	6	6	3	1	2		

[1] Great Basin Desert, western Utah, Fautin, 1946.
[2] Californian chaparral, general, Miller, 1951:547–548.
[3] Providence Mountains area, Johnson, Bryant and Miller, 1948:241–243.
[4] Mojave Desert, general, Miller, 1951.
[5] Eastern base, San Jacinto Mountains, Grinnell and Swarth, 1913; Dixon, MS.
[6] Colorado River area, Grinnell, 1914.
[7] Organ Pipe Cactus National Monument, Arizona, Hensley, 1954:195 (see text).
[8] Organ Pipe Cactus National Monument, Arizona, Huey, 1942.
[9] Papago Indian Reservation, Arizona, Sutton and Phillips, 1942.
[10] Lower California, Lat. 27° N, Bancroft, 1930.
[11] Guadalupe Mountain area, Texas, Burleigh and Lowery, 1940.
[12] Black Gap Wildlife Area, southeastern Brewster County, Texas, Thompson, 1953.
[13] Burnham Flat-Grapevine Spring area, Chisos Mountains, Texas, Dixon, MS.
[14] Sierra del Carmen area, Coahuila, Miller, 1955.
[15] Brushland section, Bexar County, Texas, Quillin and Holleman, 1918.

fall, limitation of rain to a single season, and lower winter temperatures are the principal factors involved." Inspection of the totals for desert scrub bird species in the several columns in table 3 suggests that the influence of these contrasts in vegetation structure on avifaunal composition is a controlling one. In the "Arizona Upland" section of the Sonoran Desert (Shreve, 1951:60) the "standard" desert scrub avifauna is augmented by a number of species most of which are closely associated with the towering saguaro cactus (*Carnegia gigantea*). The relationship to structural diversity in one locality may be seen in Hensley's (1954:195) listing of censuses of breeding birds of four plots representing increasing complexity of vegetation in southern Arizona. No species was found nesting in a pure stand of creosote bush, whereas the highest densities and greatest representation of species occurred on plots traversed by "washes" lined by arborescent mesquites, palo verdes, and ironwood. The densities in pairs per 100 acres on Hensley's "open desert" plot (intermediate in structural diversity) are given in table 3 for comparison to the census values in tables 1 and 2. In population density and number of species, the sample is comparable to that for the Black Gap study plot. (The absence of the Trilling Nighthawk and the Poor-will from Hensley's plots is surprising in view of Huey's, 1942:366, comments on their abundance in that vicinity.)

The presence of more ecologic niches, or ways of life in the sense of Elton (1927:63), is evident in the more diverse avifauna of the Arizona Upland desert. Occurring in the same stands in that association there may be several species of the same family; examples are found among the doves, woodpeckers, and *Myiarchus* flycatchers, and in the presence of four species of *Toxostoma* in the same vicinity, as listed by Sutton and Phillips (1942:62). In contrast, one species per family is the rule in the birds of Chihuahuan Desert scrub as here delimited, with the exception of the finch assemblage and the doves. The two species of thrashers are sparsely distributed and segregated as to habitat. This avifauna is a depauperate one, not distinguished by any unique species or combinations of species (except for the greater prevalence of the Varied Bunting). The simpler composition seems clearly related to the structure of the vegetation.

The vegetation and avifauna of the Chihuahuan and Mojave deserts present certain parallels to one another, and, along with the western section of the Sonoran Desert (the

Colorado Desert of many authors), they stand in contrast to the Arizona Upland area. However, many of the populations are more or less continuously distributed throughout the western desert area, whereas there is a distinct vegetational break between the Sonoran and Chihuahuan deserts (Shreve, 1951:23). In addition to avifaunal composition, there is a contrast in the roles played by Screech (*Otus asio*) and Elf owls in the high elevation deserts. Miller and Miller (1951:161) stated that Screech Owls "... occur widely across the deserts of the southwestern United States and the northwestern states of México;" however, they (p. 174) commented upon the rarity of this species in many parts of the Mojave Desert, and in the Big Bend area of Texas the Screech Owl is restricted to the oak belt in the mountains, and the Elf Owl is virtually so. In the Chihuahuan Desert hummingbirds are more restricted in their habitat distribution, and it is my impression that there are fewer diurnal raptors present.

DERIVATION OF DESERT SCRUB AVIFAUNAS

The absence of physiological and morphological specializations for conditions of extreme aridity has been noted by Udvardy (1958:62), who attributed this lack of avian specialization to the relatively recent origin of the North American deserts. This conclusion was supported (1) by the interpretation of Axelrod (1950) that woody vegetation of the deserts was segregated out of more generalized floras with increasing aridity at the close of the Tertiary, and (p. 262) "... became adapted to regional desert climate in post-Middle Pliocene time," and (2) by the physiological investigations of Bartholomew and his associates. The colonization of this unfavorable environment appears to have been accomplished principally by behavioral adjustments (see Hensley, 1954:22 and Dawson, 1954:107–117) rather than physiological specializations (see Bartholomew and Cade, 1956:409–411, and Bartholomew and Dawson, 1958:154). Conceivably, however, factors other than time alone could have been operative in restricting the development of specializations for existence in desert scrub. The differentiation of the Abert Towhee (*Pipilo aberti*) from Brown Towhee stock, as reconstructed by Davis (1951:98–99), indicates that the Sonoran Desert must have been in existence for a period sufficient to permit the evolution of that species at least. Davis concluded that populations of Brown Towhees were crowded into riparian thickets of the lower Colorado River drainage by the encroachment of grassland, and that the differentiation of *P. aberti* took place along the streamcourses. Thus the isolation necessary for speciation was provided by discontinuities in vegetation. Perhaps the progenitors of the Lucy Warbler (*Vermivora luciae*) also were forced to enter riparian timber (inhabited in southwestern Utah today, according to Behle, 1943:15) or mesquite forest, where their evolution could have proceeded in isolation (see Grinnell, 1914:99).

We should be cautious in supposing that species now inhabiting a given region evolved there, for Miller (1943) reported the occurrence of the Gilded Flicker (*Colaptes chrysoides*), a species now found only west of the continental divide, from a Pleistocene deposit in Nuevo León in northeastern México. Nevertheless a number of species, such as the Elf Owl, Gila Woodpecker (*Centurus uropygialis*), several species of thrashers, and the Lucy Warbler, appear to have centers of distribution or abundance in the more varied sections of the Sonoran Desert. Regardless of their area of origin, these are essentially geographic (and ecologic) representatives of widespread groups that filled vacant niches that existed there but not in other desert regions, a view advanced by Swarth (1920:14). However, the desert scrub vegetation as a whole presents few opportunities for diverse ways of life, and apparently it came to be occupied by a few widely ranging species that possibly broadened their ecologic amplitude in the absence of competitors. The populations of most of these species probably were connected with others of their

species at least intermittently by continuity of desert scrub with woodland at higher elevations or with arid subtropical scrub to the south or east. Species ranging into the deserts from centers of abundance in woodland today include the Ladder-backed Woodpecker, Ash-throated Flycatcher and Scott Oriole. Examples of species that may have entered the deserts originally from arid subtropical scrub include some that exhibit definite altitudinal limits in the Chisos Mountains of Texas, such as the Trilling Nighthawk, Black-tailed Gnatcatcher, Verdin and Pyrrhuloxia. The geographic distribution of these species in the southwestern United States, and the occurrence of all but the gnatcatcher in "tropical" areas of Sonora (van Rossem, 1945) support this contention. Apart from the ground-dwelling quails and thrashers, few species are restricted to desert scrub vegetation (see table 3 and Miller, 1951:543–544), a fact that seems related to Axelrod's (1950:255) observation concerning woody plants that "large numbers of arid subtropical scrub species also make up an integral part of Sonoran and Chihuahuan desert vegetation." Thus, it would appear that the occupancy of desert scrub by a few euryoecious species (resulting in reduction of ecologic opportunity) and the incompleteness of their isolation from conspecific populations in other more or less arborescent formations have hampered evolution in new directions in birds occurring in the desert scrub of the southwestern United States.

SUMMARY

Breeding-bird population data from two plots in desert scrub in the Big Bend area of Texas, censused for 2 and 3 years, respectively, revealed little change in species composition from one year to the next, but some fluctuations in density values. The plots are considered representative of open desert scrub of the Chihuahuan Desert. The avifauna of that scrub is shown to be depauperate in relation to that of the deserts of southern Arizona, consisting of species that range widely through the deserts and continguous woody plant formations. Comparison of the avifaunas of several desert areas reveals a relationship between species composition and structural diversity of vegetation. The colonization of desert scrub by euryoecious bird species whose populations were incompletely isolated from those inhabiting other woody plant formations is suggested as a factor that may have hampered the evolution of specializations for life under extreme desert conditions.

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