DENSITIES AND SPECIES COMPOSITION OF BREEDING BIRDS OF A CREOSOTEBUSH COMMUNITY IN SOUTHERN NEW MEXICO

RALPH J. RAITT AND RICHARD L. MAZE
Department of Biology
New Mexico State University
Las Cruces, New Mexico 88001

Studies of breeding bird densities in the deserts of North America have not been numerous. Search of the literature reveals only three: one in the Colorado Desert (Hutchinson and Hutchinson 1941, 1942), one in the Sonoran Desert of southern Arizona by Hensley (1954), and one in the Chihuahuan Desert in the Big Bend region of western Texas by Dixon (1959). The last author reviewed the results of these studies and of the more numerous faunistic works for the region. In none of these papers have the breeding birds of the desert areas of the upper Rio Grande Valley received detailed attention. The present study was undertaken to determine species composition, habitat preferences, and population densities of breeding birds on a square mile of creosotebush desert immediately east of the Rio Grande Valley in southern New Mexico. The investigations were conducted in 1964 and 1965 east of Las Cruces, Dona Ana County.

STUDY AREA

LOCATION, TOPOGRAPHY AND SOILS

Section 13, T23S, R2E, located about one-quarter mile northeast of Tortugas Mountain, Dona Ana County, New Mexico, was selected as the study area. This site was chosen because it is representative of southern New Mexico desert communities (Gardner 1951) and, more broadly, of the Chihuahuan Desert (Shreve 1942) and because vegetational analyses have been conducted on the area (Singh, 1964).

The size of the area (640 acres) is larger than is recommended by Kendeigh (1944) for bird censuses of either forests or fields; however, preliminary work led us to believe that the open nature of the terrain and vegetation would permit adequate coverage of such a large area and that the low densities of many of the species of birds would, in fact, necessitate the use of a large sample area in order to measure their density with satisfactory accuracy.

The area is in the gently sloping alluvial "mesa" between the Organ Mountains to the east and the Rio Grande Valley to the west. Elevations range from 4260 to 4400 feet above sea level. Numerous east-west intermittent water courses have dissected the area to a depth of from several feet to about 30 feet. Most of these arroyos are small with V-shaped cross sections, but two large flat-bottomed ones are present (figs. 3 and 4). Most ridge-crests are nearly flat and are covered by typical "desert pavement" overlying gravel soils and often a well-developed caliche layer (Gile 1961). Arroyos, on the other hand, contain alluvial silts and sandy loams, with coarse gravel in the actual water courses.

CLIMATE

The climate of the region is arid. The United States Weather Bureau station at New Mexico State University, about four miles from the study area, has recorded a long-term mean annual precipitation of 8.01 inches. Annual amounts vary considerably; in 1964 the total was only 3.62 inches, whereas in 1965 it was 8.29 inches. Showers are often confined to small areas, and some water reaches the study area through runoff from rainfall occurring in areas upslope. Most of the rain falls from June through September during the growing season. There is no permanent free water on the area, and any free water is ephemeral indeed. The nearest permanent water is at least three miles away.

Mean temperatures were 60.0°F in 1964 and 61.3°F in 1965. In 1964 extremes were 6°F on 10 January and 106°F on 3 July. Similar extremes were recorded in 1965: 11°F on 4 March and 100°F on 8 August. Growing seasons average 206 days; there were 178 frost-free days in 1964 and 208 in 1965.

VEGETATION

Creosotebush (*Larrea divaricata*) dominates the vegetation throughout the study area. Other typical desert shrubs are subdominants. Gardner (1951) and Fosberg (1940) have described the vegetation of the general region.
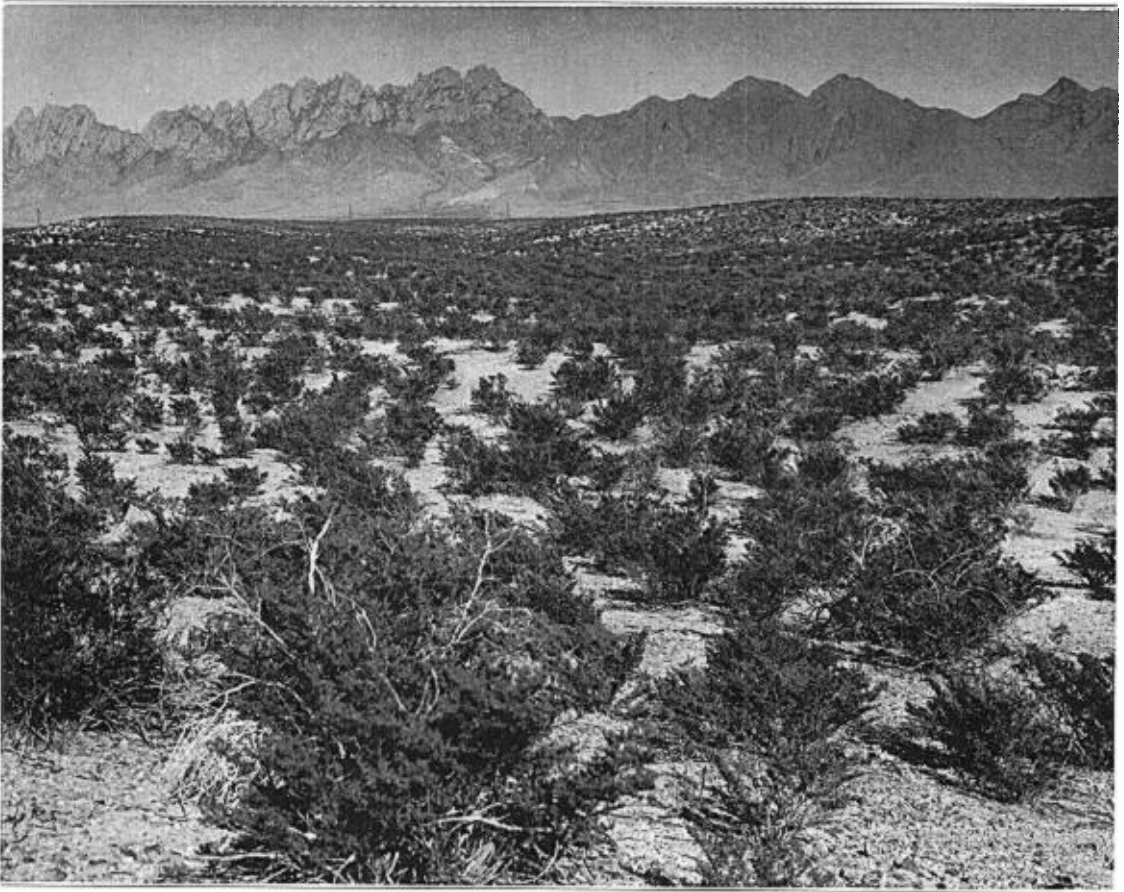
For purposes of analysis of distribution of

FIGURE 1.   View of a portion of the study area, facing east from south of largest arroyo near east-west mid-point (see fig. 3). Topography and vegetation are typical of upland areas. Shrubs are creosotebushes. A minor arroyo runs across picture in rear foreground. Organ Mountains are in background.

birds within the area we have recognized three kinds of plant communities, each of which is under obvious topographic and edaphic control. The predominant type occupies the tops and gently sloping sides of the divides between arroyos. It is characterized by low, well-spaced shrubs of two principal species: creosotebush and range ratany (*Krameria parvifolia*); few other perennial plants and few annuals are present (fig. 1).

The second type occupies the bottoms of the numerous small arroyos. The vegetation there is similar to that on the flats, but an additional subdominant, *Acacia constricta*, is more abundant, and both it and the dominant creosotebush reach greater stature and higher density in these small watercourses. Singh (1964) studied the vegetation of these ridges and small arroyos and found the three species mentioned above to be the only ones of significant importance; he found a total ground cover of the shrub canopies of 19.6 per cent and a mean height of the dominant creosotebush of 65.8 cm (fig. 1).

The third type of habitat is that found along

the larger arroyos, especially the one that very nearly bisects the section from northeast to southwest. Strips of vegetation along arroyo banks and on islands within them are characterized by shrubs of more varied species composition, of higher density and tendency toward clumping, and of greater stature than those in small arroyos or on ridge tops. I. W. Dodson (unpublished data) found as important woody species in the largest arroyo, Apache plume (*Fallugia paradoxa*), brickell bush (*Brickellia laciniata*), Mormon tea (*Ephedra trifurca*), desert willow (*Chilopsis linearis*), and little-leaf sumac (*Rhus microphylla*) in addition to the three dominants of the divides. His canopy-cover measurement was 29.1 per cent, considerably higher than for the divides, in spite of the inclusion in his sample units of rather large segments of the bare sand and gravel of the watercourse proper. Creosotebush is dominant even there, but individuals are taller (average 73.6 cm). Herbaceous vegetation is far more abundant and varied along the large arroyos. As far as diversity and density of birds are concerned,
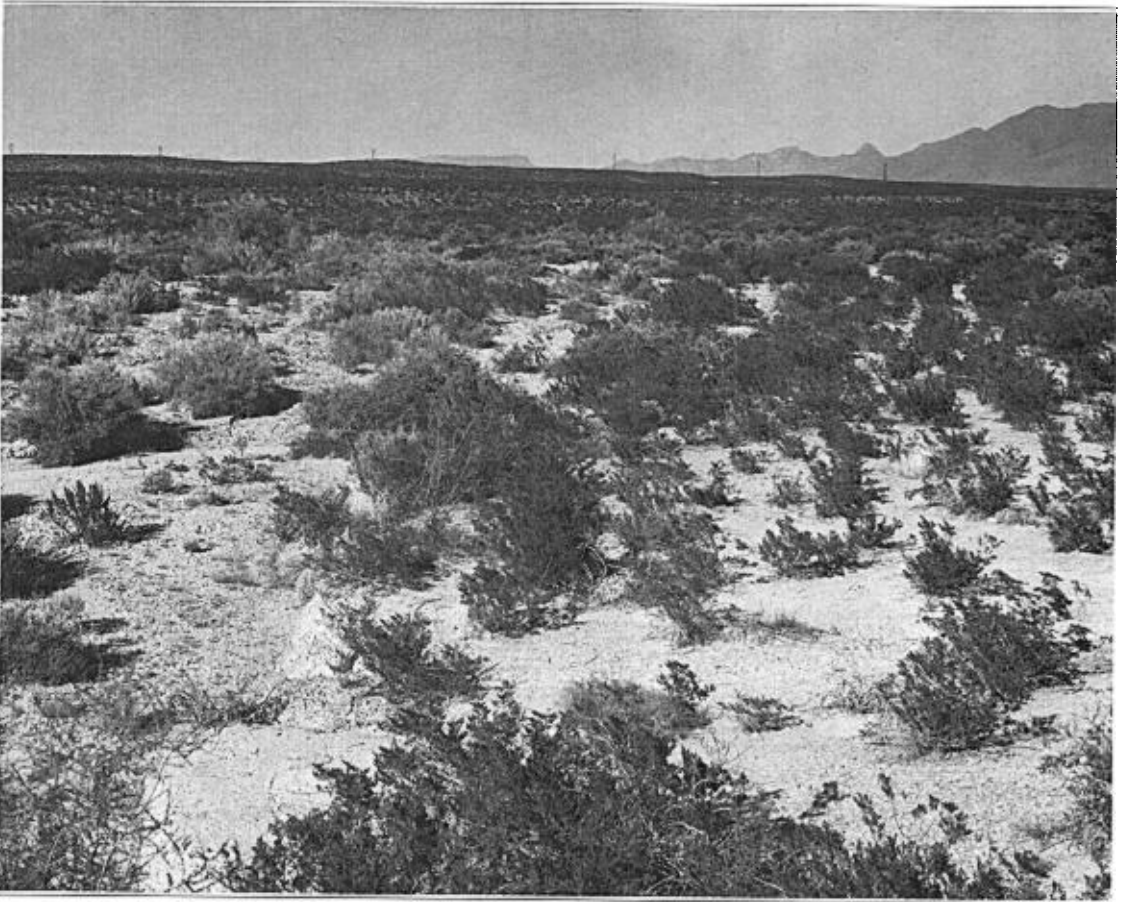
FIGURE 2. View of a portion of the study area, facing northeast from same point as in figure 1, diagonally across the largest arroyo (see fig. 3). Creosotebush and *Acacia constricta* are plants in foreground. Darker plants throughout are creosotebushes. In arroyo proper are principally apache plume and brickell bush. A single desert willow, approximately 10 feet tall, stands in the left background. Vegetation of arroyo at this point is typical of large arroyos generally.

the important differences between the vegetation of the large arroyos and of the divides are the clumping of shrubs with dense canopies (*Rhus* and *Fallugia*) to form small thickets, the addition of species of greater height, especially *Chilopsis* which reaches 20 feet, and the greater production of annual herbaceous plants (fig. 2).

As Dixon (1959:399) has stated, the inclusion of this degree of vegetational diversity is contrary to usual practices in bird censuses. However, both Dixon and Hensley (1954), the other principal worker on desert bird densities, used census plots as diverse as ours in topography and vegetation. The principal justification for this choice of study areas is that the typical desert upland *bajada*, or alluvial slope, is a heavily dissected surface with a "fine grained" pattern of dry washes and arroyos. References to the maps of figures 3 and 4, which show only relatively large arroyos, will confirm this statement; Hensley (1954:190) has also described this topographic phenome-

non. Thus, it would be difficult and, perhaps, unreasonable to choose a study area of any size (*i.e.*, one much larger than the average territory size of some of the breeding birds) that did not contain arroyos of varying size with divides between them. This heterogeneity of topography produces similar heterogeneity in vegetation. The three types of vegetation that we have recognized and just described are, we feel, sufficiently intimately intermingled to permit considering them as a single complex ecological unit with internal variation. An additional unifying feature is that creosotebushes dominate the vegetation in each subtype and co-dominants in each are shrubs.

METHODS

The principal method of investigation used was similar to that described by Kendeigh (1944). The area was systematically searched by the junior author, and locations of individual birds, pairs, families, singing individuals, and nests were marked on maps. This procedure was repeated five times in each of the two
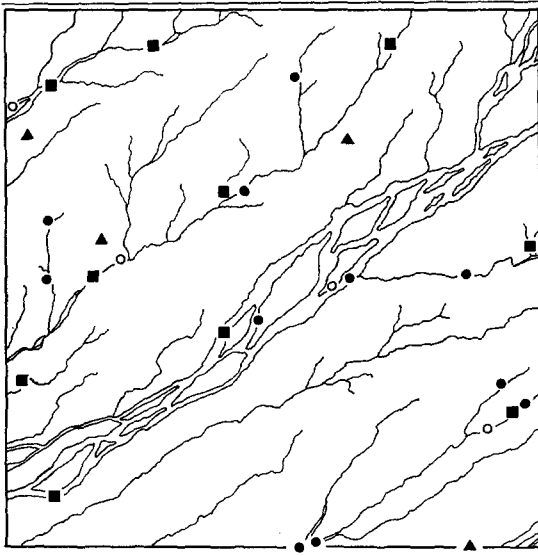
FIGURE 3. Map of the study area (section 13, T23S, R2E) in southern New Mexico showing drainage patterns and nesting sites of the four most abundant breeding species during 1964. Nest sites are represented as follows: solid triangles, Mourning Dove; solid squares, Verdin; open circles, Black-tailed Gnatcatcher; and solid circles, Black-throated Sparrow.

breeding seasons, between 10 May and 23 August 1964 and between 26 March and 12 July 1965.

Orientation within the area and mapping were facilitated by the prior division of the area into a grid marked by numbered steel stakes 100 feet apart. Increased accuracy and a certain saving of field time were afforded by the exchange of information with two other workers; David R. Moore was studying behavior and ecology of the Verdins (*Auriparus flavi-*
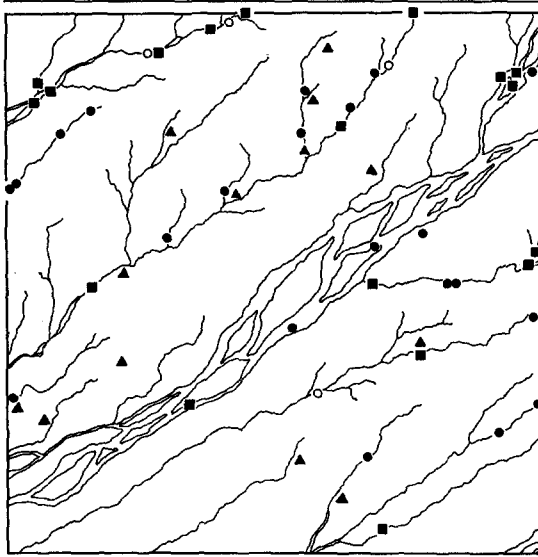

FIGURE 4. Map of study area in southern New Mexico showing drainage patterns and nesting sites of the four most abundant breeding species during 1965. Symbols as in figure 3.

TABLE 1. Density of breeding birds nesting on the study area in 1964 and 1965.

Species	Total breeding pairs		Breeding pairs per 100 acres	
	1964	1965	1964	1965[a]
Scaled Quail	1	1	0.2	0.2
Mourning Dove	5	8	0.8	1.3
White-throated Swift	0	1	0.0	0.2
Verdin	16[b]	17	2.5	2.8
Cactus Wren	0	2	0.0	0.3
Crissal Thrasher	4	1	0.6	0.2
Black-tailed Gnatcatcher	3	9	0.5	2.0
Loggerhead Shrike	0	1	0.0	0.2
Black-throated Sparrow	25	63	3.9	10.5
Totals:	54	103	8.5	17.7

[a] Calculation of densities per 100 acres for 1965 based on a total area of 600 acres rather than 640 acres as in 1964. Human interference resulted in a shrinkage of the available habitat between 1964 and 1965.
[b] Figures for Verdin densities for 1964 are relatively more accurate than for other species because of information received from David R. Moore.

ceps) on the area concurrently, and Donald B. Heckenlively was studying song in the Black-throated Sparrows (*Amphispiza bilineata*). The ability to cross-reference our findings with theirs on the two most abundant species was helpful.

Preliminary survey of the breeding avifauna in 1963 by the senior author and George I. Child indicated that the usual methods of enumeration of singing males would be unsuitable for most of the species on the area because they do not have a distinctive primary song or are only weakly territorial, or because their occurrence on the area is too sparse and irregular. For these reasons this more intensive study was from its beginning directed toward location of active nests; thus the values on density that follow, except in the case of the Black-throated Sparrow, are principally based on numbers of nests. The conspicuous singing behavior of male Black-throated Sparrows allowed mapping of territories in this species.

In all cases allowance was made for renesting in that the numbers of pairs assumed to be breeding were equal to the maximum number of active nests present at any one time. In a few cases observation of a pair in a restricted area over a period of more than a week was taken as sufficient evidence of its establishment for breeding even though a nest was not found; in these instances, also, possible error associated with renesting was taken into account. The estimations of density of breeding pairs made by these methods would appear to be conservative but generally comparable to those made by counting singing territorial males.

RESULTS

SPECIES COMPOSITION

Regular census procedures resulted in definite evidence of breeding on the area for nine species. A list of these species with estimates of breeding densities in each year is given in table 1. Five species were present in some numbers in both 1964 and 1965 and thus may be considered to comprise the basic avifauna. Each of the others was noted in only one of the two breeding seasons or, in the case of the Scaled Quail, occurred in very low density each season; these species must be considered

TABLE 2. Habitat distribution of nests in 1965.

Species	Major[a] arroyo	Minor[a] arroyo	Upland[a] area
Scaled Quail	X[b]	?	?
Mourning Dove	0	3	10
White-throated Swift	0	0	1
Verdin	11	8	0
Cactus Wren	2	0	0
Crissal Thrasher[c]	4	0	0
Black-tailed Gnatcatcher	2	2	0
Loggerhead Shrike	0	1	0
Black-throated Sparrow	3	18	0
Total:	22	32	11

[a] From field observations and measurements on aerial photographs major arroyo habitats are estimated to include 5 per cent of the area, minor arroyos 10 per cent, and upland areas 85 per cent.
[b] Adults and young seen but no nests observed.
[c] Crissal Thrasher data given for 1964. No nests were observed in 1965.

TABLE 3. Placements of nests observed on the study area in 1965.

Breeding species	Plant species utilized[a]	Height of nests[b]
Mourning Dove	—	13 nests on ground
White-throated Swift	—	1 nest under rock
Verdin	15 whitethorn 3 sumac 1 desert willow	5.04 ± 1.05 (12)
Cactus Wren	1 sumac 1 cholla	4.67 ± 0.58 (3)
Crissal Thrasher[c]	4 sumac	3.50 (1)
Black-tailed Gnatcatcher	3 sumac 1 graythorn	2.88 ± 0.48 (4)
Loggerhead Shrike	1 graythorn	3.25 (2)
Black-throated Sparrow	18 creosotebush 2 graythorn 1 apache plume	1.12 ± 0.98 (17)

[a] Numerals indicate numbers of nests in each kind of plant.
[b] Heights are in feet and include mean ± SD, with number of samples in parentheses.
[c] Data are for 1964. None observed in 1965.

as minor faunal elements. Two other species should also be considered as a part of the breeding avifauna even though acceptable evidence of their breeding on the area was not obtained in 1964 and 1965. Roadrunners (*Geococcyx californianus*) are generally but sparingly distributed throughout this region, and two adults with a juvenile were seen on the study area in the summer of 1963. Lesser Nighthawks (*Chordeiles acutipennis*) were seen often in both years, and three nests of this species were found on the area in 1963. Gambel Quail (*Lophortyx gambelii*), Rock Wrens (*Salpinctes obsoletus*), Scott Orioles (*Icterus parisorum*), and Brown-headed Cowbirds (*Molothrus ater*) are possible breeders on the area, for all were seen during the breeding season, but no definite evidence of reproduction was noted.

DENSITIES

Census results (table 1) require only slight comment at this point. As described previously, the figures for most species represent numbers of active nests and therefore are probably conservative. Although numbers of Black-throated Sparrows are based on territories occupied by singing males and are thus less conservative, the conspicuous singing behavior of these males in open country and crosschecks with results of other field workers on the area add to confidence in their accuracy. Almost certainly the general orders of magnitude of variation in density among species are as indicated by the data. The higher values for 1965 are certainly at least partly due to increased effectiveness of methods—including earlier beginning of census work—resulting from the experience gained in 1964. Since the results of 1965 are more reliable, they will be used for comparisons to data from other regions.

ECOLOGICAL VARIATION WITHIN THE STUDY AREA

Mapped locations of nests (figs. 3 and 4) and notes as to habitat (table 2) and species of plant in which the nests were built (table 3) provide the basis for ecological comparison of species and of analysis of variation in usage by birds of the various habitats within the area.

These data help to explain at least part of the variation in density among the species. The Black-throated Sparrow was the most abundant species, and it also showed the broadest ecological amplitude within the area. The maps (figs. 3 and 4) indicate that although they did not leave arroyos for nesting in 1964 and 1965, Black-throated Sparrows nested farther up in the smaller arroyos than did other species. (Old nests from previous years in upland areas indicated that at times they do leave arroyos.) During the study only Mourning Doves (*Zenaidura macroura*) used the divides between arroyos for nesting, but they did not nest in the other habitats to the extent that Black-throated Sparrows did (table 2). Perhaps the key to the ubiquitousness of Black-throated Sparrows is their ability to use creosotebushes (table 3). This shrub is dominant in all three major habitat types and is virtually the sole plant species in the upland type. No other bird species built nests in these shrubs. Another factor bearing on the wide distribution of Black-throated Sparrows is their ability to subsist with very low moisture intake (Smyth and Bartholomew 1966). Verdins were second in density; they also made

broad use of the area but were limited for actual nesting by the occurrence of thorny or spinescent shrubs over four feet tall. The most widespread of such plants on the area is white thorn (*Acacia constricta*); it is also the species most frequently used (table 3). This species does occur in all three habitat types, but on the uplands and in the smallest arroyos plants are not tall enough to serve as nest sites for Verdins; and presumably this lack of suitable nest plants is responsible for the absence of Verdin nests from these habitats. Dispersion patterns of large shrubs in the large arroyos may also have limited the densities of Verdins. In spite of the average high densities of large shrubs in the large arroyos, Verdin densities are not high even though observations in areas of sparse occurrence of large shrubs indicated that a pair of Verdins requires as few as one large shrub of suitable life form (*e.g.*, *Acacia*, *Prosopis*, *Rhus*) in a territory. Probably the clumped dispersion of shrubs in these arroyos results in some potential territories with inadequate nesting shrubs while other territories contain an excess of shrubs dominated by single territorial pairs.

It is, of course, very likely that distribution and abundance of Black-throated Sparrows and Verdins and the other species as well are not under sole control of distribution and abundance of potential nest sites. The aforementioned tolerance of Black-throated Sparrows to low moisture intake is one example of a different controlling factor, perhaps accounting for the smaller territories than in Verdins. In general, lack of data on other potential controlling factors precludes further speculation.

All Mourning Dove nests found on the area were on the ground, in contrast to predominant tree nesting by doves in the nearby riparian thickets along the Rio Grande. The utilization of the resources of the study area by Mourning Doves is different from that by other birds (except nighthawks) for it is almost solely for nesting; feeding and watering were carried on principally outside the area.

Densities of other species were so low that data were too few to reveal patterns for individual species. However, the several sparsely distributed insectivorous species, Cactus Wren (*Campylorhynchus brunneicapillus*), Crissal Thrasher (*Toxostoma dorsale*), and Black-tailed Gnatcatcher (*Polioptila melanura*), did appear to be restricted to portions of larger arroyos with dense shrubs for both nesting and feeding.

In summary, the general pattern of utilization of the area is a concentration of pairs of several species in those arroyos with the heaviest vegetation, with a trend of decreasing density and decreasing species diversity from these larger arroyos through smaller ones and finally to upland, where there were no full-time breeding residents. Although three different habitat types can be recognized on the area and these habitats differ in kinds and densities of breeding birds, it seems realistic to regard the bird community as a single heterogeneous one. As explained earlier, the habitat types are too intimately intermixed for meaningful areal subdivision, and the breeding birds of small arroyos and upland habitats are merely increasingly depauperate representatives of the avifauna of large arroyos.

DISCUSSION
FAUNISTIC COMPARISONS

Dixon (1959) recently compared species compositions of avifaunas of various North American deserts, and we will rely heavily on his findings for comparative data. Since communities of the sort in which this study was done are often considered as portions of the Chihuahuan Desert (Benson and Darrow 1954: fig. 2; Shelford 1963:fig. 15–1), the logical first comparison is with other faunas of this region. Dixon's own work was carried on in the Chihuahuan Desert, and his principal faunistic table (1959:table 3) is based on a composite list of species breeding in desert areas of southeastern New Mexico, western Texas, and northwestern Coahuila.

We have amended this list for our faunistic comparisons in table 4. Following Dixon further we have eliminated from consideration diurnal raptors and species that require special geological features; the latter group includes the White-throated Swift (*Aeronautes saxatalis*), the one pair of which bred on the area in 1965, and Rock Wrens, which were seen on the area, probably as visitants, in the breeding season. Of the remaining 14 species that breed on the area or in similar contiguous communities, all but one are included in the list based on other Chihuahuan avifaunas. This single exceptional species, the Gambel Quail, breeds irregularly and sparsely in the larger arroyos of these mesas, although they must be considered marginal habitat because it reaches much higher densities in riparian shrublands and *bosques* in the Rio Grande floodplain and in the canyon bottoms at the bases of mountains. It was not included in Dixon's list because it reaches the easternmost limit of its range in central New Mexico and extreme western Texas (Aldrich and Duvall 1955) and is thus absent from most of the

TABLE 4. Species composition of avifaunas of three desert bird censuses.

Species[a]	Southern New Mexico[b]	Western Texas[c]	Southern Arizona[d]
Scaled Quail	X	X	
*Mourning Dove	X	X	X
White-winged Dove			X
*Roadrunner	X	X	
Elf Owl		X	
*Lesser Nighthawk	X	X	
*Poorwill	X[e]	X	
*Ladder-backed Woodpecker		X	
*Ash-throated Flycatcher		X	X
*Verdin	X	X	X
*Cactus Wren	X	X	X
*Mockingbird		X	
Curve-billed Thrasher		X	X
Crissal Thrasher	X		
*Black-tailed Gnatcatcher	X	X	X
Phainopepla			X
*Loggerhead Shrike	X	X	X
Scott Oriole	X	X	
Brown-headed Cowbird	X	X	
Pyrrhuloxia		X	
*House Finch		X	X
*Black-throated Sparrow	X	X	X
Additional Species	1	0	6
Total Species	14	19	17

* Considered by Dixon (1959) to be members of "standard" desert avifauna.
[a] List is modified from that of Dixon (1959:table 3) of desert scrub species of Big Bend region of western Texas.
[b] Species known to have been breeding on or adjacent to the creosotebush census area of the present study.
[c] Species found by Dixon (1959:tables 1 and 2) to be breeding on either of his two census areas in the Big Bend region.
[d] Species found by Hensley (1954: table 10) to be breeding on any one of his census areas in Organ Pipe National Monument.
[e] Not encountered in censuses but almost certainly a member of breeding avifauna.

Chihuahuan Desert. It is, however, a common component of avifaunas of the Sonoran and Mojave deserts.

The principal conclusion to be drawn from comparison of our species list with Dixon's table is that the avifauna of the creosotebush communities of southern New Mexico is a poor representation of those of the other Chihuahuan Desert areas. Only 13, or 14 if the doubtful Poorwill (*Phalaenoptilus nuttallii*) is included, of the 28 species regarded by Dixon as members of the Chihuahuan avifauna are regular breeders in this New Mexico desert. Furthermore, three of the "standard" desert scrub species are missing. Perhaps the standard desert avifauna should be reduced to those species that can tolerate even the relatively poor desert scrub of area such as ours.

For most of the absent species some indica-

tion of the reasons for their absence can be obtained from their distribution patterns. Four species do not breed even in the general area. These are the Elf Owl (*Micrathene whitneyi*), Bell Vireo (*Vireo bellii*), Varied Bunting (*Passerina versicolor*), and Lark Sparrow (*Chondestes grammacus*) (Bailey 1928; A.O.U. 1957; Ligon 1961). The remaining species all breed within a few miles of the study area, either on the lower slopes or canyons of the Organ Mountains or on the floodplain of the Rio Grande, or both. Black-chinned Hummingbirds (*Archilochus alexandri*), Ladder-backed Woodpeckers (*Dendrocopos scalaris*), Ash-throated Flycatchers (*Myiarchus cinerascens*), Mockingbirds (*Mimus polyglottos*), Pyrrhuloxias (*Pyrrhuloxia sinuata*), and House Finches (*Carpodacus mexicanus*) are common breeders in both mountain canyon mouths and floodplain thickets (*bosques*). These two habitats have in common several features that are not possessed by the creosotebush communities, the most important of which is the presence of trees and dense stands of tall shrubs. All the bird species listed previously require tall plants for foraging or nesting or both. Their absence from the study area and other creosotebush communities appears to be a result of the extreme scarcity of any plants over six feet tall. Only desert willows regularly reach appreciably above this height, but they are widely dispersed along the major arroyos, and the canopy they provide is, thus, markedly discontinuous.

Floodplain and canyon habitats also contain more ground cover on the average and are more likely to have available free water than the creosotebush-covered mesas, but these two factors are probably less important than the presence of clumps of tall shrubs or trees in controlling species distributions. Evidence for this conclusion is that the bird species in question do obviously use tall shrubs and trees for nesting, roosting, and foraging. Furthermore, they may be found inhabiting floodplain or canyon thickets where surface moisture is as low and herbaceous ground cover and free water are just as scarce as on the mesas, whereas these same bird species are absent from oases on the mesas, such as cattle tanks, where water is always available and where herbaceous plants are dense, but where trees are not found.

Additional support for this view lies in Dixon's (1959:399) statement that Ash-throated Flycatchers and House Finches depended on the tall yuccas present in his study area. Such yuccas are uncommon in southern New Mexico and are rare on our study area. He also

mentions that Mockingbirds and Pyrrhuloxias centered their activities around dense arroyo shrubs (3–9 feet tall).

Several other species listed in table 4 do not nest in creosotebush communities but do nest in either floodplain or mountain canyon habitats, but not in both. Brown Towhees (*Pipilo fuscus*) and Bewick Wrens (*Thryomanes bewickii*) are regular inhabitants of canyon mouths at the base of the Organ Mountains (elevation above 5500 ft) but do not nest below this level in our area. White-winged Doves (*Zenaida asiatica*) and Phainopeplas (*Phainopepla nitens*) nest in small numbers in the Rio Grande Valley but in no other neighboring areas. The breeding distribution of Curve-billed Thrashers (*Toxostoma curvirostre*) in the general area is poorly known; certainly they are uncommon, perhaps as a result of the scarcity of cholla cacti, but they are absent from the mesas and present at the edge of the valley. Factors limiting these species to their respective habitats are not obvious, but it seems as if at least the Phainopepla would find suitable habitat in mesa arroyos if tall shrubs were more abundant in them, as members of this species live in such situations in other desert regions.

In attempting to make further general comparisons and evaluations concerning the desert avifauna of southern New Mexico, we have encountered difficult problems stemming from general ecological and biogeographical questions. Some of these are the diagnostic features and boundaries of the Chihuahuan Desert and other such subdivisions, the nature of aboriginal or climax communities, and even the meaning of the term "desert." Not surprisingly, these long-standing general questions will not be answered here; but perhaps the data on bird distribution will contribute to eventual answers. Specifically, the question is what should be considered as the desert scrub avifauna of this region. If this avifauna is assumed to include only those forms inhabiting creosotebush-dominated communities of the upland slopes or *bajadas* such as that of our study area, then it includes only 14 species (still excluding diurnal birds of prey and those species dependent upon special geological features). If the floodplain and mountain canyon habitats are included, then at least eight additional species from Dixon's list would be added, as would several others that might be considered as desert forms; these latter include the Screech Owl (*Otus asio*), Western Kingbird (*Tyrannus verticalis*), Hooded Oriole (*Icterus cucullatus*), Cassin Sparrow (*Aimophila cassinii*), and probably

others. Still more species would be added if desert scrub-savanna habitats were included. Thus, the inclusion or exclusion of certain habitats makes the difference between an avifauna of 14 species and one of perhaps twice that number.

It is probably pertinent to emphasize at this point that the kind of vegetation included within our study area is typical of large areas of what is termed Chihuahuan Desert. A large proportion of the creosotebush-tarbush (*Larrea-Flourensia*) vegetation type of Küchler's (1964) vegetation map of the United States is composed of communities very similar to that of our study; on his map the regions indicated as bearing trans-Pecos shrub savanna (*Flourensia-Larrea*) and grama-tobosa shrubsteppe (*Bouteloua-Hilaria-Larrea*) also contain large areas with similar vegetation. Likewise, extensive areas of Chihuahua and Durango support creosotebush-dominated communities of similar structure and plant species composition (Raitt, personal observation). If the type of vegetation on the study area is typical of the Chihuahuan Desert, then the avifauna is probably typical also. Since all that appears to be lacking for several species of birds are some trees or arborescent shrubs, it might be expected that some areas would support slightly richer avifaunas by virtue of the presence of denser stands of desert willow or of some of the larger yuccas or agaves or of tall mesquite, in response to local edaphic variations. These tentative extrapolations and qualified generalizations are certainly inadequate substitutes for statements based on quantitative data. Field studies to obtain such data on both vegetation and birds are greatly needed for this somewhat neglected region.

One corollary of the foregoing discussion of what is the "typical" Chihuahuan Desert community is that the vegetation and avifaunas of Dixon's study area in the Big Bend region of Texas are extraordinarily luxuriant and diverse for this desert subdivision. This conclusion is supported by Dixon's finding of floristic elements typical of Tamaulipan thorn shrub vegetation in addition to ones typical of Chihuahuan Desert. These same southern plant species—*Porlieria angustifolia*, *Diospyros texana*, and *Lippia ligustrina*—are tall shrubs with dense foliage, the life form that we have postulated as limiting the occurrence of bird species in our area. Dixon (1967, *in litt.*) has informed us that the Black Gap area of his study shows greater edaphic diversity than the other areas; he believes that this factor and the longer growing season correlated with lower altitude (2500 ft) and lower latitude

are responsible for the greater vegetational complexity.

The question remains as to whether the bird species confined to floodplains and mountain canyons should be included as parts of the general desert avifauna of this region. A case could be argued for including them. Many are regular inhabitants of more than one of the major variations of the desert shrub biome; several are "standard" desert species common to all broad North American desert avifaunas. In the habitats in which they breed in southern New Mexico, sclerophyllous, thorny, or spinescent plants, usually classified as xerophytes, are at least important co-dominants. The floodplain habitats include arborescent mesquite (*Prosopis juliflora*), screwbean (*Prosopis pubescens*), *Atriplex canescens*, and the introduced salt cedar (*Tamarix pentandra*), among others, as dominant species (see Campbell and Dick-Peddie [1964] for a description of this vegetation). The lower mountain canyons are bordered by vegetation that is dominated by trees including the "desert" species, hackberry (*Celtis reticulata*) and soapberry (*Sapindus saponaria*), and shrubs such as mesquite, *Mimosa biuncifera*, and apache plume. These habitats also support populations of all the birds species of the creosotebush communities.

On the other hand, most communities of both of these habitats contain species of both plants and birds characteristic of more mesic zones. In the floodplains these other forms are ones that are usually riparian, including, among plants, cottonwoods (*Populus fremontii*), willows (*Salix* spp.), seep willow (*Baccharis glutinosa*), arrowweed (*Pluchea sericea*), and even cattails (*Typha*) and other emergents, and, among birds, Flicker (*Colaptes cafer*), Bullock Oriole (*Icterus bullockii*), Red-winged Blackbird (*Agelaius phoeniceus*), Yellow-breasted Chat (*Icteria virens*), Yellow-throat (*Geothylpis trichas*), Summer Tanager (*Piranga rubra*), and Blue Grosbeak (*Guiraca caerulea*). Mountain canyons support species principally of higher elevations; these include such plants as gray oaks (*Quercus grisea*), junipers (*Juniperus deppeana*), and *Garrya wrightii* and such birds as the Flicker, Scrub Jay (*Aphelocoma coerulescens*), Gray Vireo (*Vireo vicinior*), and Black-headed Grosbeak (*Pheucticus melanocephalus*).

Thus, taking into account physical features, structure, and species composition of the vegetation, and bird-species composition, these communities constitute a mixture of riparian and desert characteristics. Although they con-

tain all the desert bird species of the region and many desert plants, they are too mesic and contain too many mesic species to be unhesitatingly included among the communities of the desert scrub. Perhaps a separate type of community, the desert-riparian, should be designated in recognition of their peculiarity. In fact, practically all the desert birds species of this region (and many of the plants) are riparian in one sense. All are found in these obviously riparian communities; some are confined to them; those that do penetrate the creosotebush areas do so for varying distances along the arroyos; and only Black-throated Sparrows leave the arroyos for actual nesting (excepting Lesser Nighthawks and Mourning Doves, which feed and obtain water in more mesic situations). This restriction of desert species to riparian and arroyo habitats may be related to Udvardy's (1958) opinion that the North American desert avifauna was only recently derived from avifaunas of forest communities, an opinion that Dixon (1959) also found evidence to support.

One additional complication involves the successional status of the desert shrub communities of southern New Mexico. Gardner (1951 and personal communication) has amassed an impressive amount of evidence from accounts of early explorers and naturalists and from his own field work that a very large percentage of the area now dominated by shrubs in what is called the Chihuahuan Desert supported desert grassland in presettlement time. From very restricted sites at the margins between mesa slopes and valley floodplains the shrub communities have in this century expanded at the expense of communities dominated by grama grasses (*Bouteloua* spp.). Brush has expanded also in the valley proper of the Rio Grande where vegetation has changed from predominant cottonwood-tall grass savanna to the present dense *bosque* thickets. The effects that such drastic vegetational changes have had on bird populations must have been manifold, yet very little is known concerning them. Studies of birds inhabiting remnants of desert grassland might give some indication of the changes, but such studies have yet to be made. It appears probable that the desert shrub avifauna that now dominates such large areas was formerly confined to small areas at valley edges. Certainly the successional history of the landscape should be taken into account in designing future studies and in interpreting results of all studies.

The problem remains as to which group of species should be used in comparisons as the

typical group of desert scrub species of southern New Mexico. Obviously the use of species lists from broad studies including varied habitats could well obscure important regional similarities and differences. The problem is probably best solved by comparing the species list from the study area proper only with those of other study areas of similar topography. The study areas of Dixon (1959) in west Texas and the three areas of Hensley (1954) in southern Arizona are the only creosotebush desert areas of which we know that appear to be comparable to ours in being limited areas located on lowland desert slopes dissected by dry arroyos. All three groups of study areas would appear to be included in the "lower bajada" category of Benson and Darrow (1954:fig. 1). Of the 14 species present on our area, 12 were also on the Texas areas and 6 occurred on the Arizona areas (table 4). One, the Crissal Thrasher, was unique to the New Mexico plots, but it was found near Dixon's study areas. Nineteen species were recorded on the areas of western Texas; 10 of these were shared with southern Arizona, 12 with southern New Mexico, and 4 were unique. Seventeen species were found by Hensley in Sonora Desert study areas; of these, 6 were shared with New Mexico, 9 with Texas, and 7 were unique.

As discussed previously, the absence in our area of many of the species present in Dixon's may be explained by the absence of trees and tall, dense shrubs. The Sonoran Desert avifauna of Hensley's plots in southern Arizona (Organ Pipe National Monument) is, of course, richer than that of southern New Mexico, but in numbers of species it is not as rich as that of the Big Bend. As compared with the two "Chihuahuan Desert" faunas it contains a larger number of unique species. The study areas of New Mexico and west Texas supported avifaunas more similar to each other in terms of numbers of species shared than either one is to the Arizona fauna, but the Arizona and Texas faunas are more similar in total numbers of species. The similarity between Texas and New Mexico avifaunas is presumably due to their closer geographical locations as portions of the same broad desert subdivision and of the Rio Grande drainage; the similarity in diversity between Texas and Arizona is probably due to the fact that each supports a vegetation of diverse life forms, including dense tall shrubs, probably in turn because of similarities in climate, and especially a longer growing season than in New Mexico. This longer growing season is probably a result of both lower elevation and lower latitude.

The failure of these comparisons to show a richer fauna in the Sonoran Desert is puzzling. Using these same studies plus results of additional studies that we have rejected for comparative purposes because of their broad, faunistic nature, Dixon (1959) found appreciably higher numbers of species in several Sonoran Desert areas than in his own and other Chihuahuan areas. He attributed this greater diversity to greater vertical stratification of the vegetation, a general principle with which we agree and for which we have also found evidence. That comparisons of broader avifaunas show greater differences than comparisons of limited study areas is perhaps attributable to greater areal diversity in vegetation—that is, more different subhabitats occurring in an areal mosaic—in the Sonoran Desert than in the Chihuahuan. However, we have found no evidence from plant ecology that bears on this speculation. More detailed studies are necessary to determine the regional variation in this vegetational mosaic and its influence on bird diversity, as compared with the influence of vertical diversity of plant life forms at single sites.

MacArthur and MacArthur (1961) and MacArthur, MacArthur, and Preer (1962) have discussed problems of bird-species diversity in relation to habitat diversity and have analyzed some data for bird populations and habitats of the eastern United States. Lack of data prevents us from following their procedures for the desert areas.

Dixon (1959) has provided an excellent comparison of the bird-species compositions of other creosotebush desert areas as reported in the literature, and we can add little to his analysis, especially as these other studies are all of the broad, faunistic type. The 14 species of the New Mexico area constitute what appears to be the poorest creosotebush desert fauna reported, but it would appear probable that large areas of the central Mojave Desert, at least those portions where Joshua Trees (*Yucca brevifolia*) are absent, might well support as few species, or fewer.

POPULATION DENSITY

Comparison of the density of breeding pairs on our area with results of censuses of other desert areas gives a series of increasing density that encompasses a tenfold change. Dixon's (1959) Government Spring area is lowest with 10 and 15 pairs per 100 acres; our New Mexican area is next with 17.7 pairs per 100 acres (table 1); followed by Dixon's Black Gap area with 30, 40, and 51 pairs per 100 acres in different years, and Hensley's (1954)
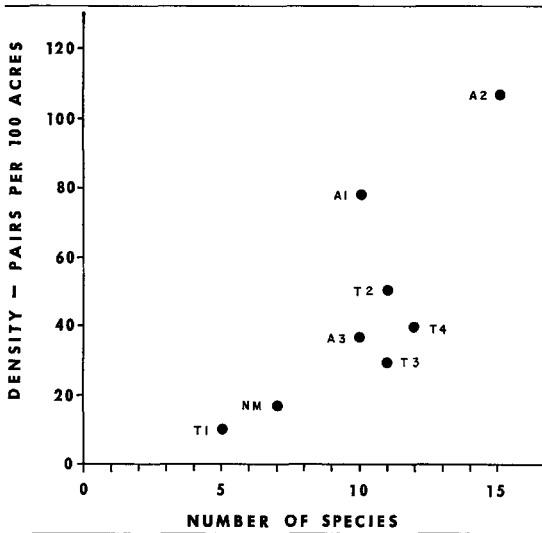
FIGURE 5. Total breeding density in relation to the number of species contributing to the density. NM indicates result of the study. A1, A2, and A3 indicate Hensley's (1954) areas 1, 2, and 3 in southern Arizona. T1 indicates Dixon's (1959) Government Spring study area. T2, T3, and T4 indicate Dixon's results on his Black Gap study area in 1956, 1957, and 1958, respectively.

Area 3 (open desert) with 37 pairs per 100 acres; and finally by Hensley's dry-wash sites, Area 3 and Area 2, with 80 and 109 pairs per 100 acres, respectively.

It is apparent from descriptions of the various areas that the order of localities in the above list of sites with increasing density is similar to that in a list of sites of increasing complexity of vegetation, and of increasing amounts of available moisture and, very probably, of increasing primary productivity. From previous discussions it is also apparent that the order of sites also follows closely the order of sites with greater numbers of breeding species.

The implications of these similarities are that, in these desert regions, increasing moisture allows greater diversity and productivity of vegetation which in turn allow both greater diversity and greater density of breeding birds.

This relationship is, of course, well known, and it is not surprising to find evidence of it here. The correlation between density and diversity of birds, however, need not have been close. For example, high density may be achieved without high diversity, and the two characteristics may be affected by quite different characteristics of the vegetation. In an effort to explore further the apparent correlation we plotted the density of birds in each plot for each year against the number of species actually contributing to the census (fig.

5). We omitted the species included as "visitants" in the tables of Dixon and Hensley and those species known to breed in the vicinity of our study area but not actually censused. (These species were included for purposes of completeness in the previous considerations of species composition.) The form of the scatter in this graph and the correlation coefficient ($r = 0.794$ with 6 d.f.) confirmed the relationship. Visual examination suggests a nonlinear relationship, and, in fact, a somewhat higher correlation coefficient (0.877) is obtained if the logarithm of the density is used on the ordinate.

The census results of Hutchinson and Hutchinson (1941, 1942) were obtained in the Colorado Desert on a site that is obviously more mesic than the others that we have considered. Density and number of species were both higher, and points representing their two censuses fall near a regression line fitted to the data in figure 5.

Because the number of species is an imperfect measure of diversity, we calculated a species diversity index for each community by the method of MacArthur and MacArthur (1961) in an effort to obtain an improved correlation between diversity and density; however, just the opposite result was obtained, for the regression of density on diversity index is not statistically significant. Perhaps this lack of correlation is due to the fact that the diversity indexes were of necessity based on somewhat different kinds of data for areas of somewhat different size and were not, therefore, truly comparable.

Statistical correlation does not necessarily indicate causation. However, from the data at hand, we can at least hypothesize that for desert scrub avifaunas an increase in density is achieved through addition of species. It seems obvious that the latter is in turn achieved through changes in vegetation that result from increased available moisture. Without quantitative information on characteristics of the vegetation, this line of reasoning on causation cannot be extended.

Udvardy (1957) discussed the relationship between number of species and breeding densities in a variety of North American community types. His graph for desert and chaparral habitats combined (fig. 1) shows a rather poor correlation, but he was apparently able to obtain data from very few actual desert studies, for he shows only two points with density below 100 pairs per 100 acres and number of species below 20. For forest communities Udvardy did find that, in general, increase in overall density is accompanied by

increase in the number of species, but that in temperate forests the number of species levels off, while in tropical forests it continues to rise arithmetically. The suggestion of a curvilinear relationship in our data would indicate similarity to temperate forests. Whether a single "species-density" curve applies to bird communities of even North American deserts, let alone for both deserts and forests, is a question of some ecological importance, but it cannot be answered without additional comparable data.

The many places in the foregoing discussions where deficiency of data was either pointed out or implicit is indicative of the great need for much additional study of avian densities in relation to vegetation in desert areas.

SUMMARY

Censuses of breeding birds were carried out in 1964 and 1965 on a one-square-mile tract of desert scrub in southern New Mexico. Variation in the vegetation on the area permits recognition of three different types or habitats: major arroyo vegetation, small arroyo vegetation, and undissected upland or "divide" vegetation. These are under obvious control of soil moisture and constitute a series of increasingly xeric conditions. All three types are dominated by creosotebush, but the more mesic habitats contain vegetation with denser and taller shrubs and richer floristic composition.

Census results yielded definite evidence of breeding for nine bird species; an additional six almost certainly breed on the area or in similar nearby communities. Black-throated Sparrows attained the highest breeding densities and widest distribution within the area, presumably in part because they were the only birds to use creosotebushes for nesting. Verdins also were abundant but were restricted for nesting to sites with tall, thorny shrubs. Mourning Doves nested on the ground and were the only birds that nested in numbers in open upland vegetation. Other species nested in low densities and only in larger arroyos.

The avifauna of the area is poorer in species than those of other North American desert shrub communities. It is probably typical of Chihuahuan Desert scrub avifaunas and thus is more similar to those of western Texas than to those of southern Arizona. The absence of trees or tall shrubs accounts for absence of some birds species found on other deserts. Problems involved in faunistic comparisons of desert avifaunas are discussed.

Total density of breeding pairs (17.7 per 100 acres in 1965) was also low in comparison with other deserts. Variation in density in desert areas is correlated with available moisture, diversity and productivity of vegetation, and number of breeding bird species. Increase in total density is achieved by addition of species under conditions of greater vegetational diversity and productivity.

ACKNOWLEDGMENTS

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