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ECOLOGICAL DISTRIBUTION OF SPINY LIZARDS

(SCELOPORUS) IN BIG BEND NATIONAL PARK, TEXAS

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ECOLOGICAL DISTRIBUTION OF SPINY LIZARDS (SCELOPORUS) IN BIG BEND NATIONAL PARK, TEXAS

By

Teddy L. Brown

B. S., University of New Mexico, 1965

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

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in the Graduate School of
The University of New Mexico
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ECOLOGICAL DISTRIBUTION OF SPINY LIZARDS (SCELOPORUS) IN BIG BEND NATIONAL PARK, TEXAS

By

Teddy L. Brown

ABSTRACT OF THESIS

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ABSTRACT

The ecological distribution of the four species of spiny lizards (Sceloporus) occurring in Big Bend National Park, Texas, was studied in the summers of 1968 and 1969. A total of 219 lizards was observed or collected by shooting with a pistol or rubber bands, by hand, and by use of can traps. The most abundant species was S. merriami (92 specimens observed or collected), second was S. poinsetti (63 specimens), third was S. magister (38 specimens), and least abundant was S. undulatus (26 specimens).

Five general communities are described: Rio Grande floodplain, desert scrub, desert grassland, pinyon-juniper-oak woodland, and ponderosa pine—Douglas-fir—Arizona cypress forest. Habitats within each are described on a vegetational or physiographic basis. The largest number of species and individuals of Sceloporus was observed in the desert scrub community (138 specimens) and the least number in the ponderosa pine—Douglas-fir—Arizona cypress forest (3 specimens).

Competition and habitat displacement within the genus Sceloporus and between Sceloporus and other iguanid lizards are discussed in relation to the abundance of preferred habitat.

No species of Sceloporus was restricted to only one community; except for S. magister, the species ranged into four communities each. No species was found in all communities.

Similarities in ecological distribution of Sceloporus and Cnemidophorus (whiptail lizards) were noted in the park and are discussed.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Objectives

Of the sixty-four species of amphibians and reptiles known to occur in Big Bend National Park, the four species of spiny lizards (Sceloporus magister, S. merriami, S. poinsetti, and S. undulatus) were selected for ecological study because of their wide ecological distribution in the park and the relative abundance of individuals. An attempt was made to observe, collect, and note relative abundance of the four species in as many different environments as possible in order to determine if the factors governing ecological distribution of spiny lizards could be applied to that of other herptiles in the park.

Earlier Investigations

Most of the earlier investigations in the Big Bend area were involved with searching for minerals and with surveying. Investigations of a biological nature were first concerned with collection and inventory, but recent emphasis has been placed on studies of ecological relationships carried out over longer periods of time.

Vegetational studies in the park include those of Palmer (1928) and Muller (1937) in the Chisos Mountains and Wells (1965) in the Dead Horse Mountains. McDougall and Sperry (1951) published a useful guide to the plants of the park. Interest in this area as a proposed national park produced a survey of vegetational types and their condition in 1936 and 1937, and permanent vegetation plots were established by the National Park Service in 1948. An ecological survey of the park was

undertaken in the years 1955-57 to determine what changes in the ecological situation had taken place since the removal of large herds of sheep and cattle with the establishment of the park in 1944.

Investigations of the herpetofauna of the park include those of Bailey (1905), Strecker (1909), and Brown (1950), all of whom listed species and locality records from the area. Murray (1939) and Schmidt and Smith (1944) reported on collections from the Chisos Mountains and Big Bend region, respectively. Smith (1937) described Sceloporus merriami annulatus from the Chisos Mountains. Degenhardt and Steele (1957) reported Trimorphodon vilkinsoni from the park. Minton (1958) summarized data from other collections from the Big Bend and added data from his own field work in the area. Degenhardt and Milstead (1959) reported a second specimen of Tantilla cucullata. Degenhardt and Degenhardt (1965) discussed the host-parasite relationship between the snake Elaphe subocularis and the tick Aponomma elaphensis. Degenhardt (1966) presented a method for counting diurnal ground lizards based on work done in the park in 1955-59; this work was repeated in 1968-69 to determine what changes in lizard populations had taken place as a response to vegetation changes during the ten year interval. Brown, Degenhardt, and Easterla (in press) discuss the relationships between the snakes Tantilla cucullata and T. diabola in the Chisos Mountains, and Smith and Werler (1969) discussed the relationships between the latter and the Mexican form T. rubra.

Description of the Area

Location and Physiography

Big Bend National Park is located in southern-most Brewster County, Texas, within the great U-shaped bend in the course of the Rio Grande which forms the international border between Texas and the Mexican states of Chihuahua and Coahuila. The park lies within the Mexican Highland Section of the Basin and Range Province (Hunt, 1967), Dice's (1945) Chihuahuan Biotic Province, and Milstead's (1961) Big Bend Biotic District. Total area of the park is 706,558 acres.

The park (Fig. 1) is bordered on the east by the Santiago and Dead Horse (Sierra del Caballo Muerto) mountains, a northward extension of the higher Sierra del Carmen of Coahuila. A series of north-south trending tilted fault blocks of Cretaceous limestone, the Dead Horse and Santiago mountains average 3,500-4,500 ft in elevation, reaching a maximum of 5,800 ft on Sue Peaks in the Dead Horse Mountains. The dipping slopes are gentle, but there are steep cliffs along fractures, and the entire surface is very rough due to severe erosion of the limestone (Fig. 4).

The Chisos Mountains (Fig. 2) and smaller surrounding volcanic peaks occupy the center of a large structural trough bordered on the east by the Sierra del Carmen and on the west by the Mesa de Anguila in the United States and the Sierra Ponce in Chihuahua. The Chisos and nearby peaks are composed of extrusive and intrusive Cenozoic igneous rocks which have penetrated and deformed the overlying strata of sandstones, volcanic ash, and conglomerates, which are capped in places

by remnants of a formerly extensive lava flow. Erosion has formed the extrusives and intrusives into dome-shaped peaks; the lava cap remains as square-faced peaks and mesas. The highest point in the Chisos and in the park is Emory Peak (7,835 ft). None of the other surrounding volcanic peaks exceeds 5,000 ft in elevation. Numerous dikes and sills radiate from the southern portion of the Chisos Mountains.

The Rio Grande has cut three canyons (Santa Elena, Mariscal, and Boquillas) through the Cretaceous limestones of the Mesa de Anguila, Mariscal Mountain, and the Sierra del Carmen, respectively. Each canyon averages about 1,500 ft in depth, with almost vertical walls. Although roads and trails lead to near the entrances and mouths of the canyons, they are passable only by boat. Santa Elena Canyon is 17 miles long, Mariscal Canyon, 7 miles, and Boquillas Canyon, 25 miles. The floodplain of the Rio Grande, which is generally less than a mile wide, was extensively cultivated by settlers in the late 19th and early 20th centuries, a practice discontinued on the American side with the establishment of the park in 1944. Elevations along the Rio Grande are the lowest in the park, ranging from about 1,700 ft in Boquillas Canyon to 2,300 ft in Santa Elena Canyon, 107 river-miles to the west.

Soils are of varied texture and generally poorly formed. In general, soil particle size increases with elevation and steepness of slope. Finer alluvial soils are found along the Rio Grande and larger arroyos; larger rocks and boulders are found in scattered outcrops on the desert and in talus slopes in the mountains.

All drainage in the park is to the Rio Grande through intermittent streams such as Bone Spring and Nine Point draws in the north, Tornillo Creek in the east, and Terlingua Creek and its tributaries in the west.

Climate

The climate is arid to semiarid. Temperature and rainfall data are recorded at all ranger stations, but are complete only for the stations at Panther Junction (3,750 ft) and in the Chisos Mountains Basin (5,100 ft). In general, winters are mild and sunny with little precipitation. Summers are hot, June and July being the warmest months, when clear skies and a dry atmosphere contribute to daily maximum temperatures occasionally exceeding 100°F in most areas of the park and at times exceeding 110°F at lower elevations. The clear skies and dry atmosphere also help produce a large amount of radiational cooling at night; as a result, 24-hour temperature ranges of 30 F° or more are not unusual. The daily maximum occurs usually between 3 and 5 PM, and the daily minimum shortly after sunrise. Temperatures were recorded daily on a Taylor hygrothermograph at the Chihuahuan Desert Research Station (K-Bar Ranch) during the summers of 1968 and 1969 and are summarized in Table 1 (p. 13).

Precipitation in the park ranges from less than 10 inches annually at low elevations to nearly 20 inches on Emory Peak in the Chisos Mountains. Maximum rainfall occurs in late summer and early fall, largely in the form of convectional thundershowers. Temperatures at this time are cooler by day but warmer at night as a result of increased cloudiness and

TABLE 1. Summary of temperatures recorded at the Chihuahuan Desert Research Station (K-Bar Ranch) in the summers of 1968 and 1969 (temperatures in °F)

Year and month	Mean daily maximum	Mean daily minimum	Two-year maximum	Two-year minimum	No. days maximum < 90°F
1968					
9-30 June	95.3	69.5	104	64	0
1-31 July	91.2	68.5	98	64	12
1-25 August	92.8	71.5	97	67	3
1969					
12-30 June	95.9	74.2	103	62	2
1-31 July	93.5	74.3	98	64	1
1-24 August[1]	94.3[1]	75.9[1]	100[1]	70[1]	1[1]

[1] 20-day record only; no temperatures recorded 7-10 August because of malfunction of hygrothermograph.

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greater atmospheric humidity. Fog and low clouds are common during this rainy saeson, and at times the clouds cloak the Chisos Mountains from Emory Peak down to about 4,000 ft.

Characteristic of arid and semiarid climates is the large variability of amounts of precipitation received from year to year. 1968 was a "wet" year in the park; many stations recorded two to three times the amount of rainfall usually received for the summer. The spring and summer of 1969 were very dry, however, as shown by the following example: in 1968, water flowed from the covered Government Spring (3,900 ft) at the north base of the Chisos Mountains into a nearby pond that measured about 40-50 ft by 10-20 ft and which supported a dense growth of willows, figs, and grass; frogs (Rana pipiens) and their tadpoles were frequently seen in the pond. In late July 1969, the spring, which is an outlet for subsurface water from the Chisos Mountains, stopped flowing and the pond dried completely two weeks later.

The relationship between summer temperatures and summer precipitation is shown in Table 1 (p. 13). The increased rainfall in the summer of 1968 resulted in cooler temperatures both day and night. Higher maxima and minima in 1969 are a result of the reduced rainfall and cloudiness. Note the number of days with maxima of less than 90°F in 1968; compare this number (15) with the number of days in the same column from 1969 (4). During a two-week period in late June and early July 1969 maximum temperatures of over 110°F were recorded at Castolon (2,169 ft), and for most of this period maxima were in the range of 115-117°F. Temperatures in the Chisos Mountains were not much cooler: a maximum of 99°F was experienced in the Basin (5,100 ft) on 21 June.

METHODS AND MATERIALS

Field work was carried out during the summers of 1968 (9 June to 26 August) and 1969 (3 June to 24 August). Short field trips to the area were made 10-20 April 1968 and 3-7 April 1969.

Specimens were collected by shooting with a .22-caliber pistol using dust shot, by shooting with B. F. Goodrich size 107 rubber bands measuring 6.5 X 0.5 inches, and by hand, sometimes with the aid of a "mechanical fingers" device used to extract lizards from rock crevices. Lizards were also caught in can traps, each consisting of two round one-gallon Xerex antifreeze cans with the bottom of one removed and the can spot-welded to the other to form a cylinder about 6.5 inches in diameter and 16 inches deep. Six of these traps were placed near K-Bar: three at distances of 30-50 yards north of the house and three near the house. I also placed three traps in Upper Green Gulch in the Chisos Mountains at about 5,000 ft elevation in 1968; these were unproductive and not used in 1969. Each can trap was buried in the ground so that the lip was flush with the surface. No difference in numbers or types of animals caught in the traps was noted whether or not the traps were covered with large rocks or with a piece of sheet metal. Holes were punched in the bottom of each trap for water drainage.

Not all lizards observed were collected, partly because they escaped capture as a result of my collecting technique, and partly because I did not want to decimate populations. Those lizards collected were killed (if not already dead) by

drowning in 70% ethanol, injected with and fixed in 10% formalin, and later transfered to 55% isopropanol for deposition in the Herpetology Division of the Museum of Southwestern Biology at the University of New Mexico.

All photographs except Fig. 1 were taken with a Canon single-lens reflex camera using either a Canon 135mm f/2.5 telephoto lens or a Canon 35 mm f/2.5 wide-angle lens. I used Kodak Kodachrome II (ASA 25) and Kodak black-and-white Tri-X Pan (ASA400) films. Fig. 1 was reproduced by a local printing business from my original drawing.

Plants were identified in the field by using McDougall and Sperry's Plants of Big Bend National Park (1951). No plant collection was made.

RESULTS

Communities and Habitats

Five general communities were identified within the park: Rio Grande floodplain, desert scrub, desert grassland, pinyon-juniper-oak woodland, and ponderosa pine—Douglas-fir—Arizona cypress forest. The first is of my own usage, the others are after McDougall and Sperry (ibid., p.1). Within each community I recognized different habitats, some on a vegetational basis and others on a physiographic basis. Trees, shrubs, fence posts, and park service road signs were considered to be arboreal habitats. Rock face habitats include large boulders, talus slopes, and cliff faces. I considered buildings, walls, and other man-made structures of stone or similar material to be a separate habitat in each community.

The communities and habitats are described below. Only a few of the major plants of each community are included in these descriptions.

Rio Grande Floodplain (Fig. 3)

This community lies at the lowest elevations in the park, from 1,800 ft near Boquillas Canyon to 2,200 ft just inside the mouth of Santa Elena Canyon. The floodplain is contained by steep canyon walls and rocky hills. Vegetation is most dense along the river bank, and consists of a growth of canes (Arundo donax and Phragmites communis), salt cedar or tamarisk (Tamarix), willows (Salix), seep-willows (Baccharis), and mesquite (Prosopis glandulosa). A few cottonwoods (Populus) grow at Rio Grande Village Campground. Ground cover is largely

Bermuda grass (Cynodon). Vegetation in areas away from the river includes creosote bush (Larrea divaricata), tornillo (Prosopis odorata), mesquite, and saltbush (Atriplex), growing in scattered clumps and not usually as dense as the vegetation closer to the river. There is little ground cover between the clumps of shrubs.

Desert Scrub (Figs. 4-7)

This is the most extensive community in the park, found on desert flats, arroyos, and hills at elevations between 1,900 ft and 4,000 ft. The dominant plant is creosote bush, occurring in nearly all areas of the community. Other species of plants in association with creosote on the desert flats include ocotillo (Fouquieria splendens), lechuguilla (Agave lecheguilla), tarbush (Flourensia cernua), mesquite, and scattered tree-like Torrey yuccas (Yucca torreyi). Several species of cacti, among them prickly pear (Opuntia engelmannii), purple-tinged prickly pear (O. macrocentra), cholla (O. imbricata), and strawberry cactus (Echinocereus stramineus), are common on the desert areas, and their fruits provide food for a variety of animals.

In arroyos the water table is often high enough to permit a dense growth of several large shrubs, including apache-plume (Fallugia paradoxa), mesquite, tasajillo (Opuntia leptocaulis), little-leaf sumac (Rhus microphylla), guayacan (Porlieria angustifolia), acacias (Acacia), allthorn (Koeberlinia spinosa), and such spiny shrubs as Condalia and Zizyphus. Many of these bear out the saying that "in the Big Bend, everything either sticks, stings, or stinks." A few trees are found in arroyos, among these are Mexican buckeye (Ungnadia speciosa),

desert willow (Chilopsis linearis), Texas persimmon (Diospyros texana), and ash (Fraxinus). Cottonwoods, mesquite, tornillo, and walnuts (Juglans) grow near isolated springs in the desert arroyos where there is a permanent water supply. Grasses are generally restricted to arroyos. Tobosa grass (Hilaria mutica) once covered large areas of now-barren Tornillo Flat, but coverage was reduced to a few clumps along the arroyos by over-grazing, cutting the grass for hay, and extensive periods of drought before the national park was established. A park service program to re-establish the grass has proven successful in a few places (Maxwell, 1968, p. 37).

Limestone areas, such as the Santiago and Dead Horse mountains, have a slightly different flora than the desert flats. On alluvial flats and in arroyos desert scrub vegetation (creosote-lechuguilla-ocotillo) is dominant, but is replaced on steeper slopes and rock faces (cliffs and canyon walls) by dense growths of hechtia (Hechtia scariosa, a member of the pineapple family), blind prickly pear (Opuntia rufida), and resurrection plant (Selaginella). Giant dagger yuccas (Y. carnerosana) over 10 ft tall grow on hillsides in association with other tree-like yuccas (Y. torreyi, Y. rostrata, Y. elata), and are especially noticeable at Dagger Flat (Fig. 7). Sotol (Dasylirion leiophyllum) is found in some rocky areas, but is more typical of the type of desert grassland which replaces the desert scrub vegetation at higher elevations in these areas and which giant dagger yuccas and sotol form a type of "forest" at elevations from 3,800 to 5,800 ft. The very top of the Dead Horse Mountains has a mixture of this yucca-sotol "forest"

and a few scraggly junipers (Juniperus pinchotii) and mottes of semi-deciduous oaks (Quercus), according to Wells (1965, p. 258).

Outcrops of igneous rocks are widespread in the park, especially along fault lines. The Chihuahuan Desert Research Station (K-Bar Ranch) is located near three rocky outcrops along the Lone Mountain anticline to the west of Tornillo Creek and about 2 miles southeast of Panther Junction (park headquarters). Vegetation on the flats between the rocky hills is largely creosote-lechuguilla-ocotillo, that of the large arroyos on each side of the house consists of mesquite, spiny shrubs (Condalia, Zizyphus), and persimmons, and the hillsides are covered with a yucca-lechuguilla-sotol-grass association. These varied habitats at this locality are occupied by three species of Sceloporus (S. magister, S. merriami, and S. poinsetti). This locality is illustrated in Fig. 6.

Desert Grassland (Fig. 8)

This community is found on the lower slopes and canyons of the Chisos Mountains and the upper slopes of most of the other mountains in the park, largely at elevations of 3,500 to 5,000 ft. Sotol and beargrass (Nolina erumpens) are the most conspicuous large plants here, but other shrubs such as acacias, algerita (Berberis trifoliolata), and the tree-like yuccas (Y. elata, Y. torreyi) are common. Grasses form a dense growth in many places and include such species as chinograss (Bouteloua breviseta), gramas (B. gracilis, B. eriopoda), and muhly (Muhlenbergia). Mexican buckeye, yellow-trumpet (Stenolobium incisum), and some trees typical of higher and lower elevations

extend into this community along arroyos.

Pinyon-juniper-oak Woodland (Fig. 9)

This is the most widespread community in the Chisos Mountains, found from around 5,000 ft to over 7,800 ft. Trees and shrubs common here are Mexican pinyon (Pinus cembroides), oneseed juniper (Juniperus monosperma), drooping juniper (J. flaccida), alligator juniper (J. deppeana), Emory oak (Quercus emoryi), Graves oak (Q. gravesii), Texas madrone (Arbutus texana), evergreen sumac (Rhus virens), and the spectacular century plant (Agave scabra). In the sheltered canyons with more mesic conditions are found bigtooth maple (Acer grandidentatum) and several species of oaks endemic to the Chisos Mountains. Open places in the woodland are covered with several species of grasses. Numerous igneous outcrops, cliffs, and talus provide suitable habitats for many herptiles.

Ponderosa pine—Douglas-fir—Arizona cypress Forest (Fig. 10)

This community of large trees is restricted to the heads of canyons and higher elevations in the Chisos Mountains. Ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) are found in moist areas of Pine, Juniper, and Boot canyons, and are separated by over 250 airline miles from the nearest stands in southern New Mexico. Arizona cypress (Cupressus arizonica) seems less restricted than the other two forest species in Juniper Canyon; it is common on the north-facing slope between 6,000 and 7,000 ft. On Emory Peak is a stand of 222 quaking aspens (Populus tremuloides).

Distribution of Species

Table 2 (p. 23) shows the distribution of Sceloporus collected or observed during this study. The large total from the desert scrub community is a reflection of the extensiveness of the community and the excellent habitats afforded Sceloporus .

Sceloporus magister (Desert Spiny Lizard)

The subspecies S. m. bimaculosus occurs in the park in the Rio Grande floodplain and desert scrub communities. Eight specimens (2 males, 2 females, 4 juveniles) were collected, all from the desert scrub, but 37 others were observed in this community and near the Rio Grande. This is a wary lizard, difficult to approach before it scurries for shelter in dense brush or in a rodent burrow. Four were captured in can traps at K-Bar Ranch, and three more were released after marking, or escaped. A large male was caught in a live-trap for mammals at K-Bar, and a juvenile was taken in the kitchen one evening.

Primarily a ground-dweller, none were observed on cliff faces or on large rocks in the open areas, but three were seen on rocks along the banks of Estufa Canyon (2,700-3,000 ft), a deep wash that cuts through deposits of consolidated gravels to the east of K- Bar Ranch. The lizards escaped into dense growths of tasajillo and mesquite rather than seek shelter in the rocks. S. magister also forages in trees such as mesquite, cottonwood, and ash. Dr. William G. Degenhardt tells of having seen these lizards sunning on the vertical flower stalks of lechuguilla, and I've taken specimens on fence posts in desert grassland near Las Cruces, New Mexico.

TABLE 2. Distribution of Sceloporus in Big Bend National Park by community and habitat (numbers are totals of lizards collected or observed)

Community and habitat	S. magister	S. merriami	S. poinsetti	S. undulatus	Total
Rio Grande floodplain					13
Dense vegetation	6				
Open vegetation	1				
Arboreal	1				
Limestone rock faces		2			
Buildings, walls, etc.	1	2			
Desert scrub					138
Creosote flat	4				
Creosote-lechuguilla-yucca	4			5	
Arboreal					
Arroyos	16	4			
Limestone rock faces		20	1		
Igneous rock faces		51	12		
Buildings, walls, etc.	5	2	10	4	
Desert grassland					40
Lechuguilla-grass-shrubs				2	
Sotol-grass-beargrass				5	
Arboreal			5	1	
Limestone rock faces					
Igneous rock faces			22		
Buildings, walls, etc.		5			
Pinyon-juniper-oak woodland					25
Open grassy areas		1		3	
Arboreal			1	2	
Igneous rock faces		5	10	2	
Buildings, walls, etc.			1		
Ponderosa pine—Douglas-fir—Arizona cypress forest					3
Open areas					
Arboreal				2	
Igneous rock faces			1		
Buildings, walls, etc.					
Total	38	92	63	26	219

S. magister was observed or captured at elevations from 1,800 ft along the Rio Grande to 3,500 ft near K-Bar Ranch, where it is sympatric with, but ecologically separated from, S. merriami and S. poinsetti.

The largest specimen collected was a male that measured 97 mm in snout-vent (SV.) length (240 mm total length) and was trapped in the mammal live-trap at K-Bar Ranch. The smallest was a juvenile 33 mm in SV. length (74 mm total length) caught 2 July in the kitchen of K-Bar Ranch and was probably recently hatched.

Sceloporus merriami (Canyon Lizard)

Two subspecies of S. merriami have been reported from the park. S. m. merriami is supposedly confined to the limestone areas of the Santiago and Dead Horse mountains; S. m. annulatus is largely an inhabitant of igneous rocky outcrops over the rest of the park, although two S. m. annulatus were collected in a bat cave on the southeast face of Mariscal Mountain, a long anticlinal limestone ridge. Other workers have differentiated the two subspecies in the field on the basis of general coloration (S. m. merriami is pale, S. m. annulatus is dark), condition of gular bars (faint, separate, and confined to the medial gular area in S. m. merriami; distinct, confluent, and extending to the labials in S. m. annulatus), amount of contact between the dark medial borders of the blue abdominal patches in males (separate in S. m. merriami, confluent in S. m. annulatus), and the presence of subcaudal crossbands (faint or absent in S. m. merriami, dark and distinct in S. m. annulatus). Specimens were examined in the laboratory

for differences in head scalation described for the two subspecies by Smith (1946, p. 188-190). Variation in most characters was seen in most populations, but more adequate samples are needed for assignment of separate populations to one subspecies or the other. Those lizards from Santa Elena Canyon closely resemble S. m. merriami in most characters. This subspecies was reported by Smith, Williams, and Moll (1963) from El Fortin and Alamo, Chihuahua, 125 miles west of previous localities. They state (p. 213) that "possibly this [population from El Fortin and Alamo] represents a still different race of the species, standing in much the same relation to m. merriami as m. australis does to m. annulatus". The population in closed canyon, 14 miles east of Redford in nearby Presidio County, shows a mixture of characters of S. m. merriami and S. m. annulatus. Of 14 specimens collected there 25 June 1968 by Dr. and Mrs. Degenhardt and myself, four could be recognizable as S. m. merriami, five as S. m. annulatus, and five as intermediate between the two in most characters. More field work is necessary to determine the status of all the subspecies of S. merriami.

These lizards are almost strictly rock-dwellers; only a very few individuals were observed in other habitats, except those on buildings and walls. One was collected on ferns in shade provided by the overhang of a large boulder near the mouth of Pulliam (Maple) Canyon in the Chisos Mountains. Axtell (1959, p. 99) reported that in Black Gap Wildlife Management Area, S. m. merriami was collected on igneous boulder and cliff habitats as well as in similar limestone habitats, but

the lizards were more abundant in the limestone habitats. S. m. annulatus does not occur in this area, thus S. m. merriami has entered this habitat usually occupied in nearby areas by S. m. annulatus.

I collected specimens 1,875 ft at the old Boquillas Ranger Station near Rio Grande Village Campground to about 5,600 ft in Pulliam (Maple) Canyon. The largest of 67 specimens (33 males, 33 females, 1 juvenile) collected was a male from Grapevine Hills that measured 56 mm in SV. length. The juvenile was collected 4 July 1968 near K-Bar Ranch and was just 20 mm in SV. length (49 mm total length).

S. merriami is sympatric with S. poinsetti to an extent such that both can be found on the same boulders and even in the same crevices where they take shelter when disturbed.

Sceloporus poinsetti (Crevice Spiny Lizard)

This species is adapted for life on boulders and in crevices by means of its flat body and thick, rough scales. This lizard's large size and black-and-white banded tail permitted observation and identification from distances of up to 75 ft. A large number of specimens was collected on cloudy days or during midday by my simply looking in rock crevices most likely to harbor these lizards; the problem was to extract the lizards. A "mechanical fingers" device was helpful, but lizards too reluctant to leave their comfortable crevices lost tails, toes, or limbs, and it was necessary to kill two specimens in the crevices in order to extract them in a condition suitable for preserving.

At K-Bar Ranch two large S. poinsetti lived on the walls and under the roof of the garage, and would wedge themselves between one wall and the doorpost of the garage's sliding door. Another favorite place for these two lizards was on the walls of the house near the air conditioner and an oleander bush. Juveniles were frequently caught in a can trap located between the house and the garage. One juvenile was found in the living room of the house.

I observed this species at elevations from 2,650 ft near Glenn Springs to 7,200 ft on the South Rim of the Chisos Mountains. It may inhabit the rocks near the summit of Emory Peak (7,835 ft), as I've collected this species at about 8,400 ft in the Magdalena Mountains, Socorro County, New Mexico, in a habitat very similar to that on Emory Peak. Habitat seems suitable for this form at elevations below 2,000 ft in the vicinity of Boquillas Canyon, though none were seen.

The largest specimen of 14 collected (2 males, 6 females, 6 juveniles) was a female that measured 110 mm in SV. length and 214 mm total length, with a regenerated tail. Three small juveniles (31, 33, and 34 mm SV., respectively) were caught at K-Bar Ranch in June 1968; the first in the living room, the second in a can trap, and the third was found dead in a mop bucket outside the kitchen door. It has been noted by several herpetologists that S. poinsetti in this area (near the center of its range) are not as large as those from other parts of its range. I collected several individuals on the edge of the San Agustin Plains, Catron County, New Mexico, all of which measured over 100 mm in SV. length; the largest was 135 mm SV.

Two observations of unusual activity by these lizards were made during this study. In July and August 1968, four individuals were seen on two wooden park service signs at Basin Junction (4,000 ft). Two lizards were on each sign and each seemed to favor a certain portion of its sign--the top, the face, or the posts holding the sign. On 24 August two of the lizards seen on their customary sign during a mild thundershower made no attempt to seek shelter during the short period of time Dr. Degenhardt and I observed them. A large S. poinsetti was seen in Upper Green Gulch (5,500 ft) in the Chisos Mountains at 12:15 AM on 23 August 1969 by Bill Butler and myself. The lizard's tail and posterior part of the body were protruding from a crevice in the rock face of a road cut. When touched, the lizard retreated into the crevice and couldn't be reached.

Sceloporus undulatus (Eastern Fence Lizard)

The subspecies S. u. consobrinus occurs at a few scattered localities in the park. I observed specimens at Dagger Flat (3,400 ft), in Pine Canyon (5,000-6,000 ft) and other areas in the Chisos Mountains, at Grapevine Spring (3,050 ft), and on Burnham Flat (3,400 ft) about 3.1 miles north of Government Spring. Dr. Degenhardt observed this species in 1969 on his study quadrat at 4,200 ft in Lower Green Gulch on the north slope of the Chisos Mountains. Records indicate that S. undulatus is common in the Chisos Mountains, but I had little luck in observing them there, possibly because of their extreme wariness.

In Pine Canyon this lizard is often seen near the abundant sotol and beargrass and is quick to take shelter among them when disturbed. S. undulatus was the most arboreal species observed. It utilizes logs, pines, junipers, and madrone for habitat in the Chisos Mountains, and is found in the giant dagger yuccas on Dagger Flat. These lizards are extremely wary in the yuccas and would not allow me to approach before they disappeared under the dead leaves of the plants. This species is apparently absent from the Rio Grande floodplain, a habitat in which this lizard is abundant in other parts of its range. Its absence here may be because of the presence of the much larger S. magister, a known predator of smaller lizards.

The largest S. undulatus of four collected (2 females, 2 juveniles) was a female that measured 66 mm in SV. length and 160 mm total length. The smallest specimen was a juvenile that measured 31 mm SV. length and 75 mm total length, caught 17 August 1968 in Upper Green Gulch by Mrs. Paula B. Degenhardt.

DISCUSSION

Of the four species of Sceloporus in the park, three (S. merriami, S. poinsetti, and S. undulatus) utilize rocky habitats to some extent; the fourth (S. magister) is largely a ground-dweller that sometimes becomes arboreal. The most saxicolous species is S. merriami; only five specimens were observed in non-rocky habitats, but four of these were on buildings or walls of stone or rough plaster, and the fifth was under the overhang of a large boulder. S. poinsetti is basically a rock-dweller that uses crevices for shelter, but also is found on buildings and sign posts offering crevices between surfaces. S. undulatus is quite plastic in habitat selection compared with the other species, possibly as a result of competion with them. It takes to trees and rocks in the Chisos Mountains, becomes a ground-dweller in a grassland habitat, and frequents yuccas as substitutes for trees. S. magister was seen on rocks only in Estufa Canyon, where S. poinsetti is apparently absent, and is usually an inhabitant of dense brush in the park, although in other areas of its range it is often found on rocky substrates.

Competition for food and shelter varies with the species observed. S. merriami and S. poinsetti were most often seen on the same hillsides and even on the same boulders, but only in the desert scrub community. The two selected slightly different habitats in the Chisos Mountains; S. merriami on rock faces in dry environments, and S. poinsetti on rock faces in more mesic situations. At Dagger Flat these two species occupy limestone hills surrounding the forest of giant dagger

yuccas on the flat where S. undulatus is found in and around the yuccas (Fig. 7).

At K-Bar Ranch, S. merriami and S. poinsetti are common on the rocky hillsides from the bases to the tops, and S. magister is restricted to arroyos and creosote flats. Contact between S. poinsetti and S. magister may take place occasionally. A large S. magister was seen to run across a dirt road and into some large rocks at the base of a hill occupied by S. poinsetti, and both species were caught in can traps and seen around the house or in it. S. undulatus was not observed here, but could possibly be arboreal on the persimmon trees in the arroyos. S. undulatus and S. magister might be sympatric at some localities in the park. At Burnham Flat one or two S. undulatus were seen on separate occasions in a dense patch of mesquite, and a short distance away two S. magister once dashed across a dirt road into a clump of Torrey yuccas. S. magister is common along the Rio Grande to the apparent exclusion of S. undulatus, but was not seen at Dagger Flat where S. undulatus occurs. Milstead (1953, p. 410) caught both species in the mesquite-mountain ash- cottonwood association near springs in the La Mota Mountain region. S. magister was found in mountain ash and mesquite trees but not in cottonwoods, and S. undulatus was collected in mountain ash and cottonwood trees but not in mesquite trees.

In the Chisos Mountains S. merriami, S. poinsetti, and S. undulatus are found in the pinyon-juniper-oak woodland with the tree lizard (Urosaurus ornatus), a small iguanid closely

resembling S. merriami in size, color and pattern, and habitat preference. Habitat displacement was noted among these four species. S. merriami was seen on rock faces in relatively dry environments where S. poinsetti was present on rock faces in more mesic situations. At places where both S. merriami and S. poinsetti were present, S. undulatus became arboreal. U. ornatus was found on logs in localities where all four of these species were present, as in Pine and Juniper canyons. On the flat near the mouth of Pulliam (Maple) Canyon at about 5,400 ft, S. merriami and U. ornatus were on different boulders separated from each other by at least 15-20 yards of grass and beargrass. In Pulliam Canyon itself at about 5,600 ft, S. merriami was on rocks at the base of the canyon walls and U. ornatus was on oaks and madrones. Milstead (ibid.) found S. merriami but not U. ornatus in the La Mota Mountain region in Presidio County, and Jameson and Flury (1949) reported only U. ornatus and not S. merriami in the Sierra Vieja Range in the same county. Milstead, Mecham, and McClintock found both species in 1950 on the Stockton Plateau in northern Terrell County, east of the Pecos River, but not in the same canyons. Both species occur in the same habitat in the Black Gap Wildlife Management Area bordering the park on the east, and Axtell (ibid.) found individuals of both species " on the same rock many times and noticed no sign of antagonism between individuals". I saw this same situation in a rocky canyon at the south end of the Cuesta Carlota east of Tornillo Creek.

U. ornatus is displaced in other areas where it is

sympatric with S. undulatus. In the Blue River Valley of Greenlee County in eastern Arizona, Boyle (1969, p. 23) found that he could predict the presence of S. undulatus by seeing an arboreal U. ornatus which had been displaced arboreally by S. undulatus where the two are sympatric in the valley.

S. poinsetti displaces S. undulatus into trees where the two species are sympatric in the park. In New Mexico they seem to be more ecologically compatible. In the Rio Hondo Valley in Lincoln County, Kimmons (1969, p. 90) "often found fence lizards on cliffs with crevice lizards". I've collected both species together in other parts of the state, but S. undulatus was less common on rocks and more likely to be found on old wooden buildings or dead trees where sympatric with S. poinsetti.

An important factor regarding the ability of species to coexist in the same small area may be the relative abundance of the "right" habitat or lack of it altogether. On the rocky outcrops in the desert, S. merriami and S. poinsetti may be found together on the same rock in a habitat abounding in suitable nooks and crannies in which these lizards may take shelter. Such outcrops seem to be about equal in number in the mountains compared with the desert, but S. poinsetti selects the most suitable rocks for itself and leaves less suitable rocks in drier areas to S. merriami, S. undulatus, and U. ornatus, or so it appears to this observer.

Another factor involved here may be the size of the young lizards. Young S. poinsetti are born in late spring and early

summer at a snout-vent length of about 30-35 mm (Stebbins, 1954, p. 236 and 238). The other lizards hatch in mid-summer or later from eggs laid about the time the young S. poinsetti are born, and are a bit smaller (20-30 mm SV. length) at the time of hatching (ibid., p. 244). By this time the young S. poinsetti are about 10-20 mm longer (SV. length) and have had more experience at surviving in the environment. By "getting a jump" on the others at an early age, S. poinsetti may be more successful in this environment.

Another group of lizards with an ecological distribution in the park similar to that of the spiny lizards is the genus of whiptail lizards (Cnemidophorus). As in Sceloporus, four species of Cnemidophorus are found here--C. inornatus, C. scalaris, C. tesselatus, C. tigris--and all have wide geographic distribution outside this area. C. tesselatus (a parthenogenic species) is found in the park only inside Santa Elena Canyon, but previously may have ranged over wider areas of the park, if identification of specimens from earlier collections is correct. C. scalaris and C. inornatus have ecological distributions similar to that of S. undulatus. C. scalaris is found in the Chisos Mountains and on most hills in the area that have rough surfaces and a growth of sotol and beargrass. C. inornatus is found in scattered localities in the desert and Chisos Mountains, but does not seem to reach the same elevations as C. scalaris (over 6,000 ft). Both C. scalaris and C. inornatus are found together with S. undulatus at Dagger Flat as an "island" in a "sea" of C. tigris, the most widespread and common whiptail in the park. C. tigris

inhabits almost all areas below 4,500 ft in elevation. Interaction between C. tigris and C. scalaris in a zone of contact in Pine Canyon in the Chisos Mountains was investigated by Ronald Lucchino during the summer of 1969.

Competition between lizards of the two genera may be minimal because of differences in food habits and habitat selection. Spiny lizards actively pursue their prey (active insects and other arthropods) aided primarily by their vision. Whiptails are very active in pursuit of their prey, but seem to feed to a great extent on termites and similar invertebrates that they locate in dead leaves and under objects on the ground, aided to a large degree by olfaction. Spiny lizards seem "attached" to objects such as trees, rocks, or buildings in their environment, and appear to be relaxed but alert when sunning on an object. Whiptails, on the other hand, are ground-dwelling lizards that do not often climb rocks or trees for shelter or in foraging, and are always rather "nervous-appearing" as they scurry about open areas and run from one bush to the next.

Degenhardt (1966, p. 95-96) listed several factors that may effect the numbers of ground lizards (particularly Holbrookia and Cnemidophorus) as vegetation increases in density with an increase in elevation or as a response to increased precipitation. Increased vegetation density reduces soil surface temperatues and provides increased cover that may obscure the lizard's vision, shelter predators, and prevent rapid escape when a predator is sighted. These factors may be more important to a ground-dwelling lizard than to a lizard

that routinely selects a boulder or tree as a vantage point and is thus able to escape the effect of increased vegetation cover at least at the ground level. Those Sceloporus that are ground-dwellers, such as S. magister and S. undulatus in some areas, seem to be unusually wary and difficult to approach.

SUMMARY AND CONCLUSIONS

Five communities in the park are described. The greatest number of species and individuals of spiny lizards occurs in the most extensive community, the desert scrub. Numbers of species and of individuals of Sceloporus decrease at elevations above 4,000 ft and below 2,000 ft.

S. merriami and S. poinsetti were often collected or observed in close proximity to each other in the desert scrub community, but in the pinyon-juniper-oak woodland seemed to occupy slightly different situations, S. merriami on rocks in relatively dry environments and S. poinsetti on rocks in more mesic environments. S. magister and S. undulatus were not observed in the same habitat in the park, although they have been collected together at locations in nearby areas. S. magister, S. merriami, and S. poinsetti were collected at K-Bar Ranch in different habitats.

Competition between the species of Sceloporus with each other and with other iguanids, notably Urosaurus ornatus, was noted where the species were sympatric. It was reduced by the displacement into different habitats of the species involved.

The ecological distributions of Sceloporus and Cnemidophorus are similar in many respects. Some species are restricted to desert and floodplain habitats (S. magister, C. tigris), but others are found mainly in the Chisos Mountains but maintain populations at scattered localities in the desert (S. undulatus, C. scalaris). S. merriami and C. inornatus are similar in that each is the smallest species of its genus in the park and is found in close proximity to larger species

(S. merriami with S. magister and S. poinsetti; C. inornatus with C. scalaris and C. tigris).

The following conclusions are made concerning the ecological distribution of spiny lizards in the park:

1. The largest number of species and individuals is found in the most extensive community, the smallest number in the most restricted community.
2. The number of species and individuals observed decreases at elevations over 4,000 ft and below 2,000 ft.
3. No species is restricted to only one community; all but one are found in four communities.
4. The species with the greatest geographic range (S. undulatus) is also the species which is the most ecologically adaptable, and the most geographically restricted species (S. merriami) is found generally in just one type of habitat (such as rock faces).
5. Displacement into a different habitat of one species by another may occur in some areas where they are sympatric but not in others, possibly because of differences in availability of the habitat selected by both species.
6. Other lizards may show similar types of ecological distribution in areas where several similar species are involved.

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APPENDIX

FIG. 1. Topographic map of Big Bend National Park, Texas. The circled numbers represent the following :

1. Santiago Mts.
2. Dead Horse Mts. (Sierra del Caballo Muerto)
3. Sue Peaks
4. Dagger Flat
5. Rio Grande Village Campground
6. Mariscal Mt.
7. Chilicotal Mt.
8. Chihuahuan Desert Research Station (K-Bar Ranch)
9. Panther Junction (Park Headquarters)
10. Grapevine Hills
11. Government Spring
12-16. Chisos Mts:
    12. Upper Green Gulch
    13. Basin
    14. Emory Peak
    15. Pine Canyon
    16. Juniper Canyon
17. Castolon
18. Mesa de Anguila
19. Santa Elena Canyon
20. Mariscal Canyon
21. Boquillas Canyon

FIG. 1.

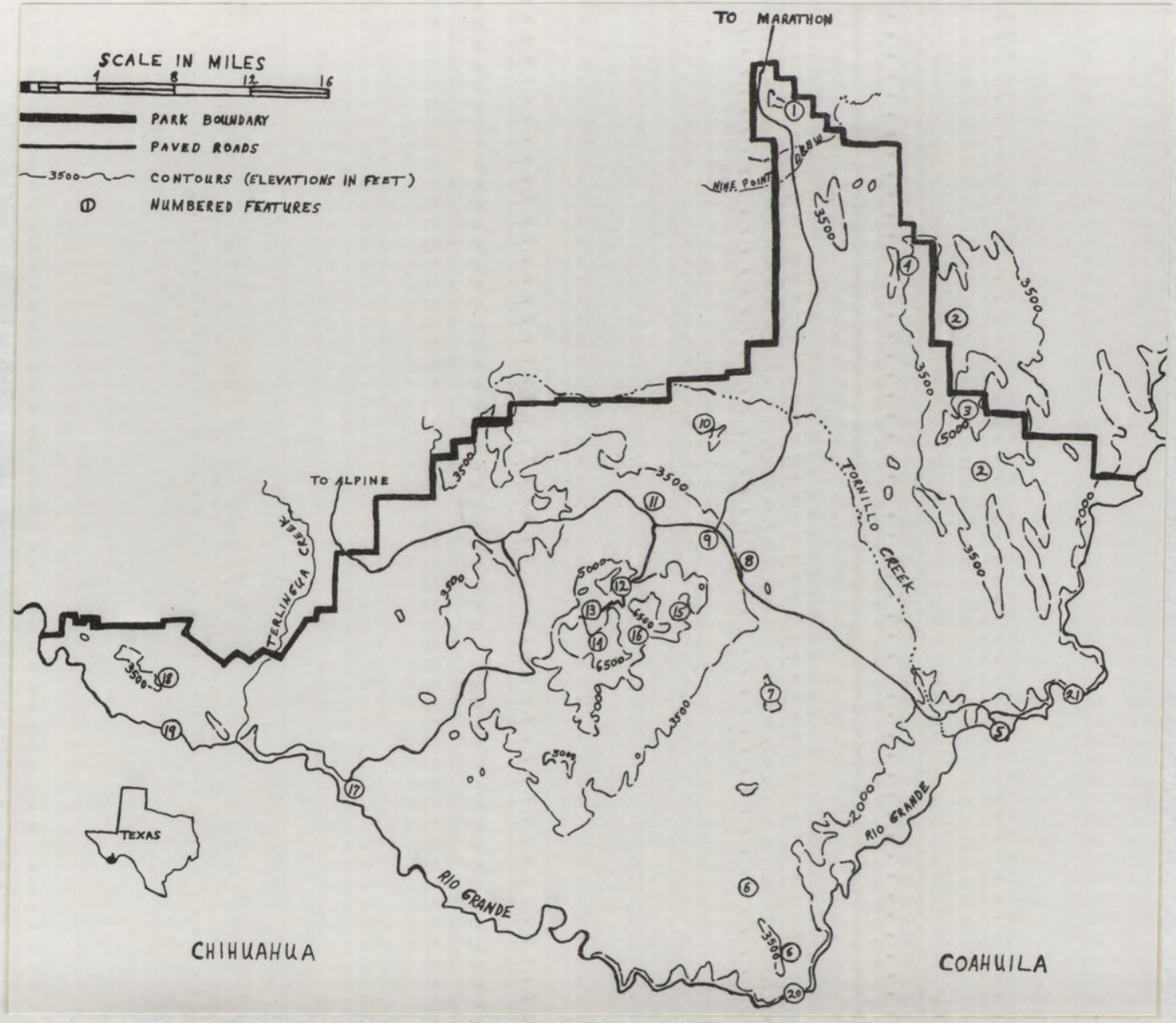
SCALE IN MILES
1
8
12
16
PARK BOUNDARY
PAVED ROADS
3500 CONTOURS (ELEVATIONS IN FEET)
NUMBERED FEATURES
TO MARATHON
TO ALPINE
HIGH POINT
6581'
TORNILLO CREEK
TERLINGUA CREEK
RIO GRANDE
RIO GRANDE
TEXAS
CHIHUAHUA
COAHUILA
3500
5000
6500
2000

FIG. 2. View of the Chisos Mountains, looking southwest from near Muskhog Spring (3,000 ft). From left to right along the crest, the highest peaks are Lost Mine Peak (7,550 ft), Emory Peak (7,835 ft), Casa Grande (7,200 ft), Pulliam Peak (6,900 ft), and Pulliam Bluff (6,800 ft). Vegetation in the foreground is creosote bush (Larrea divaricata) and the tree-like Torrey yucca (Yucca torreyi).

FIG. 3. Rio Grande floodplain near Castolon (2,100 ft). Typical dense growth of mesquite (Prosopis glandulosa) on the banks of the Rio Grande. Habitat of S. magister.

FIG. 4. Limestone cliffs near Boquillas Canyon (2,000-2,700 ft). Dominant vegetation on the slopes includes lechuguilla (*Agave lecheguilla*), hechtia (*Hechtia scariosa*), ocotillo (*Fouquieria splendens*), and sotol (*Dasylirion leiophyllum*). Habitat of *S. merriami* and possibly also of *S. poinsetti*, though none of the latter species were observed here.

FIG. 5. Desert scrub on Burnham Flat (3,400 ft), about 3.1 miles north of Government Spring. This is one of Degenhardt's (1966) lizard-study quadrats (note a white marker flag near the upper left corner of the photograph). Dominant vegetation is creosote bush (*Larrea divaricata*), lechuguilla (*Agave lecheguilla*), and scattered clumps of mesquite (*Prosopis glandulosa*). *S. undulatus* was observed near the clump of mesquite at the top center of the photograph.

FIG. 6. Outcrop of igneous rocks at K-Bar Ranch (3,400 ft). Creosote bush and chinograss (Bouteloua breviseta) are dominant between large rocks on which S. merriami and S. poinsetti are found. S. magister was seen at the base of this hill.

FIG. 7. Giant dagger yuccas (Yucca carnerosana) at Dagger Flat (3,400 ft). S. undulatus was seen in the yuccas, and S. merriami and S. poinsetti taken on the hill in the background.

FIG. 8. Desert grassland in Pine Canyon, Chisos Mountains (5,000 ft). Dominant plants include sotol (Dasylirion leiophyllum), beargrass (Nolina erumpens), prickly pear (Opuntia engelmannii), and several species of grasses. S. undulatus was observed about the bases of the shrubs and took shelter in them when pursued.

FIG. 9. Pinyon-juniper-oak woodland in Upper Green Gulch, Chisos Mountains (5,500 ft). Several species of junipers (*Juniperus*) and oaks (*Quercus*) are found in association with Mexican pinyon (*Pinus cembroides*) on the slopes of these hills and canyons composed of intrusive and extrusive igneous rocks. *S. poinsetti* and *S. undulatus* were collected on rocks and trees at this locality.

FIG. 10. Ponderosa pine—Douglas-fir—Arizona cypress forest on the north-facing slope of Juniper Canyon, Chisos Mountains (6,000-7,000 ft). Arizona cypress (Cupressus arizonica) is mixed with drooping and alligator junipers (Juniperus flaccida and J. deppeana) on the slopes and is found in the moist canyon bottoms with ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii), which are confined there to a great extent. One S. poinsetti and two S. undulatus were the only Sceloporus seen in this community.