THE INFLUENCE OF A RETURN OF NATIVE GRASSLANDS UPON THE ECOLOGY AND DISTRIBUTION OF SMALL RODENTS IN BIG BEND NATIONAL PARK

THE INFLUENCE OF A RETURN OF NATIVE GRASSLANDS UPON THE ECOLOGY AND DISTRIBUTION OF SMALL RODENTS IN BIG BEND NATIONAL PARK

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In the southwestern United States there is a delicate balance between the existing grasslands and the rodent fauna. The purpose of this investigation was to determine the influence of secondary succession of native grasslands upon the ecology and distribution of small rodents. Two methods of determining the rodent species were plot quadrates and trap lines using Sherman live traps.

Habitats, reproductive conditions, elevational effects, edaphic preference, species interaction, and ectoparasites of the small rodents were studied between June, 1969, and June, 1971, in Big Bend National Park, Texas. Rodents were captured in three different plant formations. Grassland, Desert Shrub, and Woodland formations, in that order, contained the greatest to the lowest species diversity.

The distributional relationship of rodents to plant formations was analyzed using the resemblance equation, $x^n + y^n = 1$. Comparison of grassland to desert shrub and woodland communities yielded similar values, 0.45 and 0.49, respectively. The grassland, intermediate in position geographically, was influenced by woodland rodent species from

higher elevations and by species from lower elevations in the Desert Shrub formation.

The Desert Shrub and Woodland formations had only one species (*Ammospermophilus interpres*) in common. The contrast between the two formations was evident in a similarity value of 0.06. The dissimilarity value (0.94) approached one and indicated not only rodent species' adaptation to edaphic and floristic patterns, but also geographic isolation of the Desert Shrub and Woodland formations. The contrast in floral and faunal composition of the three plant formations precluded equilibrium of rodent species.

Dipodomys merriami, *Neotoma micropus*, *Perognathus penicillatus*, and *Peromyscus eremicus* attained maximum abundance in the Desert Shrub formation. *Sigmodon hispidus*, *Peromyscus merriami*, *Reithrodontomys megalotis*, and *Peromyscus maniculatus* preferred grasslands while *Peromyscus boylii*, *Peromyscus pectoralis*, *Neotoma albigula*, and *Sigmodon ochrognathus* were common in woodlands.

Specimens were collected between 1,850 and 7,100 feet. Only one species, *Spermophilus variegatus*, was recorded from each elevational interval. Species diversity was greatest between 1,850 and 5,500 feet. Heteromyid rodents were abundant at desert elevations, while cricetid rodents were more numerous in the elevational range of the grassland and woodland.

separations were evident. Species of the genera *Sigmodon*, *Spermophilus*, and *Neotoma* were allopatric.

Winter, fall, and early spring were periods of high reproductive activity, while late spring and early summer were low periods. Average litter size for the rodent species was 4.32.

Twelve genera and 21 species, four which are new species, of chiggers (Family Trombiculidae) were collected from 19 rodent species. Definite trends were evident in host habitat preference and chigger ectoparasites. Desert shrub-, grassland-, and woodland-inhabiting rodent species exhibited similar parasite species.

Small mammal habitats have been destroyed on an ever increasing scale by the encroachment of man. It is necessary not only to determine how much stress can be placed on the balance of an ecological association, but also the capacity or extent of recovery when stress is removed and succession allowed to proceed. This has been the case in Big Bend National Park. Through severe overgrazing of grassland, the ecological balance that had existed for centuries was disrupted. Now recovery has begun and is in initial stages. This study will form the foundation through which succession to a return of the native environment can be studied for years.

ACKNOWLEDGEMENTS

I thank the National Park Service for logistic support. The success of this project was enhanced greatly by the interest and assistance of Chief Park Naturalist Roland Wauer. Appreciation is also extended Park Superintendent L. T. Peterson, Jr., for housing facilities in Big Bend National Park.

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CHAPTER I

INTRODUCTION

The Problem

In the southwestern United States there is a delicate balance between the existing grasslands and the amount of annual precipitation. Since rodents are dependent upon the grassland and other existing vegetation for existence, any serious disturbance in the ecology of the grasslands would certainly have an effect upon local populations. When Big Bend National Park, an area of 708,281 acres or 1,100 square miles, was established in 1944, the area had been subjected to 50 years of severe overgrazing by domestic livestock. Two effects were number reduction and range restriction of the pronghorn (*Antilocapra americana*), javelina (*Tayassu tajaca*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginiana*) (Borell and Bryant, 1942). Apparently the black bear (*Ursus americanus*), gray wolf (*Canis lupus*), ocelot (*Felis paradalis*), opossum (*Didelphis marsupialis*), and bighorn (*Ovis canadensis*) became extinct in the park between 1900 and 1930 (Borell and Bryant, 1942). The larger predators disappeared as the large herbivores died or migrated from the park area. There are no records concerning the impact of overgrazing on the rodents, but it is probable that they were affected to a greater extent than were the larger mammals.

Increased interest in the Chisos Mountains in 1936 and 1937 prompted the National Park Service to support a series of investigations. These were of the biological survey type where both the flora and fauna of the region were studied. Johnson (1936) and Smith (1937) reported on the wildlife of the proposed park. Marsh (1937) conducted a survey of the Santa Rosa and Sierra del Carmen Mountains of northern Coahuila to the south of the park area. Borell and Bryant (1942) published the first general study of the mammals of Big Bend National Park. Distributional and ecological data were presented, but the study was far from comprehensive. Their research revealed the environmental restriction and small populations of the rodents. Taylor, McDougall, and Davis (1944) made a general ecological survey adding to the information on mammals. Denyes (1956) investigated the vegetational relationships of the small mammals.

Other mammal surveys were conducted in the Big Bend region by Bailey (1905), Blair (1940), Blair and Miller (1949), Hermann (1950), Tamsitt (1954), Dixon (1958), Judd (1967), and Easterla (1968, 1970). Judd (1967) commented on Denyes' study and suggested that there is presently insufficient data on the distribution of small mammals in the park. A further review of the literature demonstrates this fact. The Borell and Bryant study is outdated, and Denyes, who concentrated on the desert lowlands, presented little information on the mountainous areas of the park.

It has been 25 years since the removal of the domestic livestock. The purpose of this study was to investigate the impact of the secondary succession of the native grassland upon the ecology and distribution of the rodents in Big Bend National Park. This involved the securing of breeding and reproductive data, vegetational relationships, altitudinal effects, species interactions in overlapping or interface areas, taxonomic data, and ectoparasitic information.

The habitats of small mammals have been destroyed on an ever increasing scale by the encroachment of man. It is necessary not only to determine how much stress can be placed on the balance of an ecological association, but also the capacity or extent of recovery when stress is removed and succession allowed to proceed. This has been the case in Big Bend National Park. Through severe overgrazing of the grassland, the ecological balance that had existed in the park for centuries was disrupted. Now the healing has begun and is in its first stages. This study will form the foundation through which succession to a return of the native environment can be studied for years. There are very few instances where the ecology of an area has been so destroyed, yet later allowed to repair itself.

Place Names

The names of places mentioned in the present paper are listed below. The approximate location of each place in the park is given in Fig. 1. A more exact location can be obtained by referring to the topographic map of the Chisos Mountains quadrangle, 1905 edition, of the United States Geological Survey.

BASIN (THE), 5,000-5,600 feet--head of Oak Creek
BLUE CREEK,--southwest slope of Chisos Mountains
BONE SPRING DRAW, 2,594 feet--four miles south of Persimmon Gap
BOQUILLAS, 1,800 feet--canyon on Rio Grande River
BOULDER MEADOW, 5,700 feet--northeast base of Emory Peak
BURRO MESA, up to 4,400 feet--west base of Chisos
CASTOLON, 2,100 feet--village on Rio Grande River
CHILOCOTAL MOUNTAIN, 4,104 feet--east base of Chisos
CHISOS MOUNTAINS, height to 7,835 feet--largest range in the area
DAGGER FLAT, 3,500 feet--northeast Chisos Mountains
EMORY PEAK, 7,835 feet--highest peak in the Chisos
GANO SPRING, 3,400 feet--north base of Burro Mesa
GLENN SPRING, 2,606 feet--southeast base of Chisos
HOT SPRINGS, 1,900 feet--on Rio Grande River at mouth of Tornillo Creek
JOHNSON RANCH, 2,060 feet--located on big bend of Rio Grande
JUNIPER FLAT, 5,600 feet--northeast base of Emory Peak
JUNIPER CANYON, 4,000-6,000 feet--on east slope of Chisos
K-BAR, 3,700 feet--three miles east of Panther Junction
LAGUNA MEADOW, 6,700 feet--west base of Emory Peak
LONE MOUNTAIN, 4,132 feet--near northeast base of Chisos
MARISCAL MOUNTAIN, 2,400-3,940 feet--southeast of Chisos
MESA DE ANGUILA, up to 3,884 feet--north of Santa Elena Canyon
NINE POINT DRAW, 2,600 feet--five miles west of Persimmon Gap
PANTHER JUNCTION, 3,700 feet--north base of Chisos
PERSIMMON GAP, 2,970 feet--northwest point of the park
PINE CANYON, 4,000-6,000 feet--northeast slope of Chisos
ROSILLOS MOUNTAINS, up to 5,420 feet--north of Chisos
SAN VICENTE, 1,880 feet--village on Rio Grande River southeast of Chisos

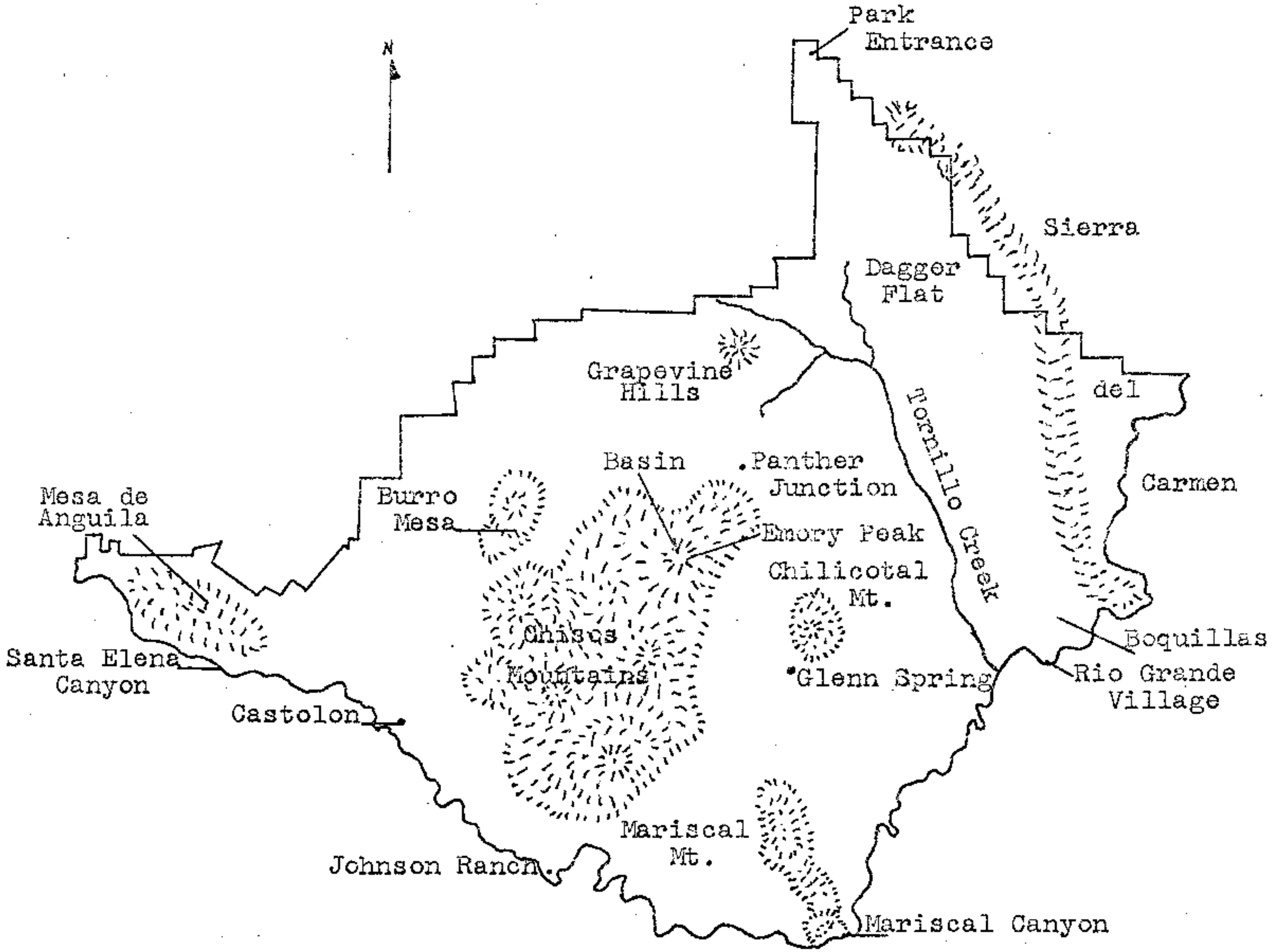

Fig. 1--Map of Big Bend National Park

TOBOSA FLAT, 2,000-3,000 feet--west of Mariscal
Mountain
TERLINGUA CREEK,--southwest of Chisos Mountains
TORNILLO CREEK,--north and east of the Chisos

Materials and Methods

One hundred aluminum Sherman live traps, nine inches long, three inches wide, and three inches high, baited with rolled oats, were used in the study. Traps were checked daily before 9:00 a.m. Each trapline consisted of 25 stations, 25 feet apart, at which one trap was placed for three consecutive nights. Thus each trapline consisted of 25 traps along a line 600 feet long. This procedure is a modification of the "Calhoun line" which is widely used in surveys of relative abundance (Calhoun and Casby, 1958). Lines were set parallel to natural physiographic features such as streams or ridges or through the middle of vegetational areas.

When selecting a study area, one assumption made was that there was an even distribution of mammals in the area--this is seldom the case. Any sampling method will have its disadvantages even in an extensive and uniform type of habitat, but where the terrain is not uniform it becomes even more susceptible to error (Drake, 1958). Murray (1957) discussed small mammal distribution in habitats which, because of their lack of uniformity, created sampling problems. He showed that in three areas of this type, there was evidence that the movement and distribution of small mammals was influenced by the habitat so that a sample would be biased, or subject to error. Sampling stations were distributed widely throughout the park and were established to sample as many habitats as possible, rather than on a random basis.

Field work was conducted in Big Bend National Park (29°, 00' to 20°, 40' N latitude) from August, 1969, to June, 1971. A total of 1,325 specimens was collected. Linear body measurements in millimeters were obtained from the specimens and include total length, length of tail, hind foot length, and height of the ear from the lower notch.

Body weights were taken to the nearest 0.1 g on a triple beam balance. Sex and reproductive status of all specimens were noted. The number of embryos and an average crown-rump length of each embryo were recorded for pregnant females.

Statistical analysis using the "Resemblance Equation" (Preston, 1962) to test for a break between faunistic homogenity and heterogenity was used in analyzing distribution.

Ectoparasites were obtained by individual removal with forceps and by combing the fur.

CHAPTER II

CHARACTERISTICS OF THE LAND

Geology

Big Bend National Park lies along the border of the United States and Mexico, and includes areas of desert lowlands and mountains. Here the Rio Grande makes a huge U-shaped bend as it forms the international boundary between the Mexican states of Chihuahua and Coahuila and the adjacent state of Texas. The park lies within the Basin and Range Physiographic Province of Fenneman (1931), a province characterized by rugged mountain ranges from 1,800 feet just below the mouth of Boquillas Canyon, to 7,835 feet at the top of Emory Peak. The intermontane flats are typical of the Chihuahuan Desert. The Chisos Mountains provide the outstanding physical feature of the area. They are of extremely rugged relief, and encircled by sharply sloping foothills which merge with the desert plain.

The area was, intermittently, a sea bed during the Paleozoic and part of the Mesozoic eras; a swampy marsh land and a semi-tropical forest in the Cretaceous period; and the scene of extensive volcanism and upheaval in the Cenozoic era. Since the volcanic mountain building, the land has been subjected to erosion, becoming the desert-mountain environment of today. Vast canyons have been cut through uplifted mesas; soluble materials have been dissolved and sands, gravels, and smaller rocks have been carried away by flood waters forming arroyos, basins, and wide plains. Concurrently the more resistant rocks were left as peaks, high ridges, spires, mesas, and cliffs (Maxwell and Dietrich, 1965). Thus, through a combination of many geological forces such as sedimentation, volcanism, weather changes, and erosion, the Big Bend area has become an area of rough landscape and arid desert.

During the Appalachian Revolution (230 million years ago at the end of the Permian period), and the Laramide Revolution (63 million years ago near the end of the Cretaceous period) the main geologic uplifts occurred in southwestern Texas (Udden, Baker and Bose, 1916). It was during the Laramide Revolution that the Rocky Mountain system and the Mexican Sierra Madre ranges were formed. The Big Bend country lies between these two major mountain ranges, but the Chisos Mountains are not as high as either the Rockies or Sierra Madre ranges. During the Tertiary period and the Pleistocene epoch, igneous rock was intruded into the sedimentary deposits of the Lower Cretaceous limestones. Unable to reach the surface, molten lava hardened to form the plug-like masses present in numerous peaks of the Chisos Mountains. Extrusive deposits of ash and lava are present in the Cerro Castolon area of the park.

The Chisos Mountains and surrounding smaller peaks are isolated elements of volcanic origin, composed primarily of various intrusive and extrusive igneous rocks. This is in contrast to surrounding ranges which are predominantly limestone.

The Chisos Mountains arise near the center of a structural trough. This irregularly shaped graben averages 40 miles in width. The floor's flatness, planed by erosion just after the Cretaceous period, is bounded by the Santiago-Sierra del Carmen Mountains on the east and the Mesa de Anguila and the Christmas-Rosillos Mountains on the west.

Weathering and water erosion carved the castle-like formations of many of the mountain tops, the mesas, and the deep canyons. The mountain slopes are usually steep and strewn with boulders and talus. Igneous rim-rocks are exposed frequently in the vertical, high cliffs on the lower flat-topped mountains, whereas the highest peaks are conical in shape forming a complex system of ridges. Numerous gorges and gaps have been cut into the rock masses.

Below the mountain peaks and slopes lies the plain of the Cretaceous trough, characterized by a variety of topographic features. Erosive action has resulted in a maze of gullies, rock outcrops, buttes, small mesas, long linear ridges, cuestas, and hogbacks, forming a badlands on the plain. Rocks are clay and shale with alternating layers of sandstone. Drainage from the mountains descends to the lowlands by a system of canyons, leading ultimately to the Rio Grande by way of several major, intermittently flowing creeks.

Soils

Carter (1928, 1931) and Denyes (1956) discussed the physical and chemical characteristics of the Big Bend soils. The soil and vegetational relationships were reported by Carter and Cory (1932). The soils are generally coarse as is typical of desert and semi-desert areas. A major portion of the surface sediments is a gravelly outwash composed of igneous and calcareous detritus. At higher elevations on the mountain slopes, rocks and boulders are more abundant, and the soil is increasingly coarse and varied. Generally, soils in the mountains are very shallow, open, and well drained, with the drier slopes supporting semi-desert and desert vegetations. Pockets of forest humus have developed locally in the high Chisos and the lower forested canyons. Denyes (1956) divided the soils into two groups--Highland and Lowland. The highland soils are characterized by their shallowness and a basic or acid reaction. The Rio Grande floodplain and some of the larger creeks have deep deposits of sand.

The soil types of the park (Denyes, 1956) include the Gila, Rio Grande, Reagan, Reeves, Ector, and Brewster series. Floodplain soils and adjacent areas of the Rio Grande and its major tributaries are of the Gila and Rio Grande series.

These soils are friable, deep, fine, sandy loams, subject to frequent flooding.

The gravelly loam soils of the basins belong to the Reeves series. This soil type contains little humus and dominates on the desert plain.

The gravelly loam of the Reagan series occupies an altitudinal range of 3,500 to 4,500 feet on the lower grassy slopes of the foothills. Here there is an underlayer of caliche with a six to ten inch layer of surface soil.

Ector series soils are found at the same elevations as the Reagan series. These are sandy loams with a silt and clay mixture.

The soils of the Brewster series are located in the highest mountains. Although sparse, these soils usually have a high humus content due to the leaf litter. In many places this fine, sandy loam is found only in crevices and depressions.

Big Bend National Park has been subjected to severe overgrazing since the late 1800's. As a result, sheet erosion has removed much of the original topsoil from the area. The soil has been undergoing a rebuilding since 1945, when livestock grazing ceased.

Climate

The climate of the park varies from arid to semi-arid, and the differences are a result of elevation. Thornthwaite (1948) classified the climate of Big Bend National Park as

E B'd. This is an arid, mesothermal climate, deficient in precipitation throughout the year. Sunlight abundance is evident in the average yearly temperature, which is 68° F, with a range of -8° to 118° F. The temperature must frequently exceed 120° F at the low elevations south of the Chisos Mountains during the summer, but no data are available for this area. Days are longest and the intensity of the sunlight greatest in June and July. Diurnal fluctuation is great. Daily variations in air temperature of more than 30° F, as well as soil-temperature variations of 70° F, are often recorded on the desert (Degenhardt, 1966). Temperatures in the higher mountain areas (Fig. 2) are about five

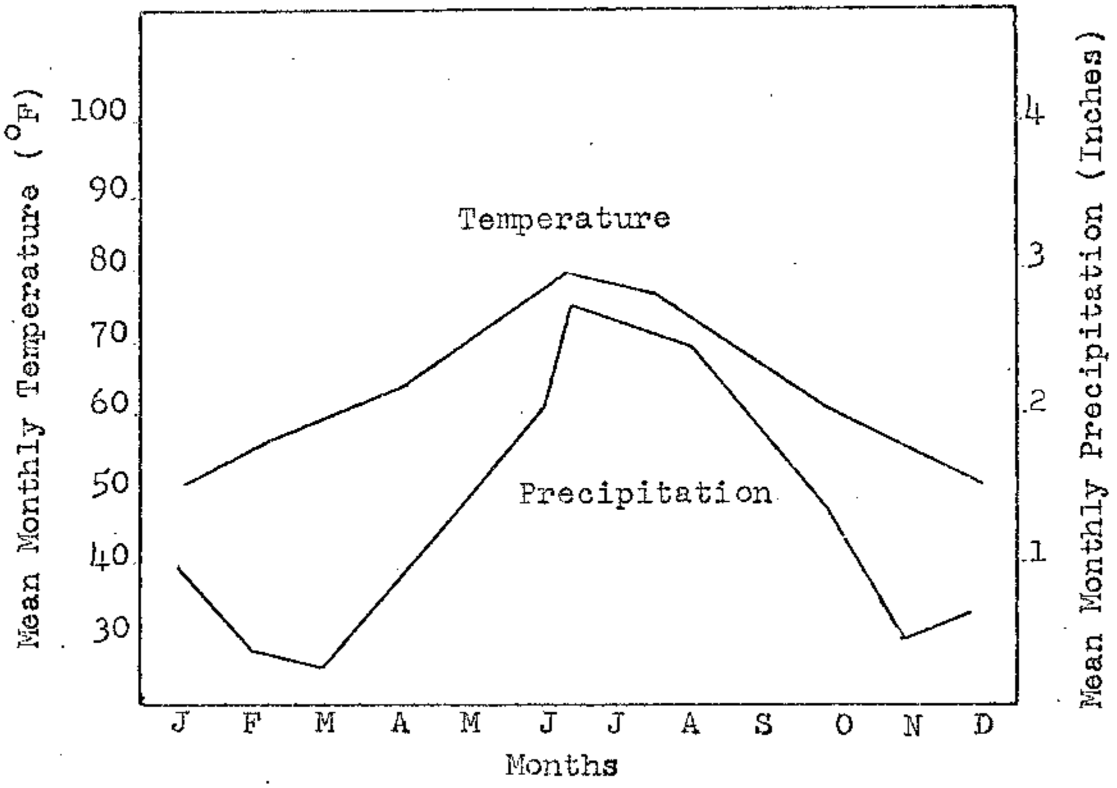

Fig. 2--Monthly temperatures and precipitation for the Basin, 5,300 ft. (Compiled from records 1947-1966. Big Bend National Park).

degrees less than those on the mountain slopes (Panther Junction), while the temperatures along the Rio Grande average five to ten degrees higher than those recorded at Panther Junction.

Precipitation is erratic throughout the park. The lower elevations surrounding the Chisos Mountains receive a total annual rainfall of less than 10 inches, the mountain slopes (Panther Junction) at an elevation of 3,700 feet average 12 inches (Fig. 3), the Basin at 5,100 feet 16 inches, and the higher elevations above 7,500 feet probably receive 20 to 25 inches a year. Rainfall may occur throughout the year because of sporadic storms during frontal passages. Most of the

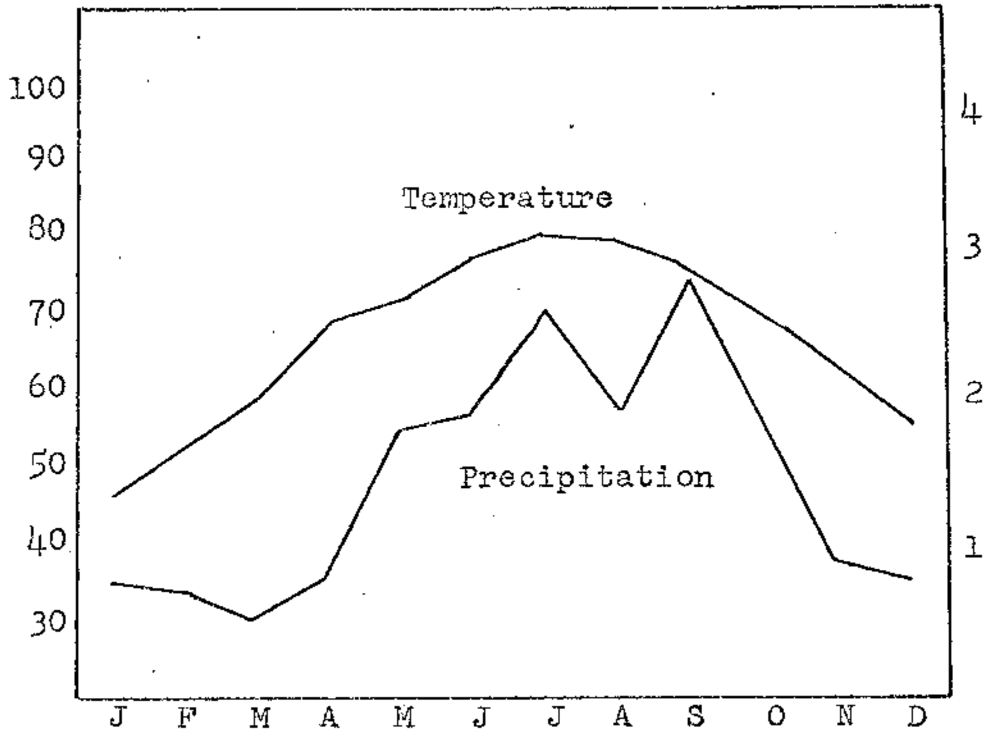

Fig. 3--Monthly temperatures and precipitation for Panther Junction, 3,700 ft. (Compiled from records 1947-1966. Big Bend National Park).

rainfall is measured during late summer and early fall. Precipitation other than rainfall occurs as snow in the higher Chisos Mountains.

Blair (1942) assigned the Big Bend of Texas to the subtropical belt of high pressure which produces xeric climates around the entire world. The center of high pressure over the Great Basin produces moisture-deficient winds from the north and northwest in the winter. A low pressure area in Arizona causes an influx of easterly winds from the Gulf of Mexico in the summer, but the winds lose most of their moisture due to passage over a vast expanse of warmer earth. However, enough moisture remains, and the upward movement of the air mass as it reaches the Chisos Mountains causes condensation and precipitation in the summer (Muller, 1937). During this period approximately three-fourths of the annual rainfall occurs.

The Chihuahuan Desert

The Chihuahuan Desert is separated from the Great Basin, Mohave, and Sonoran Deserts by the high plains in southwestern New Mexico, and the Sierra Madre Occidental in western Chihuahua. The Chihuahuan Desert is the second largest desert in North America. It includes part of eastern New Mexico and western Texas adjacent to the Rio Grande, the lower valley of the Pecos River, the eastern half of Chihuahua, the western half of Coahuila, and parts of Durango, Zacatecas, Nuevo Leon, and San Luis Potosi (Fig. 4). In Texas an area of some 19,000,000 acres is included within the Chihuahuan Desert.

This desert is characterized by a mountain-basin topography. The elevation varies from a low of 1,800 feet along the Rio Grande in Big Bend National Park to over 8,000 feet in the Davis Mountains of Texas. Nearly half of the Chihuahuan Desert is over 4,000 feet in elevation. Hard gravelly surfaces cover the majority of the desert. Limestone is more abundant than in the other North American deserts,with limestone soils occupying the greatest total area. There are large expanses of igneous soils with some localized deposits of aeolian and alluvial sandy soils. Closed basins of several square miles in area are covered by extensive alkaline flats in Chihuahua and Durango.

Low rainfall and humidity, high evaporations, and a marked diurnal temperature variation characterize the climate of the Chihuahuan Desert. The average annual precipitation is usually 10 inches or less. In the undrained basins of Coahuila the average is three inches. It is only on the mountains and slopes that rainfall exceeds 12 inches, as some mountain peaks probably receive between 20 and 25 inches annually. Summer rainfall is common, with 65 per cent to 80 per cent of the total annual rainfall being received between June and September (Shreve, 1942). Because there is usually little cloud cover, temperatures rise rapidly during

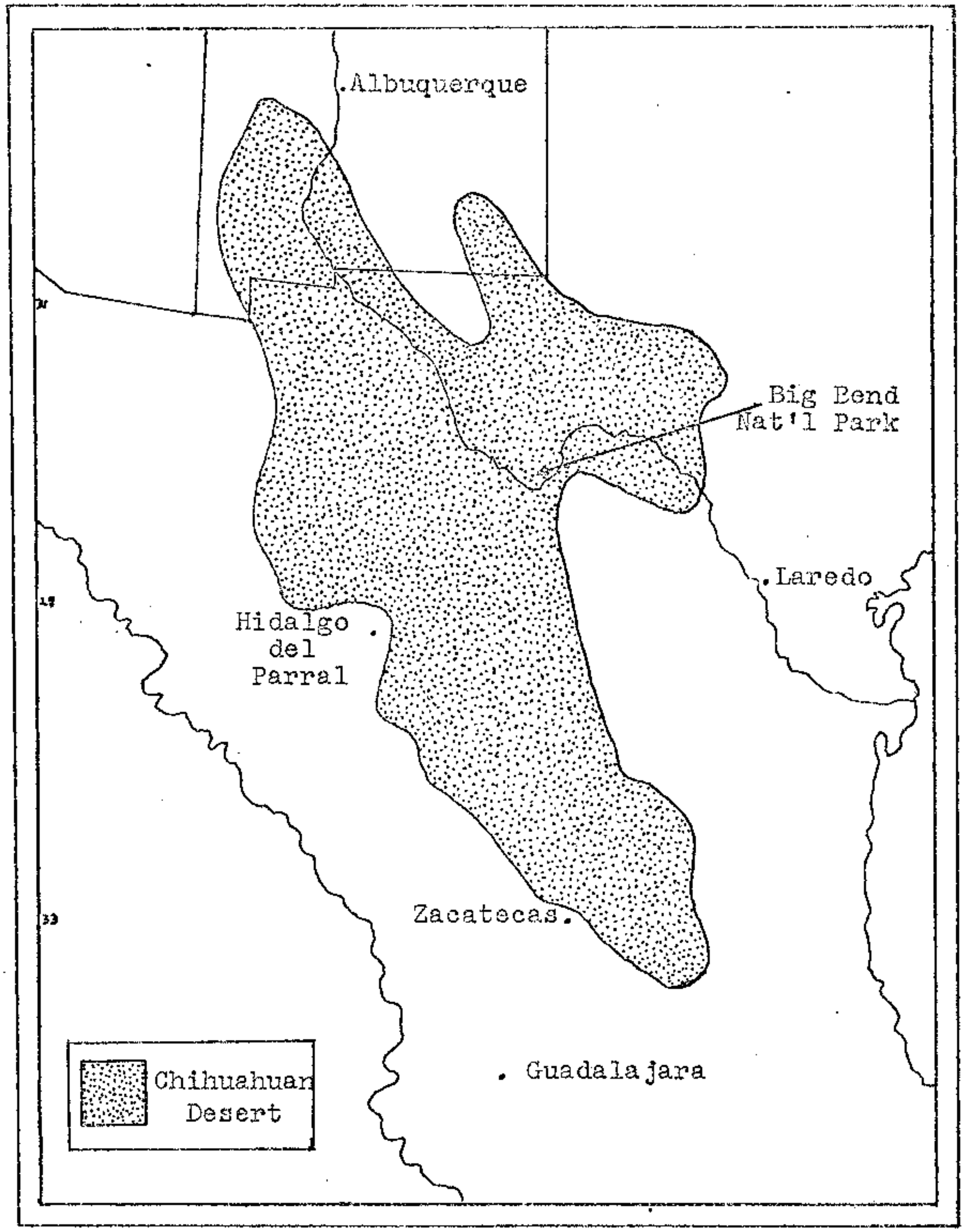

Fig. 4--Map of the Chihuahuan Desert (from "The North American Deserts" by Edmund C. Jaeger. Stanford University Press, Stanford, California, 1961).

the day, but radiation cooling at night may result in a diurnal temperature range of 50 degrees or more. Summer temperatures in excess of 100° F are not uncommon. At desert levels moderate frosts occur in the winter, with more severe temperatures and light snows above 5,500 feet.

Elevation, topography, soil, climate, and other various factors affect plant distribution and cause a variety of floristic associations. Creosotebush (Larrea divaricata), tar bush (Flourensia cernua), sotol (Dasylirion leiophyllum), lechuguilla (Agave lecheguilla), and ocotillo (Fouquieria splendens), are indicative of the desert plains. The higher elevations are characterized by an assortment of pines, oaks, junipers, and a variety of grasses.

Vegetation

The geological processes forming the mountains, the weathering and erosion reducing both the highlands and the lower slopes, the regional climate, and the local rainfall have all had a direct effect upon the kind and distribution of vegetation. Plant associations are usually found as irregular belts that are dependent on the altitude, rainfall, and local air currents. Forests are present on these mountain tops where moisture is available, but others, with unfavorable environment, are barren. Vegetation is poorly developed on the eroded lowlands, where temperatures are more severe and rainfall is minimal.

Big Bend National Park lies within the Chihuahuan Biotic Province (Dice, 1943; Blair, 1950). This province coincides to some extent with the Chihuahuan Desert and the physical and climatic features resemble those previously described for the Chihuahuan Desert. The park area was assigned to the Creosote Bush (Southern Desert Shrub) region of the United States by Shantz and Zon (1924). Tharp (1928) described the Sotol-Lechuguilla and Mountains regions of Texas to encompass the park area. Davis and Robertson (1944) recognized the Chihuahuan biotic province, but the usage of the term "Province" in their publication conformed to a greater extent to the life belts concept of Dice (1943). York (1949) designated the park area to the Rio Grande Basin district and Denyes (1956) defined the Chisos biotic district of southern Brewster County. The last researcher to define a large vegetational unit was Milstead (1961), describing the Big Bend biotic district. The Chisos biotic district of Denyes and the Big Bend biotic district of Milstead are quite similar. The district is distinguished, primarily, by an abundance of creosotebush associated with tarbush, mesquite, ocotillo, prickly pear, sotol, and lechuguilla. Lower Sonoran, Upper Sonoran, and Transition life zones are represented by the flora of Big Bend National Park.

The vegetation in Big Bend Park has been extensively studied. The first studies were inventories of the flora, but more recent investigations have emphasized ecology.

Many of these floristic studies were combined with information on the fauna. The majority of the early studies were centered on the Big Bend region and not on the park itself. Bailey (1905) reported the first basic information on the flora and fauna. Bray (1901, 1905, 1906) extensively described the desert vegetation of Trans-Pecos Texas. Palmer studied the vegetation of the Chisos Mountains (1928) and the Davis Mountains (1929). Carter and Cory (1932) investigated the soil-vegetation relationship. The flora of the Alpine area was reported by Cottle (1931, 1932). Muller (1937) described the vegetation of the Chisos Mountains. A checklist of the plants in Brewster County was published by Sperry and Warnock (1941). Hinckley worked in the Davis Mountains (1944) and in the Sierra Vieja (1947). The vegetation of the Glass Mountains was disclosed by Warnock (1946). A semitechnical guide to the plants of Big Bend Park based on Sperry's earlier works (1938, 1941) was published by McDougall and Sperry (1951). Anthony (1954, 1956) investigated the Opuntiae in the Big Bend. The affinity of the Big Bend flora to that of the Chihuahuan Desert in northern Mexico was examined by Shreve (1939, 1942), Le Susur (1945), and Muller (1947). Denyes (1956) detailed the life belts of Big Bend National Park and their associations. A recent study by Warnock and Kittams (1970) defined the plant formations and their associated communities in Big Bend National Park.

The community structure of the plants in the park has been analyzed in six reports. Borell and Bryant (1942) described four distinct associations--River Bottom, Desert Flat, Lower Foothill, and Chisos Mountains Proper. Their analysis of the vegetation was general.

Taylor et al. (1944) defined five plant communities (biomes). These were the River Floodplain, Desert Shrub, Sotol Grass, Woodland, and Forest biomes. Theirs was a general ecological survey, but was much more comprehensive than the study of Borell and Bryant (1942).

Four general plant communities were outlined by McDougall and Sperry (1951). The Desert Shrub was considered the most extensive type of vegetation in the park, and characterized by the creosotebush. The characteristic plants of the desert grassland community were chino grass and sotol, occupying the lower slopes of the Chisos Mountains. The middle and upper slopes of the Chisos were locations of the pinyon-juniper-oak woodland. The mesophytic species of the high mountains were placed in the ponderosa pine-Douglas fir-Arizona cypress forest. Denyes (1956) used natural terrestrial communities to depict three life belts. The listed life belts were the Desert Plains, Foothills, and the Encinal, with each being divided into a number of associations.

The Desert Plains life belt was characterized by typical Chihuahuan Desert species (Denyes, 1956; Shreve, 1942). The Desert Plain extended from the Rio Grande River floodplain to approximately 3,500 feet elevation. Scattered lush growth was supported by alluvial deposits along the river.

The Foothills life belt associations were found on the mountain ranges and low hills from elevations of 3,500 to 4,500 feet. In this area there was a floristic intergrading of desert forms and grassland species. The conditions for grass on the slopes were superior to the desert plains.

The steep slopes, basins, and canyons of the upper Chisos at elevations between 4,500 to 7,835 feet were characterized by tree growth and grassy meadows. This mesophytic environment was included in the Encinal life belt.

Gehlbach (1966) discussed the floristic aspects of the Chihuahuan Desert and Chisos Mountains. The vegetation in a broad belt from the Grapevine Hills up Green Gulch to the Chisos Mountains and its related canyons was described. Therophytes were common on the desert plain and phanerophytes increased in numbers on the slopes and higher Chisos. He believed the desert grassland was dominant until the arrival of the white man. The park was divided into seven vegetational formations, but the continuum of the vegetation, because of the uniqueness of the species, did not exhibit a clear replacement of one species by another. There were distinctly different areas of abundance and different distributions. The dominant species were shrubby leaf-succulent or semi-succulent species. The seven formations were the

Desert Shrub, Chihuahuan Desert, Desert Grassland, Mountain Grassland, Evergreen Woodland, Deciduous Woodland, and the Coniferous Forest.

In 1955 field botanists from Texas A&M University established more than 100 plots in the park. Research was conducted by Barton H. Warnock, and results of the vegetational analysis since 1955 have resulted in a new vegetational map (Fig. 5) of Big Bend National Park (Warnock and Kittams, 1970). Three plant formations (Desert Shrub, Grassland, and Woodland) were defined. The Desert Shrub formation contained three communities--Mesquite-Giantreed, Creosotebush, and Creosotebush-Tarbush. The Chino grama--Lechuguilla, Chinograma-Blackgrama-Skeletonleaf goldeneye, Chinograma-Candelilla, Hechita-Chinograma-Sotol, Grama-Sotol, and Giant Dagger-Sotol communities composed the Grassland formation. The Woodland formation contained semi-arid to mesophytic plant communities (Mexican Pinyon-Oak-Juniper and Ponderosa Pine-Douglas Fir). This is the most accurate vegetational analysis of the park. The mammalian-floristic relationships will be defined using this model.

A number of faunal studies also mentioned the vegetation of the area studied. These are Blair (1940), Borell and Bryant (1942), Tinkham (1948), Blair and Miller (1949), Jameson and Flury (1949), Phillips and Thornton (1949), Thompson (1953), Tamsitt (1954), Milstead (1953), Baker (1956),

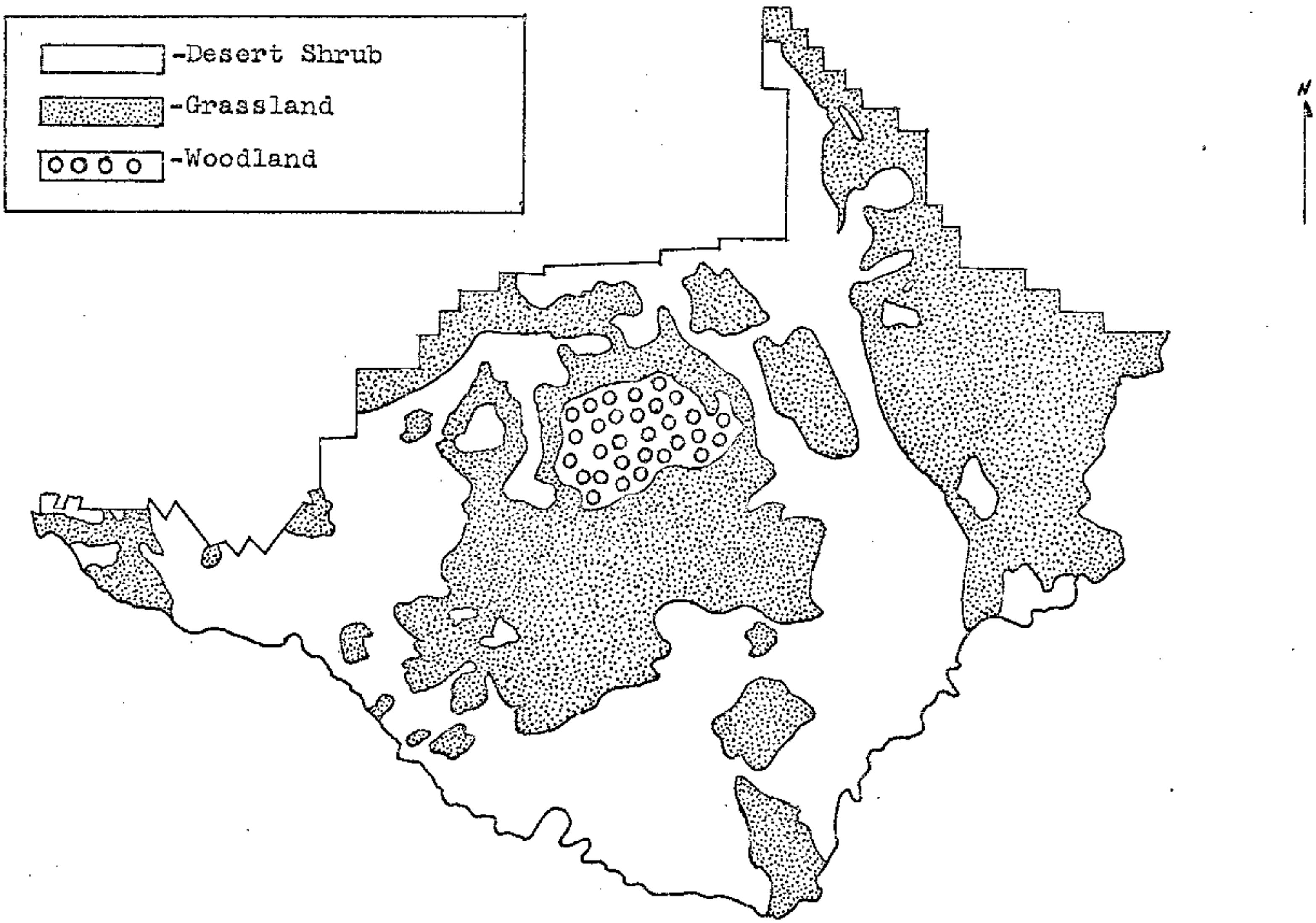

Fig. 5--Vegetation Map of Big Bend National Park, (Adapted from a map by Warnock and Kittams, unpublished).

Axtall (1959), Denyes (1956), Minton (1958), Milstead (1961), and Degenhardt (1966).

As was previously noted, the Big Bend area has undergone a series of changes through geologic history. Vegetationally a Pleistocene influence can be recognized in the park. In the Pleistocene, or "glacial" epoch, the cooling trend which had begun in the Oligocene epoch led to the formation and slow spread of lowland ice sheets in higher latitudes toward lower latitudes (Dorf, 1960). As the ice sheets spread southward from central Canada, a glacially induced climatic change occurred in the United States. There is evidence of subarctic plants and animals far to the south in North America. Occurrences of northern spruce and fir are found in the lowlands of northern and central Florida, south-central Texas, northern Oklahoma, and southern Kansas (Deevey, 1949; Davis, 1946; Potzger and Tharp, 1947). The evidence confirms that the northern forest belts migrated over extensive distances during glaciation. Since these forest belts are climatically influenced, it is evident that the climate in the southwest was much cooler than at present. Dorf (1960), in his generalized map of the climatic zones during the glacial stages of the Pleistocene, showed a subarctic climate as far south as the vicinity of El Paso. On his map, Big Bend was influenced by a cool temperate climate. Today the subarctic climate extends south in the high Rocky Mountains as far as northern New Mexico, but is centered in Canada.

The cool temperate climate is located in areas adjacent to the United States and Canadian boundary.

Harris (1970) reported the following subarctic, climatically influenced mammals from Pleistocene deposits of northern New Mexico: *Marmota flaviventris*, *Neotoma cinerea* *Lepus townsendii*, *Microtus longicaudus*, *Spermophilus richardsoni*, and *Sylvilagus nuttalli*. Findley (1965) found *Sorex nanus* in Pleistocene cave deposits in southern New Mexico. Patton (1963) reported fossil remains of *Synaptomys cooperi* in Llano, Burnet, Kendall and Dallas Counties, Texas; Dalquest, Roth, and Judd (1969) in a study of the mammal fauna of Schulze Cave in Edwards County, Texas, found *Synaptomys cooperi* with *Sorex cinereus*, *Microtus pennsylvanicus*, *Zapus princeps*, *Lepus townsendii*, and *Mustela erminea*. Cushing (1945) reported *Synaptomys cooperi* from Pleistocene deposits in San Josecito Cave, Nuevo Leon, Mexico. Hamilton (1937) stated that *Synaptomys cooperi* was definitely of boreal affinity. It is apparent from scattered fossil localities that the range of the southern bog lemming in the late Pleistocene (Wisconsin glacial period) extended from near the ice sheet south into northern Mexico.

Fossil evidence tends to support the generalized Pleistocene climatic conditions proposed by Dorf (1960). Dalquest *et al.* (1969) postulated that in the late Pleistocene the High Plains of Texas and the region extending to the base of the Rocky Mountains was similar to a modern alpine meadow.

The climate was cool, but there were no long periods of subfreezing weather. Findley (1965) suggested that a relatively mesic forest was present in southern New Mexico which probably extended south into the Trans-Pecos of Texas. This forest was possibly similar to a lower Canadian life zone habitat. Many of the Pleistocene specimens collected by Harris (1970), Finley (1965), and Dalquest *et al*. (1969), are occupants of the Transition and Canadian life zones now located several hundred miles north of Big Bend National Park.

Wells (1966), in a vegetational study of the Pleistocene composition of *Neotoma* middens, theorized that the mesophytic, montane forests of the southwest became discontinuous in the Tertiary. It is quite likely that many mesophytic, montane, coniferous species have never had a continuous distribution across the intervening lowlands. Douglas fir (*Pseudotsuga*) occurs in the Sierra del Carmen, Guadalupe, and Chisos Mountains. *Pinus ponderosa* occurs in the Chisos Mountains, but more massive stands are located in the Davis Mountains. *Pinus flexilis*, *Quercus hypoleucoides*, *Styrax youngae*, and *Viburnum affine* occur in the Davis and Sierra del Carmen Mountains, but not in the smaller Chisos Mountains.

Preserved plant materials with radiocarbon ages ranging from 11,500 to more than 20,000 years BP, were found in rock sheltered wood rat deposits at desert elevations in Big Bend National Park (Wells, 1966). The data indicated that an open, xerophilous woodland of pinyon pine, liveoaks, and junipers were present during the Wisconsin pluvial (Wells, 1970). These woodlands today are disjunct stands on the higher mountains of the Chihuahuan Desert. During the pluvial associated with Wisconsin glaciation, there was an absence of the desert climate, but the climate did not allow the strictly montane forest zone of more mesophytic conifers and broad-leaf deciduous trees to expand much beyond the narrow confines of the Chisos Mountains' central mass. In middens at 1200 meters mesophytic, montane species were absent, but middens located at 880 meters in existing desert vegetation indicated a xerophilous woodland 800 meters below present woodland vegetation.

In pluvial times, the desert flora of the Chihuahuan region may have coexisted with the woodland flora in much the same manner as characteristic desert species presently extend to remarkably high elevations within the woodland zone. Direct fossil evidence in the Pleistocene _Neotoma_ middens indicated pinyon pine (_Pinus cembroides_), juniper (_Juniperus pinchotii_), algerita (_Berberis trifoliolata_) shrubby live-oak (_Quercus pungens_ and _Q. grisea_), prickly pear (_Opuntia macrocentra_), and the more xerophytic lechuguilla (_Agave lecheguilla_), acacia (_Acacia roemeriana_), and sotol (_Dasylirion leiophyllum_) composed the same midden.

Twenty thousand years ago, a mesophytic forest occurred in the Chisos Mountains and the desert plain of today was covered by a xerophytic woodlands that merged with the forest on the lower mountain slopes. An invasion of desert species began 8,000 to 10,000 years ago (Wells, 1970), correlating with the prolonged drought that occurred with the recession of the ice sheet of the last glacial period (Casey, 1969). Desert species replaced woodland species. It is estimated that the environment of today has changed very little over the last 2,000 to 3,000 years.

Except for the large herds of stolen livestock that raiding Indians had driven across the Big Bend country, few if any domesticated livestock had ever grazed there. The valleys and hills of the area were unaffected by the increased erosion which has always followed the advent of ranching (Casey, 1969).

In 1875 Presidio County, Texas, was officially organized by the state legislature. Surveyors, sent into the area by railroad companies and private individuals, provided the first modern vegetational descriptions of the Big Bend area. They reported thousands of acres of virgin grasslands. The grass was excellent and the land well watered by streams and running springs. With this knowledge, ranchers were attracted to this last area of open range.

Captain James B. Gillett was the manager of one of the first ranches established in Big Bend National Park. He stated the following:

> It may be interesting to know at the time this ranch was established in 1885, the Terlingua was a bold running stream, studded with cottonwood timber and alive with beaver. At the mouth of Rough Run there was a grove of trees, under the shade of which I have seen at least one thousand head of cattle. Today (1933) there is probably not one tree standing on the Terlingua that was there in 1885 (Casey, 1969).

By 1900 the virgin grasslands were near the upper limits of their carrying capacity. Overstocking resulted in rapid exhaustion of every square mile of the lower rangeland. The most palatable grasses were destroyed by grazing and trampling. Mesquite, weeds, cactus, and brush that had been kept in check by periodic fires in the past invaded and crowded out the grasses.

Both overgrazing and drought were responsible for dynamic changes between 1900 and 1920 in the park area. For example, prior to this time flats were covered by tobosa grass in the Tornillo Creek area. The growth was so bountiful that the early settlers cut it for hay (Maxwell, 1968). By 1915 overgrazing and drought had reduced the grass to only a few scattered clumps. Today this area is a badland with severe erosion and very little grass.

As the grass in the lowlands disappeared, the ranchers began to search for a new source. A new era of ranching in the Chisos began about 1920 and extended to 1944, with virgin meadows at higher elevations being tapped for the first time. The favorable combinations of high elevations, mild climate, limited rainfall at the proper time, and a large variety of grasses made this a favorite ranching area.

CHAPTER III

RESULTS

Vegetational Development

Livestock removal from Big Bend National Park initiated recovery of the native flora. This recovery has progressed further at higher elevations, but at lower elevations is in initial stages. Mountain grasslands have regained much of their former distribution and abundance, extending down the canyons and ravines and expanding gradually onto the slopes. The major area of succession today is centered in the foothills of the Chisos Mountains.

Highways are an important factor influencing lower elevational recovery. Along the construction routes, existing desert vegetation has been destroyed, thereby enabling grassland invasion. Precipitation collects on the highway surfaces and drains to its margins. As a result, there is an increase in the available moisture. In conjunction with habitat alteration and increased moisture, narrow corridors of grassland into the desert have been produced. This is exemplified in Tornillo Flat where strips of grass parallel the highway margin. Along each drainage system, especially Tornillo Creek, the grassland has increased in areal coverage and is slowly invading the Desert Shrub community. The continuation of the invasion into the surrounding desert will depend upon annual precipitation.

Vegetational analysis of the grassland community conducted by Warnock (1969) emphasized the dynamics of this community. Two trends are evident in the vegetational analysis, and are summarized in Table I.

TABLE I

VEGETATIONAL PLOT COMPOSITIONS IN THE GRASSLAND COMMUNITY*

Plot	Altitude	Dominant Grasses	Per Cent Ground Cover
Lost Mine Peak	5500	*Muhlenbergia emersleyi* *Muhlenbergia setifolia*	50.0
Pulliam Canyon	5300	*Aristida glauca* *Muhlenbergia emersleyi*	36.5
Gulf Station	3700	*Bouteloua eriopoda* *Bouteloua trifida*	30.9
Lone Mountain	3500	*Bouteloua breviseta* *Bouteloua trifida*	36.7
Lone Mountain Pass	3380	*Bouteloua breviseta* *Aristida pansa* *Tridens pulchellus*	29.4
Hannold Grave	3200	*Bouteloua breviseta*	26.7
Old Boquillas Road	3200	*Bouteloua breviseta*	23.2
Dugout Wells	2990	*Bouteloua breviseta*	16.0

*Compiled from Warnock, 1969.

One trend demonstrates the altitudinal variation in ground cover. These figures were calculated by averaging the plant composition of five different transects. The highest value (50.0) at the Lost Mine Peak plot, and lowest value (16.0) at the Dugout Wells plot, were obtained on control plots located in the Woodland and Desert Shrub formations, respectively. The highest grassland community value was 36.7 at the Lone Mountain plot at an elevation of 3,500 feet. Ground cover was composed primarily of grass. The Lone Mountain plot was located near the altitudinal center of the Grassland formation. The Pulliam Canyon plot at an elevation of 5,300 ft. was located in the Woodland-Grassland ecotone, and the total ground cover percentage, 36.5, included some trees. Warnock recorded the lowest per cent coverage value, 23.2 at the Old Boquillas Road plot in the Grassland-Desert Shrub ecotone.

There was a decrease in the number of grass species corresponding to a decrease in elevation. The dominant grasses near the grassland upper limit had long stems (1.5 to 2.5 ft.) and were dispersed. In contrast, grass species of the Grassland-Desert ecotone were short-stemmed, bunch grasses.

Higher grassland altitudes were dominated by Muhlenbergia emersleyi, with Bouteloua breviseta dominating the xeric environment of the lower ecotone. Grama grass (Bouteloua) was the dominant species of the grassland, but overstory cover, and annual precipitation. Bouteloua breviseta dominated the xeric environments, and Stipa tenuissima and Bouteloua gracilis were abundant in the mesic woodland.

In 1948 the Soil Conservation Service established random plots in the Woodland, Grassland, and Desert Shrub communities to study therophytes (Warnock, 1969). The per cent ground cover for grasses, cacti, and forbs was recorded for four 10 ft. transects on each study area. The data are summarized in Table II.

TABLE II

VEGETATIONAL DEVELOPMENT OF GRASSES, CACTI, AND FORBS ON SERVICE PLOTS*

Plot	Altitude	Per Cent Ground Cover		
		1948	1956	1969
Panther Pass	5800	0.34	3.81	2.60
Green Gulch	4200	0.13	0.52	1.23
Green Gulch	4200	4.30	3.62	6.67
Green Gulch	4200	0.38	0.63	1.51
Burnham Ranch	3800	1.39	3.16	5.05
Tornillo Flat	2800	. .	0.05	0.10
Tornillo Flat	2800	. .	0.20	. .

*Compiled from Warnock, 1969.

The data from 1948 to 1969 indicate a significant increase of ground cover in all study areas with the exception of Tornillo Flat. The Big Bend area was subjected to severe drought during the early 1950's, which may explain the greater increase in ground cover for the 1956 to 1969 period than the 1948 to 1956 period. The Burnham Ranch plot exhibited the greatest increase of ground cover, 72 per cent in the 21 year period. A value of 0.20 was recorded for the Tornillo Flat plot in 1956, but no grass, cacti, or forbs were present in 1969. A comparison of Warnock's findings with the Soil Conservation Service plots indicates maximum cover by grassland between 3,500 and 4,500 feet.

In 1955, Texas A&M University (Warnock, 1969) established random plots throughout the park. For the first time the Woodland community was sampled. The plots were surveyed in 1955 and 1967, and the data is presented in Table III.

This vegetational survey yielded the first comprehensive analysis of the ecological dynamics of the Big Bend flora. The data revealed that the Woodland and Desert Shrub formations were near stabilization with regard to dominant vegetation and had approximately the same average ground cover increase from 1955 to 1967. Seventy-three per cent of the woodland plots indicated substantial change in community vegetation. In the Woodland formation Warnock noted slight changes in tree composition and a significant areal increase in ground cover by grasses. Negligible changes appeared in

TABLE III

SUMMARY OF FLORAL CHANGES FROM 1955 to 1967 ON THE TEXAS A&M VEGETATIONAL PLOTS*

Plant Formation	Number of Plots	Average Total Ground Cover in 1955**	Range of Total Ground Cover in 1967**	Average Total Ground Cover in 1967**	Range of Total Ground Cover in 1967**	Increase in Average Ground Cover from 1955 to 1967**	Number of Plots with Grass Increase
Woodland	11	289.5	22.5-480.0	565.8	81.5-1848.5	276.3	8
Grassland	14	188.8	25.5-338.5	642.1	332.0-1168.6	453.3	14
Desert Shrub	10	227.6	13.0-629.5	500.0	34.0-1140.0	272.4	6

*Compiled from Warnock, 1969.

**Measured in hundredths of a square foot.

the vegetational analysis of the desert flats. Plots located in the desert-mountain foothills exhibited an increase in ground cover. The increased cover was attributed to a proliferation of the grass species.

The grassland slopes of the Chisos Mountains had the greatest increase in average ground cover. All plots indicated a substantial increase in grasses as a ground cover component. The average ground cover increase from 1955 to 1967 for the Grassland formation (453.3) was almost two times the increase for the Woodland formation (276.3) and the Desert Shrub formation (272.4). A Grassland formation plot located at an elevation of 3,800 ft. exhibited the greatest ground cover increase from 1955 to 1967 (25.5-1168.6). Not only did the grasses increase in areal coverage, but they became the dominant plants at elevations between 3,500 and 4,500 feet.

Vegetational Influence on Rodent Distribution

The distribution relationship of the rodents to plant formations is based on approximately 16,000 trap nights. The species are assigned to the formation in which the majority of the specimens were collected. If a species occurred in small numbers in one or two isolated associations in a formation, it was not designated as a formation species. Only one specimen of _Peromyscus eremicus_ was collected in the Woodland formation; therefore, it was not assigned to that formation. _Peromyscus pectoralis_ was collected in two areas within the grassland. Five specimens were taken, but the species was not assigned to the Grassland formation. The rodent distribution in relation to the plant formations of Big Bend National Park is given in Table IV.

TABLE IV

RODENT DISTRIBUTION IN RELATION TO PLANT FORMATIONS OF BIG BEND NATIONAL PARK

Species	Desert Shrub	Grassland	Woodland
Spermophilus mexicanus		X	
Spermophilus spilosoma	X	X	
Spermophilus variegatus		X	X
Ammospermophilus interpres	X	X	X
Thomomys bottae		X	X
Pappogeomys castanops	X		
Perognathus merriami	X	X	
Perognathus penicillatus	X		
Perognathus nelsoni		X	X
Dipodomys merriami	X	X	
Dipodomys ordii	X		
Onychomys torridus	X		
Reithrodontomys fulvescens		X	
Reithrodontomys megalotis		X	X
Peromyscus eremicus	X	X	
Peromyscus maniculatus	X	X	
Peromyscus leucopus	X	X	
Peromyscus pectoralis			X
Peromyscus boylii		X	X
Peromyscus difficilis			X
Sigmodon hispidus	X	X	
Sigmodon ochrognathus		X	X
Neotoma micropus	X		
Neotoma albigula		X	X
Neotoma mexicana			X

A quantitative statement of the resemblance between the was proposed by Preston (1962). This statistical method, called the "Resemblance Equation", is used to test for a break between faunistic homogenity and heterogenity. The resemblance of the faunas of two areas is attained by the formula $x^n + y^n = 1$. In the formula "x" is the fraction of the joint rodent fauna found in one plant formation, and "y" is the fraction found in the second formation. Both "x" and "y" are positive and lie between zero and one. The value of "n" represents the resemblance degree between the two faunas.

Preston's formula can be rewritten as $x^{\frac{1}{z}} + y^{\frac{1}{z}} = 1$. This is a functional formula. In the theoretical formula, Preston substituted "n" for 1/z to simplify the "Resemblance Equation". The resemblance of two faunas is measured by "z". The value of "z" was used to correlate the rodent distribution in the plant formations. In all comparisons between rodent faunas in plant formations, the value of "z" was between zero and one. A value near zero indicates the faunas are identical, and a value of one implies no common species. Preston (1962) used a "z" value of 0.27 to designate equilibrium between the two faunas. An index less than 0.27 indicated the two areas were samples of some larger unit (perhaps their joint area). A "z" value above 0.27 but below one was indicative of some degree of interaction, but it was incomplete.

The contrasts between rodent species occurring in the individual plant formations are noteworthy. Eight species occur in both the Grassland and Desert Shrub formations. Likewise, eight species occur in both the Grassland and Woodland formations. More rodent species (17) occur in the Grassland formation than in the other two formations. Table V illustrates the affect of plant formations upon rodent distribution.

TABLE V

RODENT DISTRIBUTION IN RELATION TO PLANT FORMATIONS

Plant Formation*	Number of Rodent Species	Number of Rodent Species Common to the Two Formations (C)	Number of Rodent Species Uncommon to the Two Formations
F_1	13	$\frac{C}{1+2} = 8$	Hence $\frac{F}{1+2} = 22$
F_2	17	$\frac{C}{2+3} = 8$	$\frac{F}{2+3} = 20$
F_3	11	$\frac{C}{1+3} = 1$	$\frac{F}{1+3} = 23$

*F_1-Desert Shrub, F_2-Grassland, F_3-Woodland

The mathematical solution of the "Resemblance Equation" is solved easily by matrix analysis. In Table VI the data of Table V is presented in matrix form.

TABLE VI

THE DATA OF TABLE V REPRODUCED IN MATRIX FORM

No.	Plant Formation	F	1	2	3
1	Desert Shrub	13		22	23
2	Grassland	17			20
3	Woodland	11			

The numbers 1, 2, and 3 refer to plant formations. Dissimilar rodent species occurring in different plant formations are represented by the numbers 22, 23, and 20. The matrix is read by a horizontal-vertical junction method. For example, there is a total of 24 species in the Desert Shrub and Woodland formations (Column F). Twenty-three of these are not shared (Column 3). Therefore, only one species is common to these two formations.

Each combination of the faunas produces two values with the larger being treated as "x" and the smaller as "y". The "x" and "y" values are obtained by $\frac{F_1}{F_{1+2}}$ and $\frac{F_2}{F_{1+2}}$. The "x" and "y" value for each plant formation rodent species comparison is given in Table VII. Once again, 1, 2, and 3 refer to the Desert Shrub, Grassland, and Woodland formations, respectively.

TABLE VII

SECOND MATRIX, CONTINUING THE ANALYSIS OF RODENT DISTRIBUTION IN BIG BEND NATIONAL PARK

No.	1	2	3
		Values of y	
1		0.59	0.48
2	0.77		0.55
3	0.56	0.85	
	Values of x		

The final analysis of vegetational influence upon the distribution of rodents in Big Bend National Park is presented in Table VIII. In this matrix the dissimilarity (z) of the various pairs, computed from the "x" and "y" values of the previous matrix, are listed above the sloping line. The values of "z" are obtained by applying the "x" and "y" values to Table XVII in Preston's publication (1962).

TABLE VIII

THIRD MATRIX, ANALYZING THE BIG BEND NATIONAL PARK DISTRIBUTION OF RODENTS

No.	Plant Formation	1	2	3
			Values of z	
1	Desert Shrub		0.55	0.94
2	Grassland	0.45		0.51
3	Woodland	0.06	0.49	
		Values of(1-z)		

Comparison of the Grassland to the Desert Shrub and Woodland communities yields similar values, 0.55 and 0.51, respectively. The Grassland, in an intermediate position geographically, is influenced by species from each of the contiguous formations but does not approach equilibrium with either and can be considered partly isolated from both. The Grassland is bounded at lower elevations by the Desert Shrub formation and at higher elevations by the Woodland formation. The contrast in floral and faunal composition of the three plant formations precludes equilibrium of rodent species. Some species are adapted to one formation, but not the others (Table VI).

The Desert Shrub formation and Woodland formation have only one species in common (_Ammospermophilus interpres_). The contrast between the two formations is evident in a dissimilarity value of 0.94. The dissimilarity approaches one and indicates not only species' adaptation to a plant formation, but also geographic isolation of the plant formations. Heteromyid rodents are more characteristic of the Desert Shrub formation (four species) than of the Woodland (one species). Cricetid rodents are more typical of the Woodland (seven species compared to six).

The major difference in cricetid faunas between these two formations is abundance of individuals rather than number of species. Three of the six desert species are considered rare. Only one specimen of _Onychomys torridus_ has been collected in the park. Twenty-two specimens of Peromyscus leucopus and 16 specimens of Peromyscus maniculatus have been taken. Sigmodon hispidus and Neotoma micropus were slightly more numerous with Peromyscus eremicus the most abundant (73 specimens). A total of 110 specimens of the six cricetid species was collected in the Desert Shrub formation. In contrast, 464 specimens of seven cricetid species were taken in the Woodland formation (8 Reithrodontomys megalotis, 173 Peromyscus pectoralis, 94 Peromyscus boylii, 11 Peromyscus difficilis, 64 Sigmodon ochrognathus, 106 Neotoma albigula, and 8 Neotoma mexicana).

Rodent Distribution in Relation to Edaphic Factors

Soil characteristics such as composition, size of rocks, and slope at each collection site were recorded. Soil composition and size of the associated rocks were the most important factors influencing the rodents' distributions. Sand, sand and gravel, clay and sand, rubble with a clay-loam mixture, large mixed rocks with loam, and rockpiles, were categories used in the analysis. Slope was not a major factor at lower elevations, but was important at higher elevations.

Desert areas have four major soil types. These are sand, sand with gravel, sand with clay, and rubble with clay and loam. Desert Shrub and Grassland plant formations occur on these soils. The Woodland formation has developed on shallow loam soil with a mixture of different sized rocks. There is a definite interaction between soil type and vegetational distribution. Table IX illustrates its influence on rodent distribution.

TABLE IX

SOIL INFLUENCE ON RODENT DISTRIBUTION AND NUMBER

Species	Sand	Sand and Gravel	Sand and Clay	Rubble and Clay-Loam	Mixed Rock and Loam	Rockpile
Spermophilus mexicanus	6	. .	. .	. .	. .	. .
Spermophilus spilosoma	4	3	. .	14	. .	5
Spermophilus variegatus	. .	. .	. .	. .	14	8
Ammospermophilus interpres	. .	. .	. .	2	15	. .
Thomomys bottae	. .	. .	. .	6	10	. .
Pappogeomys castanops	15	3	. .	. .	. .	. .
Perognathus merriami	8	4	. .	35	. .	. .
Perognathus nelsoni	. .	10	. .	46	50	. .
Perognathus penicillatus	156	19	. .	. .	. .	. .
Dipodomys merriami	58	. .	. .	54	. .	. .
Dipodomys ordii	16	. .	. .	. .	. .	. .
Reithrodontomys fulvescens	. .	. .	. .	. .	4	. .
Reithrodontomys megalotis	. .	. .	29	2	5	. .
Peromyscus boylii	. .	. .	. .	. .	86	11
Peromyscus difficilis	. .	. .	. .	. .	2	9
Peromyscus eremicus	40	. .	. .	76	1	. .
Peromyscus maniculatus	13	2	. .	1	. .	. .
Peromyscus leucopus	8	4	8	1	. .	. .
Peromyscus pectoralis	. .	. .	1	5	142	3
Onychomys torridus	. .	. .	. .	1	. .	. .
Sigmodon hispidus	10	. .	29	. .	. .	. .
Sigmodon ochrognathus	. .	. .	. .	. .	71	. .
Neotoma albigula	. .	. .	. .	14	104	. .
Neotoma mexicana	. .	. .	. .	. .	. .	8
Neotoma micropus	27	. .	. .	6	. .	. .
Total	361	61	66	261	504	44

The members of the family Sciuridae occupy diverse soil types. *Spermophilus mexicanus* was collected only in the sandy soil along the Rio Grande River at Rio Grande Village. Traps located near this area in rocky soils did not yield specimens. *Spermophilus spilosoma* reaches its greatest abundance on the harder clay and calcareous soils with scattered rocks and increased slope.

Soil texture influences the distribution of gophers. *Pappogeomys castanops* is limited to the sandy soil along the Rio Grande River floodplain and its major tributaries, such as Terlingua and Tornillo Creeks. *Thomomys bottae* occupies the more compact, rocky soils of the mountain slopes. The two species are not in contact anywhere, but their ranges approach each other near the Rio Grande.

Perognathus merriami and *Perognathus penicillatus* occur in sandy habitats, but only *P. penicillatus* attains maximum abundance on the sandy, flat washes in the desert. The alluvial clay and rubble soil of the Chisos Mountains' foothills is preferred by *P. merriami*. *Perognathus nelsoni* is more saxicolous occurring on shallow soils with 80-90 per cent rocks and increased slope.

Kangaroo rats are predominant on desert soils. *Dipodomys ordii* is restricted to friable sand. *Dipodomys merriami* is equally abundant on desert sand and more compact soils with surface rubble.

Six species of the genus *Peromyscus* occur in Big Bend National Park. *Peromyscus maniculatus* and *P. leucopus* are most abundant on the soils with a sand composition. Sandy areas and compact soils with rubble are occupied by *P. eremicus*. *Peromyscus boylii*, *P. pectoralis*, and *P. difficilis* prefer habitats with shallow soil and large rocks. *Peromyscus difficilis* is most abundant in rockpiles.

Sigmodon hispidus and *Neotoma micropus* are common on the friable desert soil. Mountain slopes and meadows with a loam soil mixed with rocks are the habitats of *Neotoma albigula* and *Sigmodon ochrognathus*. *Neotoma mexicana* inhabits rockpiles on steep slopes.

Altitudinal Distribution

In this study rodents were collected between 1,850 and 7,100 feet. Only one species (*Spermophilus variegatus*) was recorded from each of the elevational intervals. Species diversity is greatest between 1,850 and 5,500 feet. Fifty-nine per cent of the rodents were collected in the elevational range of the grassland (2,800-4,500 ft.). The Desert Shrub elevations exhibit a greater diversity (31 per cent) of rodents than the Woodland elevations (10 per cent). Heteromyid rodents are abundant in the desert elevations, while cricetid rodents are more numerous at the Grassland and Woodland elevations.

Within each genus the different species attain their greatest abundance at different elevations. Elevational allopatry is evident in the genera *Sigmodon* and *Neotoma*. Elevational sympatry, but not necessarily habitat sympatry, is indicated for the other genera. Table X summarizes the altitudinal distribution of the rodents in Big Bend Park.

TABLE X

ALTITUDINAL DISTRIBUTION AND NUMBER OF RODENTS COLLECTED IN BIG BEND NATIONAL PARK

Species	1850 to 2850	2851 to 3850	3851 to 4850	4851 to 5850	5851 to 6850	6851 to 7832
Spermophilus mexicanus	6	. .	. .	. .	. .	. .
Spermophilus spilosoma	8	12	1	. .	. .	. .
Spermophilus variegatus	2	1	4	8	2	2
Ammospermophilus interpres	2	4	7	10	1	. .
Thomomys bottae	3	8	. .	4	1	. .
Pappogeomys castanops	18	. .	. .	. .	. .	. .
Perognathus merriami	8	33	5	1	. .	. .
Perognathus nelsoni	15	29	28	34	. .	. .
Perognathus penicillatus	141	23	11	. .	. .	. .
Dipodomys merriami	72	40	. .	. .	. .	. .
Dipodomys ordii	16	. .	. .	. .	. .	. .
Reithrodontomys fulvescens	. .	. .	3	1	. .	. .
Reithrodontomys megalotis	3	25	. .	3	5	. .
Peromyscus boylii	. .	. .	13	48	22	14
Peromyscus difficilis	. .	. .	. .	2	5	4
Peromyscus eremicus	20	63	7	6	. .	. .
Peromyscus leucopus	21	1	. .	. .	. .	. .
Peromyscus maniculatus	11	5	. .	. .	. .	. .
Peromyscus pectoralis	. .	. .	15	142	18	3
Onychomys torridus	. .	1	. .	. .	. .	. .
Sigmodon hispidus	38	1	. .	. .	. .	. .
Sigmodon ochrognathus	. .	. .	7	36	28	. .
Neotoma albigula	. .	12	5	96	5	. .
Neotoma micropus	31	2	. .	. .	. .	. .
Neotoma mexicana	. .	. .	. .	. .	2	6
Total	393	250	106	381	89	29

Regional Influence on Rodent Distribution

The geologic evidence indicates a stabilized climate in the park area for the past 20,000 years. This time period has permitted integration of rodent faunas of Trans-Pecos Texas and northern Mexico. There are no endemic rodents and most species range over wide geographic areas. The rodent species of the major mountain groups, Chisos (Borell and Bryant, 1942), Davis (Blair, 1940), Guadalupe (Davis, 1940), and Sierra del Carmen (Baker, 1956), of the region are compared using the "Resemblance Equation" (Preston, 1962). The species distribution in each of the mountain areas is given in Table XI.

TABLE XI

OCCURRENCE OF RODENT SPECIES IN MOUNTAINS OF TRANS-PECOS TEXAS AND NORTHERN MEXICO

Species	Chisos	Davis	Guadalupe	Sierra del Carmen
Eutamias dorsalis				X
Eutamias canipes			X	
Ammospermophilus interpres	X		X	X
Spermophilus mexicanus	X	X		
Spermophilus spilosoma	X	X	X	X
Spermophilus variegatus	X	X	X	X
Cynomys ludovicianus		X	X	
Sciurus niger				X
Thomomys bottae	X	X	X	X
Pappogeomys castanops	X	X	X	X
Perognathus merriami	X	X	X	X
Perognathus flavus		X		X
Perognathus hispidus		X	X	

TABLE XI--*Continued*

Species	Chisos	Davis	Guada-lupe	Sierra del Carmen
Perognathus penicillatus	X	X		X
Perognathus intermedius		X	X	
Perognathus nelsoni	X	X		X
Dipodomys ordii	X	X	X	
Dipodomys merriami	X	X	X	X
Dipodomys spectabilis		X	X	
Dipodomys nelsoni				X
Reithrodontomys montanus		X		
Reithrodontomys megalotis	X	X	X	X
Reithrodontomys fulvescens	X	X		X
Peromyscus eremicus	X	X		X
Peromyscus maniculatus	X	X		X
Peromyscus leucopus	X	X	X	
Peromyscus boylii	X	X	X	X
Peromyscus pectoralis	X	X	X	X
Peromyscus difficilis	X			X
Onychomys torridus	X	X	X	
Sigmodon hispidus	X	X		X
Sigmodon ochrognathus	X	X		X
Neotoma micropus	X	X	X	
Neotoma albigula	X	X	X	X
Neotoma mexicana	X	X	X	X
Microtus mexicanus			X	
Erethizon dorsatum	X	X	X	X
Total Number of Species	26	30	23	25

The data on rodent species occurring in the mountains of Trans-Pecos Texas and northern Mexico are given in Table XII.

The Davis Mountains are located near the geographic center of the region and have the greatest species diversity. In each comparison, the number of common species is similar--likewise, the number of uncommon species.

TABLE XII

DATA ON RODENT DISTRIBUTION IN TRANS-PECOS TEXAS AND NORTHERN MEXICO

Mountain Groups*	Number of Species	Number of Rodent Species Common to the Two Mountain Groups	Number of Rodent Species Uncommon to the Two Mountain Groups
F_1	26	$C_{1+2} = 24$	Hence $F_{1+2} = 32$
F_2	30	$C_{1+3} = 17$	$F_{1+3} = 32$
F_3	23	$C_{1+4} = 21$	$F_{1+4} = 30$
F_4	25	$C_{2+3} = 20$	$F_{2+3} = 33$
		$C_{2+4} = 20$	$F_{2+4} = 35$
		$C_{3+4} = 12$	$F_{3+4} = 36$

*F_1- Chisos Mts.; F_2- Davis Mts.; F_3- Guadalupe Mts.; F_4- Sierra del Carmen Mts.

The mathematical solution of the "Resemblance Equation" is solved by matrix analysis. The data of Table XII is presented in matrix form in Table XIII.

TABLE XIII

THE DATA OF TABLE XII REPRODUCED IN MATRIX FORM

No.	Mountain Group	F	1	2	3	4
1	Chisos	26		32	32	30
2	Davis	30			33	35
3	Guadalupe	23				
4	Sierra del Carmen	25				36

Each combination of mountain faunas produces two values with the larger being treated as "x" and the smaller "y". The numbers 1, 2, 3, and 4 coincide with the Chisos, Davis, Guadalupe, and Sierra del Carmen Mountains, respectively, in Table XIV.

TABLE XIV

SECOND MATRIX, CONTINUING THE ANALYSIS OF RODENT DISTRIBUTION IN TRANS-PECOS TEXAS AND NORTHERN MEXICO REGION

No.	1	2	3	4
			Values of y	
1		0.81	0.74	0.86
2	0.97		0.70	0.71
3	0.81	0.91		0.63
4	0.86	0.86	0.69	

Each mountain group is a separate entity and is isolated by an intervening area of the Chihuahuan Desert. The theory (Wells, 1966) that the Trans-Pecos region of Texas was once a continuous woodland helps explain the current rodent distribution. The resemblance of the rodent distribution in the mountain groups is given in Table XV.

TABLE XV

THIRD MATRIX, ANALYZING THE TRANS-PECOS
TEXAS AND NORTHERN MEXICO REGION

No.	Mountain Group	1	2	3	4
			Values of z		
1	Chisos		0.14	0.36	0.22
2	Davis	0.86		0.28	0.32
3	Guadalupe	0.64	0.72		0.61
4	Sierra del Carmen	0.78	0.68	0.40	
			Values of (1-z)		

Most of the mountain groups have values of "z" near 0.27 indicating approximately perfect equilibrium at the species level. The pair 1-2 with an index of 0.14 is almost identical in species composition. The two areas are samples of a larger faunal unit and perhaps their joint area should be a faunal unit.

The Sierra del Carmens are geographically nearer the Chisos Mountains than the Davis Mountains, but a higher "z" value (0.22) is calculated for the Chisos-Sierra del Carmen comparison. The rodent fauna of the Chisos Mountains is more similar to the Davis Mountain fauna ($z = 0.14$). The Rio Grande may act as a filter barrier which may explain, in part, this discrepancy in "z" values.

The mountain group most dissimilar to the Chisos is the Guadalupe Mountains. The "z" value of 0.36 indicates that, although the Guadalupe Mountains are geographically the most remote range, species diversity is not significant. Apparently the two faunas are near equilibrium, having 17 species in common.

Hershkovitz (1958) suggested an arrangement for classifying mammalian genera so that their affinities were associated with definite zoogeographical regions. His groupings were as follows: genera whose geographic range include a tropical zoogeographical region of either the Western or the Eastern Hemisphere and a Holarctic subregion of the other Hemisphere are called cosmopolites; genera which are confined to one zoogeographic region (endemic) or which may spread to another region (excurrent) as regionalitès; and genera of uncertain geographic derivation but which live in two contiguous regions as varicants.

The rodent genera which occur in Big Bend Park were arranged so that their affinities were associated with definite zoogeographical regions. Using Hershkovitz's classification, the 16 native rodent genera of the Trans-Pecos and northern Mexico region are as follows: eight (50 per cent) are Nearctic regionalites; one (6 per cent) is cosmopolites; one (6 per cent) is Neotropical regionalites; three (19 per cent) are Nearctic-Palearctic varicants; and three (19 per cent) are Nearctic-Neotropical varicants. The theory that the Chihuahuan biotic province is of Mexican affinity does not apply to the rodent fauna of the Trans-Pecos Texas and northern Mexico region.

The most important result of matrix analysis of the rodents of Trans-Pecos Texas and northern Mexico is clarification of the rodent faunal affinity of Big Bend National Park. The species composition of the park fauna is not derived from a single geographical fauna, but is the result of interaction and invasion from different geographical areas. The near equilibrium of the four mountain groups supports this assumption. Faunal affinities with the Great Plains, Southwestern United States, Gulf Coastal Plain, Western United States, and Northern Mexico can be distinguished.

Reproductive Activity

Reproductive activity was exhibited in one hundred and sixty-five of the females examined. The presence of embryos, definite placental scars, enlarged uteri, and lactation were evidences of breeding. Winter, fall, and early spring are the periods of high reproductive activity, while late spring and early summer are low periods (Fig. 6).

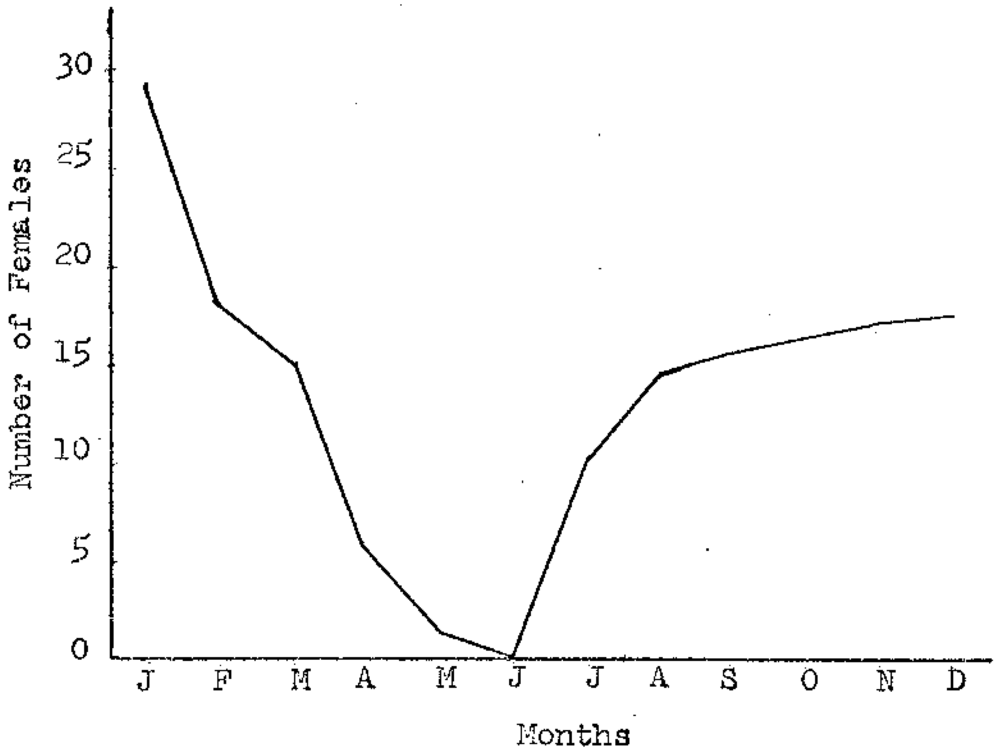

Fig. 6--Number of females demonstrating reproductive activity for each month of the year.

The low number of reproductively active females can be correlated with a period of environmental stress. The latter part of April, May, and June are the months in which food availability is lowest. The food supply increases in late fall due to increased moisture from late summer and early fall precipitation. Habitat and vegetational deterioration reaches a maximum in the spring, but during the study period, May and June precipitation did not occur. The first substantial rainfall was not recorded until July. The combination of an inferior habitat, rising temperatures, and lack of precipitation depressed the reproductive activity. The reproductive activity of the different species is similar in that species at lower elevations breed at approximately the same time as the higher elevation species.

The nine months of reproductive activity are July to March. The climate moderates in the latter portion of summer, with an increase in precipitation and a decrease in the average maximum temperature. There is a corresponding renewal of vegetation with habitat improvement. Winter temperatures are mild and of short duration. The highest number of reproductively active females recorded was in January. This indicates that the winters in Big Bend Park, on the average, are not sufficiently severe to restrict reproduction. Reproductive data of males correlates with that for females.

Two peaks, December to January and March to May, are evident in the number of juveniles collected. These peaks correspond to the late fall and early winter breeding periods of the females.

Ninety-six females of the families Heteromyidae and Cricetidae were pregnant. The litter size ranged from a maximum of seven (Peromyscus leucopus) to a minimum of one (Dipodomys merriami, Dipodomys ordii, and Neotoma albigula). The average litter size of high elevation species was slightly larger (3.50 to 3.36) than that of desert species (Table XVI).

TABLE XVI

LITTER SIZE OF RODENTS

Species	Mean Number of Embryos	Range	Number of Females Examined
Perognathus merriami	3.66	3-5	3
Perognathus nelsoni	4.00	4	2
Perognathus penicillatus	3.50	2-5	6
Dipodomys merriami	2.50	1-5	18
Dipodomys ordii	2.75	1-5	4
Reithrodontomys megalotis	3.80	2-4	5
Peromyscus boylii	5.00	. .	1
Peromyscus eremicus	3.10	2-5	10
Peromyscus leucopus	7.00	. .	1
Peromyscus maniculatus	2.00	. .	1
Peromyscus pectoralis	3.33	3-4	3
Sigmodon hispidus	3.33	3-4	3
Sigmodon ochrognathus	3.57	3-5	7
Neotoma albigula	1.81	1-3	21
Neotoma mexicana	2.00	. .	1
Neotoma micropus	3.00	2-4	4

Species Interaction

Species collected in the same trap line were assumed to have some degree of interaction. The most common interactions are probably caused by food, habitat, and edaphic preferences of the rodent populations. Species with a diverse ecological distribution interact with a larger number of different species. Ten different species are associated with Neotoma micropus in the desert and lower grassland habitats, but Neotoma mexicana interacts with only three species in the upper Woodland formation (Table XVII).

TABLE XVII

SUMMARY OF SPECIES INTERACTION

Species	Spermophilus spilosoma	Spermophilus variegatus	Ammospermophilus interpres	Thomomys bottae	Pappogeomys castanops	Perognathus merriami	Perognathus nelsoni	Perognathus penicillatus	Dipodomys merriami	Dipodomys ordii	Reithrodontomys megalotis	Peromyscus boylii	Peromyscus difficilis	Peromyscus eremicus	Peromyscus leucopus	Peromyscus maniculatus	Peromyscus pectoralis	Sigmodon hispidus	Sigmodon ochrognathus	Neotoma albigula	Neotoma mexicana	Neotoma micropus
Spermophilus spilosoma					x			x	x						x							x
Spermophilus variegatus			x																			
Ammospermophilus interpres		x					x							x			x			x		
Thomomys bottae							x															
Pappogeomys castanops	x							x	x						x							x
Perognathus merriami							x	x	x					x						x		x
Perognathus nelsoni			x	x		x						x		x			x		x	x		
Perognathus penicillatus	x				x	x			x	x				x	x							x
Dipodomys merriami	x				x	x		x		x				x								x
Dipodomys ordii								x	x					x								
Reithrodontomys megalotis																x		x	x			x
Peromyscus boylii							x						x				x		x	x	x	
Peromyscus difficilis												x					x			x	x	
Peromyscus eremicus			x			x	x	x	x	x							x			x		x
Peromyscus leucopus	x				x			x								x						x
Peromyscus maniculatus											x				x			x				x
Peromyscus pectoralis			x				x					x	x	x					x	x	x	
Sigmodon hispidus											x					x						x
Sigmodon ochrognathus							x				x	x					x			x		
Neotoma albigula			x			x	x				x	x	x	x			x		x			
Neotoma mexicana												x	x				x					
Neotoma micropus	x				x	x		x	x		x			x	x	x		x				

Dipodomys merriami and *Dipodomys ordii* were collected in the same trap line at Tornillo Flat and at the mouth of Santa Elena Canyon. At Tornillo Flat individuals of the two species were taken in alternating traps. Edaphic preference was the factor causing their interaction.

Perognathus merriami was sympatric with *Perognathus penicillatus* and *Perognathus nelsoni*, but *P. nelsoni* and *P. penicillatus*, due to edaphic preference, were allopatric. *Perognathus merriami* and *P. penicillatus* occurred together at three localities in the Desert Shrub formation. *Perognathus nelsoni* and *P. merriami* were sympatric on the rocky slopes of the Grassland formation.

Pinyon Pine-Juniper slopes of the Woodland formation were areas of interaction for *Peromyscus pectoralis* and *Peromyscus boylii* (Table XVIII). The area of sympatry was

TABLE XVIII

NUMBER OF SYMPATRY STATIONS FOR
THE GENUS *PEROMYSCUS*

Species	*P. difficilis*	*P. boylii*	*P. pectoralis*	*P. leucopus*
P. maniculatus	. .	. .	. .	1
P. boylii	3	. .	. .	. .
P. eremicus	. .	. .	1	. .
P. pectoralis	3	5	. .	. .

between 5,500 and 7,000 feet. Peromyscus pectoralis and P. boylii were collected in association with P. difficilis at higher elevations. Peromyscus eremicus occurred with P. pectoralis on the grassland slopes of Pine Canyon at an elevation of 5,000 feet. The specimen of P. pectoralis was the only one collected in a grassland community. The distributions of P. leucopus and P. maniculatus are sympatric along the Rio Grande River, eight miles southwest of Rio Grande Village.

Sigmodon hispidus and Sigmodon ochrognathus are allopatric. Their park distribution is in grassland habitats, but elevational influence on the grass species ecologically separates the species. Sigmodon ochrognathus occurs in Stipa meadows, and Stipa grass in the park grows only at altitudes above 5,000 feet. Desert grasses, burro (Scleropogon brevifolius), tobosa (Hilaria mutica), and chino (Bouteloua breviseta), at elevations below 3,000 ft. are inhabited by S. hispidus. Populations of S. hispidus are located only in areas of dense ground cover. As the grassland secondary recovery continues, the distribution of S. hispidus will probably expand. It is possible that S. hispidus and S. ochrognathus may some day be sympatric in Green Gulch.

Neotoma micropus, Neotoma mexicana, and Neotoma albigula are allopatric. Five miles separate the distributions of N. micropus and N. albigula north of Panther Junction.

Neotoma micropus inhabits the upper Desert Shrub formation at an elevation of 3,700 feet. *Neotoma mexicana* is restricted to rockpiles and talus near the summit of Emory Peak (7,000 ft.), and *N. albigula* inhabits the surrounding forested slopes. The ranges of *N. albigula* and *N. mexicana* approach within one-quarter mile at the north base of Emory Peak.

Rodent Ectoparasites

Studies of chigger mites found on 19 species of rodents in Big Bend National Park have revealed new species of *Euschoengastia*, *Euschoengastoides*, *Otorhinophila*, and *Pseudoschoengastia*. The four new species will be described in subsequent publications. Twenty-one species representing 12 genera were collected. *Neotoma albigula* was parasitized by the greatest number of chigger species (13). Eleven species were recorded from *Perognathus nelsoni*, and 10 from *Perognathus merriami*. Only one species was recovered from *Spermophilus variegatus*, *Ammospermophilus interpres*, *Thomomys bottae*, *Pappogeomys castanops*, and *Peromyscus maniculatus* (Appendix I). Small samples of these rodent species explain the lack of chigger parasites--not parasite preference for the host.

Chiggers were obtained throughout the year, although larger sampling may prove seasonal incidence for certain hosts. For example, no winter incidence was recorded for *Dipodomys ordii* or *Sigmodon hispidus*. The overall incidence of trombiculid infestation was approximately 75 per cent. Multiple parasitism occurred more often than single larva infestation (90 per cent to 10 per cent). No appreciable tissue damage due to chigger infestation was observed, but extensive and prolonged parasitism will result in dermatosis.

The ear conchae exhibit the greatest amount of parasitism. The species of the genus Euschoengastoides, for instance, appear to occupy different areas of the conchae; the periphery, middle portion, and even the ear drum area are infested with "pockets" of chiggers. The genital and thigh regions are secondary in infestation. A preference is displayed for the openings of the reproductive and digestive systems. In heteromyid rodents, especially Perognathus merriami, the soft tissues of the cheek pockets are parasitized.

Chigger mites were identified by Dr. Richard B. Loomis.

CHAPTER IV

DISCUSSION

General Habitat Relationships

Rodent distribution in Big Bend National Park is the result of climatic and environmental interaction. Rodents are an integral part of most terrestrial ecosystems. Vegetational type, soil texture, and many other factors can influence the distribution and population size of rodents. Successional changes in plant communities alter rodent density and species composition. Paleoecological data indicate that the ranges of rodents in the Pleistocene correlated with climatic changes. The present ranges have resulted from post-Pleistocene climatic shifts, altered vegetation, and the adaptability of the rodents. Statistical analysis of the Trans-Pecos Texas and northern Mexico rodent faunas gives credence to the theory (Wells, 1966) that southwestern Texas had a similar continuous vegetation after the Wisconsin pluvial. The time interval is sufficiently long to allow the integration of rodent species with different faunal affinities.

A prolonged drought is theorized as the factor that initiated vegetational changes in the southwest some 10,000 years ago (Wells, 1966). The changes are demonstrated presently by desert and mountain plant formations with an intermediate grassland. Desert plant species, as invaders, occupy a lower successional stange, and certain rodent species (Dipodomys merriami, Dipodomys ordii, Neotoma micropus, Perognathus penicillatus, and Peromyscus eremicus) attain maximum abundance in this habitat. Other species, Sigmodon hispidus, Perognathus merriami, Reithrodontomys megalotis, Peromyscus maniculatus, and Neotoma albigula, attain greater numbers in higher stages of plant succession where dense cover is present. These species occur in the grassland and woodland communities.

In the absence of human influence and environmental alteration, a faunal survey is species indicative for a time period of stabilized climate and flora (Baker, 1956). The original rodent distribution in the park is unknown because no faunal surveys were conducted before habitat alteration by livestock. The effects of overgrazing remain evident today. The eroded, barren flats of the Tornillo Creek area once supported grasslands which were utilized for hay production (Maxwell, 1968). Habitat destruction is a factor in the current distribution of rodents in the park.

Changes in community structure due to overgrazing or habitat destruction have been discussed by several authors (Baker, 1940; Raun, 1966; Getz, 1970). This change in Big Bend Park surely altered rodent distribution and community composition. Since overgrazing occurred first in the lower

Chisos foothills and the desert, grasses were restricted to higher elevations. Additional environmental stress probably occurred as ecologically distinct species were forced to occupy the same areas. In the lower desert, rodents were probably isolated in small grassland remnants along drainage systems. The present association of Sigmodon hispidus and Peromyscus maniculatus along road beds and drainage patterns is an example. My theory is that desert forms were isolated from woodland species in the mountains by an inferior environmental hiatus--this hiatus being created by overgrazing and habitat destruction. Secondary grassland succession has improved the intervening environment and both rodent number and species diversity have increased.

Vegetative conditions in the Chisos were at an all-time low in 1944 (Casey, 1969). Secondary succession was delayed by droughts in the latter 1940's and early 1950's, with a subsequent drought in 1965; however, there is evidence for grassland recovery in the high mountains. Stipa grass in Laguna Meadow is widespread and forms a dense ground cover. Grasslands have advanced down the slopes of the Chisos Mountains and are encountering desert invaders on the lower slopes. There have been 27 years of secondary succession. Gardner (1950) observed that desert grassland protected from severe overgrazing for 30 years exhibited a grass density increase of 110 per cent. Even after 30 years protection the area was not completely healed, but there was no active erosion. Warnock's (1969) data indicate an increase on the grassland plots of average ground cover from 188.8 hundredths of a square foot in 1955, to an average cover of 453.3 hundredths of a square foot in 1967. Big Bend Park, in complete absence of domestic livestock grazing, exhibited a 241 per cent increase in average ground cover in the Grassland formation in 11 years. The average ground cover increase was less for the Woodland and Desert Shrub formations.

The environmental deterioration must have reduced rodent population sizes. The study of Borell and Bryant (1942) was based on 218 specimens collected by Borell plus previously collected specimens in museums. The 218 specimens were collected over a period of two years with 89 actual trapping nights. An average of 2.45 specimens per night was collected. No statement was available concerning the number of traps set each night, but from a personal viewpoint, 2.45 specimens indicate low rodent populations. Seventy-six of the 218 specimens were heteromyid rodents which are common and easily trapped. Even after a 1970 summer low of .009 per cent specimens for 100 trap nights, my overall trapping success was seven per cent. Baker (1940) obtained two specimens in 92 trap nights on severely overgrazed pasture land in Colorado County, Texas, and 14 mice in 99 trap nights on ungrazed pasture land. Borell and Bryant (1942) studied the mammal fauna when the park was overgrazed. My study was conducted after considerable recovery of the grassland environment. An increase in rodent density is evident.

The locality trapped has a great influence on the number of rodents collected. Rodent population densities are not evenly distributed, varying greatest in the desert environments. The creosote-lechuguilla-ocotillo plant community did not yield an abundance of specimens. The largest number of specimens collected in one night in the desert community was obtained in a cholla cactus-sand association. The isolated desert grass areas along the roads and water systems have high densities. Rodent populations in the Grassland and Woodland plant formations are more evenly distributed. Woodland densities are highest in grassy meadows, such as Laguna, Juniper Flat, Boulder, and Pine Canyon. Slopes surrounding the meadows have a decrease in grass cover and number of individuals. In Pine Canyon Meadow four species (*Sigmodon ochrognathus*, *Peromyscus pectoralis*, *Peromyscus boylii*, and *Neotoma albigula*) are common in the area, but only *P. boylii*, in small numbers, was collected on the adjacent rocky slopes.

When rodent capture is categorized according to plant communities, soil type, and per cent of average ground cover in the trap area, significant differences are apparent in rodent distribution (Appendix II). The species of rodents are assigned habitat affinities based on the habitat categories in which capture per species is greatest. These categories are assumed to represent the type of habitat most favored by the species.

Spotted ground squirrels, *Spermophilus spilosoma*, are inhabitants of dry, rocky or sandy areas. Though approximately 40 per cent of the soil surface is devoid of vegetation, plants present include creosote, cholla, and prickly pear. *Spermophilua mexicanus* occurs only in the sandy environments of Rio Grande Village in a Bermuda grass community. Ecologically these two species are distinct. *Spermophilus mexicanus* is confined to a short grass community with most sand, while *S. spilosoma* occupies drier, rocky soils with decreased ground cover. Tamsitt (1954) found *S. spilosoma* burrows in gravelly soil at Black Gap, but Baker (1956) noted this species' preference for deep soils with a minimum of rocks in Coahuila. *Spermophilus variegatus* is the most widespread rodent in the park. Individuals were observed in Mariscal Canyon at an elevation of approximately 2,200 ft. and on the rockpiles near the north base of Emory Peak (7,000 ft.). Rock squirrels were collected or observed only in rocky habitats in the Grassland and Woodland formations.

The distribution of the saxicolous Texas antelope squirrel ranges from the river bottom up to 6,100 feet. *Ammospermophilus interpres* is the most ecologically diverse rodent in the park, occurring in all three plant formations.

Two gophers are present. Chestnut-faced pocket gophers, Pappogeomys castanops, are restricted to pale, deep, fine-textured soils covered by various Desert Shrub plant species along and adjacent to the Rio Grande River and its tributaries. Botta pocket gophers, Thomomys bottae, are abundant on the dark, rocky soils of the mountain slopes within the upper grassland and oak-pine belts. The two gopher species are geographically allopatric on this area. Borell and Bryant (1942) stated that in a few places the ranges of the chestnut-faced and Botta pocket gophers overlapped, but specific locations were not given.

Merriam pocket mice, Perognathus merriami, the rarest member of the genus in the park, occur in greatest numbers in grama grass-lechuguilla associations on the Chisos' foothills. Porter (1962) reported abundance on alluvial soils between 3,500 and 4,000 feet. Borell and Bryant (1942) found P. merriami rare in the park and collected only four specimens from a sandy flat. On this evidence they stated that apparently extensive tracts of hard, rocky soil served as barriers to the dispersal of this species. Baker (1956) reported that P. merriami was restricted to sandy soils in Coahuila. In the present investigation, 80 per cent of the P. merriami were collected on rocky soil. Apparently P. merriami exhibits a preference for rocky soil habitats in the Chisos Mountains.

The habitat affinity of the rock pocket mouse, *Perognathus nelsoni*, is the upper grassland. Rock pocket mice were most abundant on the steep, rocky slopes between 4,000 and 5,500 feet. *Perognathus nelsoni* occurs in small numbers at 3,700 ft., with *P. merriami* in a grama grass-lechuguilla association. With elevational increase, rock pocket mice increase in numbers and Merriam pocket mice decrease. The grama grass-sotol association in Pine Canyon at 5,000 ft. supports a large population of *P. nelsoni*. The range of *P. nelsoni* includes the Pinyon Pine-Juniper woodland, but populations are small. The present survey indicates *P. nelsoni* to be intermediate in population size between *P. merriami* and *P. penicillatus*. Borell and Bryant (1942) listed the rock pocket mouse as rare. They noted an elevational range between 2,300 and 4,800 feet, and typical habitat was rocky areas occasionally overgrown with grass, sotol, and bear grass (*Nolina*). Baker (1956) stated that *P. nelsoni* was an inhabitant of characteristic Chihuahuan Desert Shrub Vegetation-type and not grassland. A habitat preference of rocky, rough terrain was noted in the Black Gap areas by Tamsitt (1954).

Borell and Bryant (1942) reported overlap in the ranges of the rock pocket mouse and the desert pocket mouse in Big Bend Park, but no locality was given. I found *P. nelsoni* and *P. penicillatus* to be both geographically and ecologically allopatric, but the two species probably occur together where fine, sandy soils mantle desert areas.

Perognathus penicillatus is confined to areas of sand with Desert Shrub vegetation. The desert pocket mouse has a widespread range in the lower desert environment of the park and is by far the most abundant rodent in the Desert Shrub formation. Baker (1956) found P. penicillatus abundant in Coahuila, but northeast of Big Bend at Black Gap, Tamsitt (1954) listed the desert pocket mouse as a sparsely distributed species.

The second most common rodent of the Desert Shrub formation is Dipodomys merriami. Merriam kangaroo rats have a wider habitat tolerance than D. ordii. Sandy soils, clays, gravels, and even rocky soils are inhabited. In Big Bend Park, sandy soils are slightly favored over rocky soils (58 specimens to 54 specimens). Populations are highest in creosote and creosote-lechuguilla associations at elevations between 1,850 and 3,000 ft., and lowest in the grassland between 3,000 and 4,000 feet.

The Ord kangaroo rat, Dipodomys ordii, is found in desert situations but is not a common mammal. I found D. ordii only at Upper Tornillo Creek Bridge in a creosote flat. Borell and Bryant (1942) stated that the Ord kangaroo rat was probably confined to the river bottom. Upper Tornillo Creek is approximately 20 miles upstream from the Rio Grande River. Overland migration from the Rio Grande to Upper Tornillo Creek would be impossible due to the position of the Chisos Mountains. Dipodomys ordii must have extended its range northward via the sandy margins of the creek. The river bottom habitat, where Borell and Bryant (1942) found D. ordii, has been destroyed by flood. Deep sands have been replaced by clays and no heteromyids were found there.

Dipodomys ordii and D. merriami are sympatric along Upper Tornillo Creek. Twice as many merriami as ordii inhabit the area. Borell and Bryant (1942) reported sympatry of the two species at the mouth of Santa Elena Canyon.

The western harvest mouse, Reithrodontomys megalotis, was captured in greater numbers at the lower elevations (3,000 ft.) of the Grassland formation on sandy soil with dense ground cover. Judd (1967) reported a specimen collected in a pinyon-juniper-grass association at 5,300 ft. elevation in the Chisos Mountains. I collected four specimens in Stipa grass at 6,700 ft. in Laguna Meadow. Borell and Bryant (1942) did not find R. megalotis in Big Bend Park, nor did Tamsitt (1954) indicate this species at Black Gap. Blair (1940) reported the western harvest mouse to be one of the most widely distributed rodents in the Davis Mountains north of Big Bend National Park. Baker (1956) collected only one western harvest mouse specimen in northern Coahuila (a location 14 miles east of the southeast corner of the park).

The western harvest mouse is more abundant and widespread in distribution in Big Bend than indicated by previous publications. It is found in short-grass, short-grass-yucca, pinyon-juniper-grass, and grama-Stipa grass associations. Reithrodontomys megalotis has an elevational range between 2,500 and 6,700 feet.

Borell and Bryant (1942) reported two specimens of Reithrodontomys fulvescens collected in a sotol-grama grass association in Pine Canyon (4,700 ft.) and one specimen collected in Juniper Canyon (4,800 ft.). One specimen was trapped in Green Gulch in 1967 (Larry Brown, letter to Park Naturalist). No specimens were taken during this investigation. The fulvous harvest mouse is rare and occurs in the canyon grasslands where there is increased moisture and an evenly distributed ground cover. Blair (1940) listed three specimens from Limpia Canyon (4,300 ft.) in the Davis Mountains, but Baker (1956) stated that, in Coahuila, grassy habitats marginal to streams or cultivated fields were preferred habitats. Taylor et al. (1945) obtained two specimens on the western foothills of the Sierra del Carmen in grass near a spring. Tamsitt (1954) did not indicate the presence of R. fulvescens at Black Gap.

Peromyscus boylii is common above 5,000 ft. in rocky areas with a vegetational cover of pinyon, juniper, oak, and brush. Grassy meadows at higher elevations yielded few specimens. All specimens were collected on rocky soil. Peromyscus pectoralis occurs within the same elevational range as P. boylii. The white-ankled mouse is most abundant between 5,000 and 6,000 ft. in the pinyon-oak associations, whereas *P. boylii* is obtained in maximum numbers in the more mesic forest above 6,000 feet. Although *P. pectoralis* and the brush mouse are found together in the Chisos Mountains, the white-footed mouse is usually found in more open grass associations. *Peromyscus boylii* is most abundant among rocks near oak, pine, and juniper trees. Rarely was *P. pectoralis* taken either on the exposed slopes of the higher elevations or in desert situations below 4,500 feet. Zonally, *P. pectoralis* occurs intermediately between *Peromyscus eremicus*, *Peromyscus maniculatus*, and *Peromyscus leucopus* at lower elevations. Tamsitt (1954) found *P. pectoralis* to be the rarest mouse at Black Gap, and he did not collect a specimen of *P. boylii*. Habitats similar to the Chisos Mountains in the Davis and Sierra del Carmen Mountains yielded specimens of *P. boylii* and *P. pectoralis* (Blair, 1940; Baker, 1956).

The rock mouse, *Peromyscus difficilis*, has not been reported previously from Big Bend National Park or Trans-Pecos Texas. Eleven specimens were captured on exposed rocky slopes and among boulders at the north base of Emory Peak (7,000 ft.). Rock mice were found in rockpiles where the crevices and ground are blanketed with a thick layer of oak leaves. Texas Madrone (*Arbutus texana*) and several species of oak (*Quercus* spp.) are the dominant plants at this locality. *Neotoma mexicana* and *P. boylii* are also present in the rockpile habitat. Hoffmeister and De La Torre (1961) .

reported specimens from New Mexico and the Sierra del Carmen Mountains in Coahuila, but no specimens from Texas. According to their records, a hiatus exists between New Mexico and northern Coahuila. The presence of P. difficilis in Trans-Pecos Texas is confirmed and some clarification of the southwestern distribution of the rock mouse has been achieved.

Peromyscus eremicus is an ecologically diverse species. Specimens were collected in creosote, creosote-lechuguilla, grama grass-lechuguilla, lechuguilla-ocotillo, prickly pear, and grama grass-pinyon-juniper associations in the three plant formations. Creosote flats, desert grama grass-lechuguilla, and prickly pear associations at elevations between 1,800 and 3,500 ft. are preferred habitats. Cactus mice occupy the drier mountain slopes to an elevation of 5,500 ft., but population densities decrease with elevational increase. This species prefers rocky soils but occurs both on sandy and clay soils. Borell and Bryant (1942) recorded an elevational range between 1,850 and 3,500 ft. for P. eremicus in desert environments and stated that eremicus was the most common species of the genus Peromyscus in Big Bend Park. Tamsitt (1954) indicated small populations at Black Gap, and Blair (1940) collected only four specimens in the Davis Mountain region. Baker (1956) stated that P. eremicus was the most widespread, as well as most common, Peromyscus in Coahuila. The distribution information on P. eremicus implies that this species is abundant in the eastern portion of the Chihuahuan Desert from Big Bend Park south into Coahuila.

Peromyscus maniculatus was found on desert plains and the lower foothills of the mountains. Specimens were taken as low as 1,850 ft. in elevation and as high as 3,500 feet. Deer mice occur along arroyos, creeks, and on the floodplain of the Rio Grande River in deep to shallow soils and where mesquite (Prosopis glandulosa), cane (Phragmites), cacti, and grassy cover exists. Trapping records indicate deer mice occur in greatest numbers in areas of moderate grass with higher soil moisture content than the surrounding desert plain. Evidently P. maniculatus is ecologically limited in distribution by soil texture and moisture. Blair (1940) collected the majority of specimens in grass associations of the Davis Mountains. Baker (1956) failed to take P. maniculatus on the drier slopes that supported thick stands of lechuguilla, but recorded them from grass-prickly pear associations. Borell and Bryant (1942) recorded specimens from along the Rio Grande River floodplain and near the edge of a small pond in adjacent weeds and grass.

In Big Bend National Park, Peromyscus leucopus has a riparian distribution. All specimens were collected in the Rio Grande River floodplains, where trees and brush produced a semi-woodland environment in association with grass. Borell and Bryant (1942) collected specimens in similar habitats. Blair (1940) reported P. leucopus occurred in woodland at an elevation of 5,500 ft. in Limpia Canyon. Baker (1956) failed to collect specimens of P. leucopus in western Coahuila. No specimens were collected in Black Gap, to the north of Big Bend Park (Tamsitt, 1954).

Five miles southwest of Rio Grande Village, P. leucopus and P. maniculatus inhabit thickets along the Rio Grande River. Peromyscus maniculatus occupies the open grassy areas and P. leucopus occurs in suitable brush with moderate grass. In this sympatric area, P. leucopus populations are higher than populations of P. maniculatus. Neither species occurs in large numbers in the park.

The hispid cotton rat, Sigmodon hispidus, inhabits grassy environments at lower elevations, especially in moist areas along streams where grassland recovery has progressed more rapidly. There is considerable grass along the margins of the Panther Junction-Marathon highway and extensive grassy tracts are present at Tornillo Creek and Bone Spring Draw. The largest hispid cotton rat population occurs adjacent to Upper Tornillo Creek with a smaller population at Bone Spring Draw. Sigmodon hispidus is restricted to areas of moderate to dense grass cover. Borell and Bryant (1942) proposed a river bottom distribution for this species, based on four specimens. I collected only two specimens in river bottom habitat and observed runways on a sandy knoll in Mariscal Canyon. Thirty-one specimens were collected in grassy habitats 20 miles from the Rio Grande River. No specimens have been collected in northern Coahuila adjacent to Big Bend Park (Baker, 1956) or north of the park at Black Gap (Tamsitt, 1954). Seven specimens were collected by Blair (1940) in grass associations in the Davis Mountains. Evidently hispid cotton rats are more numerous and widespread than in previous years, correlating with grassland recovery.

Sigmodon ochrognathus occurs in Grassland and Grassland-Woodland formations in Big Bend Park. Populations of yellow-nosed cotton rats are present in Laguna Meadow, Pine Canyon, Juniper Flat, and Boulder Meadow. Specimens in the Texas A&M collection were taken in Green Gulch and at Boot Springs. *Sigmodon ochrognathus* occurs between elevations of 5,000 to 7,000 feet.

The dominant grass at all collection sites is *Stipa*. In Laguna Meadow sideoats grama (*Bouteloua curtipendula*), *Stipa tenuissima*, and *Stipa neomexicana* are present. Pinyon Pine (*Pinus cembroides*), Alligator Juniper (*Juniperus deppeana*), Ponderosa Pine (*Pinus ponderosa*), and Douglas Fir (*Pseudotsuga menziesii*) are dominant trees where *S. ochrognathus* occurs. Juniper Flat was the only collection site where oaks were dominant. The yellow-nosed cotton rat is most abundant in *Stipa* grass-pinyon-juniper or *Stipa* grass-Ponderosa pine-Douglas fir associations in the park. In contrast, other investigators (Blair, 1940; Baker, 1956; Baker and Greer, 1962; Hoffmeister, 1963; Baker, 1969) indicated a habitat affinity with oak or oak-juniper woodland in association with a variety of grass species. None mentioned Stipa grass as a dominant where specimens were collected.

Dark, loose loam soils with few large rocks compose the substrate at Boulder Meadow, Juniper Flat, and Laguna Meadow, but in Pine Canyon a hard, rocky, clay soil exists. All four sites have a relatively flat terrain. Rocky soils with a slope of as much as 40 degrees were inhabited by S. ochrognathus in Arizona (Hoffmeister, 1963). Canyon valley floors with thick grass were occupied in Coahuila (Baker, 1956) and in Durango (Baker and Greer, 1962). Generalizing habitat preference for this species, Baker (1969) stated that S. ochrognathus lived chiefly on rocky slopes with scattered clumps of grass. My data indicate a preference for flat meadows with a loose, loam soil. Extensive trapping on the rocky slopes surrounding the meadows failed to yield a specimen of the yellow-nosed cotton rat.

Burrows of the yellow-nosed cotton rat were examined in Laguna Meadow. Five burrows had an average diameter of 30 mm. Each burrow was marked by a fan-shaped mound of dirt and a runway leading into the grass. Surface runways are conspicuous near the burrow openings. Evidence of the presence of S. ochrognathus is the runway, which extends from the burrow several feet before branching. Dense stands of Stipa grass provide a canopy over the runway. Because of upper level covering, a yellow-nosed cotton rat can traverse many feet of the runway without exposure from above. Runways average two inches in width and 75 ft. in length. Baker and Greer (1962) found 11 openings from a single burrow system into surface runways. I found only one. In Arizona, a rocky soil prevented the digging of burrows by S. ochrognathus, but abandoned burrows made by Thomomys umbrinus were utilized (Hoffmeister, 1963). There are no pocket gophers in Laguna Meadow, but T. bottae is present in Pine Canyon. Gopher burrow utilization in Pine Canyon is not confirmed.

Baker (1969) theorized that S. ochrognathus lived under more xeric conditions than any other species of Sigmodon. A preference for dry, rocky hillside habitats and small populations were cited as reasons for his conclusion. In Big Bend National Park, the meadows where S. ochrognathus occurs are more mesic than the lower desert plains occupied by S. hispidus. Greater precipitation occurs on mountain meadows; in addition, drainage from the slopes is chanelled into the meadows. A more luxuriant growth of grass is present in the meadows than on the mountain slopes.

The common food of S. ochrognathus is grass. Grass croppings are numerous in runways. In season (late summer and early fall) the purple fruit of the prickly pear (Opuntia) is a favorite food. Purple staining of the fur around the mouth, under the chin, and upper chest is common.

In Big Bend Park, *S. ochrognathus* is associated with *Reithrodontomys megalotis*, *Neotoma albigula*, *Peromyscus boylii*, *Peromyscus pectoralis*, and *Perognathus nelsoni*. Associates in other areas are *Reithrodontomys fulvescens*, *Baiomys taylori*, *Sigmodon fulviventer*, *Liomys irroratus*, *Peromyscus eremicus*, *Sigmodon hispidus*, and *Sigmodon leucotis* (Hoffmeister, 1963; Baker, 1969).

Blair (1940) reported seven *S. ochrognathus* specimens from the Davis Mountains, and Taylor *et al.* (1945) found cuttings, burrows, and piles in the Sierra del Carmen Mountains.

Grassland and Woodland plant formations are inhabited by *Neotoma albigula*. Grama grass-prickly pear, grama grass-yucca, grama grass-oak, Stipa grass-prickly pear, and pinyon-juniper associations support populations of this species. Data analysis indicates a preference for rocky soils and brushy habitats. The availability of vegetation, which affords shelter for houses, seemed to affect their abundance more than the composition of the terrain (Davis, 1966). The white-throated wood rat ranges between 3,700 and 6,800 ft. in elevation, and occurs in greatest numbers between 4,500 and 6,000 ft. in the pinyon-juniper woodland. *Neotoma albigula* certainly is the most abundant wood rat in Big Bend Park. Borell and Bryant (1942) collected only four specimens from 5,000 to 5,200 ft. elevation, and Blair (1940) obtained two specimens in the Davis Mountains. Twenty-one specimens were trapped at Black Gap (Tamsitt, 1954).

Neotoma mexicana inhabits the talus slopes and rockpiles of Mount Emory. Specimens were trapped on and under boulders with a deep litter consisting of oak leaves in a plant association of mixed oaks and conifers. No houses were observed and it is assumed that underground dens are used. The only indication of the species' presence is droppings on rocks. The environment on Emory Peak is mesic. Lichens are present on the rocks and trees, and leaf litter is damp. The area is shaded most of the day by Emory Peak. Similar situations were inhabited by N. mexicana in Coahuila (Baker, 1956).

Mexican wood rats have not been reported previously from the Chisos Mountains. Blair (1940) collected nine specimens in the Davis Mountains; all were caught near rock masses on steep canyon walls. Baker (1956) reported specimens collected in mixed oaks with some conifers from as low as 4,800 ft. in elevation to a height of 8,000 ft. in the Sierra del Carmens. Evidently the ecological requirements of N. mexicana isolate it from the other species of Neotoma in Big Bend Park.

The gray wood rat, Neotoma micropus, is characteristic of the arid Desert Shrub formation. Individuals are common on the creosote, prickly pear, and cholla desert flats of deep sand, but also occur in brush thickets of cane and mesquite along the Rio Grande River.

Neotoma micropus is not as an elaborate nest builder as N. albigula. Only a few sticks and pieces of cactus are strewn about the nest openings. Most of the nests are underground with two or three external openings. All nests are situated in the middle of a clump of prickly pear, cholla, or catclaw (Acacia), and well protected.

Specimens of the gray wood rat were collected in the elevational range of 1,900 to 3,000 feet. Gray wood rats are most abundant in the Desert Shrub formation, but three specimens were collected at the extreme lower margin of the Grassland formation. Neotoma micropus is separated from N. albigula by the Grassland formation. Neither species demonstrates a great affinity for open grassland.

Borell and Bryant (1942) listed N. micropus as uncommon in the park. No specimens have been collected adjacent to Big Bend National Park in northern Coahuila (Baker, 1956). Blair (1940) trapped two gray wood rats in the Davis Mountains, but none were obtained at Black Gap (Tamsitt, 1954). I find the absence of N. micropus at Black Gap intriguing. The majority of Black Gap habitats are of similar composition to those preferred by N. micropus in Big Bend Park. Tamsitt noted N. albigula specimens were blue-black and gray in color. Specimens of N. micropus in the park are gray to gray-black in color, whereas N. albigula tends to be various shades of brown.

Reproduction

Rodent breeding seasons usually occur at a time most advantageous for the pregnant female and the newborn young. Even in rodents that breed at all times of the year, there is usually some period of lesser activity associated with periods of environmental stress. Late spring to early summer is the time of greatest environmental stress on rodents in Big Bend National Park, and the data indicate a phase of reduced reproduction. In conjunction with lower reproducticity, rodent populations are at a minimum in the early summer. The results of the present study show two pregnant females taken in May and none in June. Trapping results for two summers reveal 0.05 rodents taken per 100 trap nights. The increase in number of pregnant females in the late summer, fall, and early winter corresponds closely with the periods of new vegetative growth and climate moderation. There is some evidence that nutrients contained in fresh vegetation have a stimulating effect upon breeding activity (Boderheimer and Sulman, 1946). The present breeding results are generally consistent with previous data (Cockrum, 1962; Davis, 1966; Lord, 1960; Smith and McGinnis, 1968), but there are exceptions.

The number of embryos per female for 18 pregnant Merriam kangaroo rats averages 2.50 (1-5). These females were collected from August through March. Average number of young per female during this time is fairly consistent, varying from 2.77 for August to December, down to 2.28 for January to March. A reproductive study of Dipodomys merriami in southern Arizona (Reynolds, 1960) revealed an average litter size of 2.02 (1-3). Average number of young is lowest in October (1.50) and highest in September (2.18). The months of lowest reproductive activity in southern Arizona, October through March, (Reynolds, 1960), are the highest months in Big Bend National Park, indicating a significant difference in the reproductive activity of D. merriami in Big Bend and the same species in southern Arizona.

Peromyscus eremicus bears litters every month of the year except May, June, and July. The reduction in breeding correlates with the general pattern of rodent reproduction. Maximum litter size for P. eremicus is five, with an average of 3.10 (10 litters). Svihla (1932) reported a mean litter size of 2.60 in P. eremicus, based on five litters; Davis and Davis (1947) found the mean number of young in 404 litters to be 2.42; Baker (1956) obtained an average litter size of 2.70 (38 litters) for P. eremicus in Coahuila; Brand and Ryckman (1968) in a laboratory study of P. eremicus taken in southern California, reported an average litter size of 2.22 (14 litters). My data suggest a large litter size for P. eremicus and correlate with the litter size of the desert mouse in Coahuila. Evidently female eremicus produce larger litters in the eastern distributional areas than in the western areas.

Sigmodon ochrognathus breeds throughout the year in Big Bend Park. Populations usually contain more juveniles than adults. Seven pregnant females had an average litter size of 3.57 (3-5). Four female S. ochrognathus collected in southern Arizona had embryo numbers of two, three, three, and four, and laboratory raised females had an average litter size of 3.00 (Hoffmeister, 1963). Baker (1956) reported the following embryo counts for S. ochrognathus in Coahuila: two, two, six, seven, eight, and nine. Litter size of the yellow-nosed cotton rat in Big Bend Park is larger than the sizes recorded for this species in southern Arizona.

Ectoparasites

Like most ixodid ticks, larval Trombiculidae attach to their hosts only while feeding. Chiggers feed even less frequently than the other mite families; therefore, a great portion of their life span is spent off the host. Engorged mites drop from their hosts, and when ready to feed again climb to a vantage point and await the passage of a suitable host. Although the chiggers are found on various vertebrates, they are not particularly host specific.

Host selection is based on availability of satisfactory hosts to unfed, active larvae and certain chiggers have host preference based on intimate association and physiological selection and rejection (Loomis, 1970). Host preference on one to several related species seems to occur frequently. Chiggers and their hosts coincide in activity and life cycles.

Certain morphological features seem correlated with environmental factors. Larvae of desert species tend to be smaller and lack or have shorter setae on the body and legs. Seemingly these modifications are directly related to water conservation (Loomis, 1970).

No previous study of the chigger parasites on rodents in Big Bend National Park has been published. Loomis and Crossley (1963) included some records from the park in a study of the chiggers from Texas. The present investigation adds to the knowledge of host preference and distribution of chiggers in the northern Chihuahuan Desert.

The rodent distribution appears to correlate with incidence of chigger parasitism. *Neotoma albigula* and *Perognathus nelsoni* occur together in similar habitats, and nine chigger species are hosted by both species. *Peromyscus pectoralis* and *Neotoma albigula* have seven trombiculid species in common, but *Peromyscus pectoralis* and *Perognathus nelsoni*, due to habitat preference--brush versus grassland--jointly host only two species. *Peromyscus boylii*, *Peromyscus difficilis* and *Neotoma mexicana* inhabit rocky habitats at higher elevations. All three are parasitized by *Euschoengastia criceticola* and *Kayella lacerta*. *Peromyscus boylii* and P. difficilis are hosts for Pseudoschoengastia farneri. Habitat preference by these three cricetid hosts correlates with the incidence of parasite species. A similar situation exists for Perognathus merriami and Perognathus penicillatus.

In the present study, chigger infestation is independent of sex and relative age; however, evidence indicates that larger animals of all sex and age classes were more susceptible to trombiculid parasitism. If it is assumed that larger individuals tend to be more active, these results may be consistent with the interpretation.

APPENDIX I

The following is a summary of the host-parasite relationships of the rodent species in Big Bend National Park. The rodent species and the trombiculid ectoparasites collected from the specific hosts are listed.

Spermophilus spilosoma. Total chigger species, 4, as follows: *Euschoengastoides hoplai* (Loomis); *Fonsecia gurneyi* (Ewing); *Hyponeocula arenicola* (Loomis); *Leptotrombidium panamense* (Ewing).

Spermophilus variegatus. Total chigger species, 1, as follows: *Eutrombicula alfreddugesi* (Oudemans).

Ammospermophilus interpres. Total chigger species, 1, as follows: *Leptotrombidium panamense* (Ewing).

Thomomys bottae. Total chigger species, 1, as follows: *Euschoengastoides arizonae* Loomis.

Pappogeomys castanops. Total chigger species, 1, as follows: *Hyponeocula arenicola* (Loomis).

Perognathus merriami. Total chigger species, 10, as follows: *Euschoengastoides arizonae* Loomis; *Euschoengastoides* hoplai (Loomis); *Euschoengastoides similis* n. sp.; *Fonsecia gurneyi* (Ewing); *Hexidionis allredi* (Brennan and Beck); *Hexidionis harveyi* Loomis and Lucas; *Hyponeocula arenicola* (Loomis); *Leptotrombidium panamense* (Ewing);

Otorhinophila baccusi n. sp. Loomis and Wrenn; *Pseudoshoengastia* n. sp.

Perognathus nelsoni. Total chigger species, 11, as follows: *Euschoengastoides arizonae* Loomis; *Euschoengastoides hoplai* (Loomis); *Euschoengastoides loomisi* (Crossley and Lipovsky); *Euschoengastoides neotomae* Loomis; *Euschoengastoides similis* n. sp.; *Hexidionis allredi* (Brennan and Beck); *Hyponeocula arenicola* (Loomis); *Kayella lacerta* (Brennan); *Leptotrombidium panamense* (Ewing); *Pseudoschoengastia hungerfordi* Lipovsky; *Pseudoschoengastia* n. sp.

Perognathus penicillatus. Total chigger species, 9, as follows: *Euschoengastoides arizonae* Loomis; *Euschoengastoides hoplai* (Loomis); *Euschoengastoides similis* n. sp.; *Hexidionis allredi* (Brennan and Beck); *Hexidionis harveyi* Loomis and Lucas; *Hyponeocula arenicola* (Loomis); *Kayella lacerta* (Brennan); *Otorhinophila baccusi* n. sp. Loomis and Wrenn; *Pseudoschoengastia* n. sp.

Dipodomys merriami. Total chigger species, 8, as follows: *Euschoengastoides arizonae* Loomis; *Euschoengastoides hoplai* (Loomis); *Fonsecia gurneyi* (Ewing); *Hexidionis allredi* (Brennan and Beck); *Hexidionis harveyi* Loomis and Lucas; *Hyponeocula arenicola* (Loomis); *Otorhinophila baccusi* n. sp. Loomis and Wrenn.

Reithrodontomys megalotis. Total chigger species, 2, as follows: *Hexidionis harveyi* Loomis and Lucas; *Pseudochoengastia whartoni* Brennan.

Peromyscus eremicus. Total chigger species, 9, as follows: *Sasacarus whartoni* (Hoffmann); *Euschoengastoides loomisi* (Crossley and Lipovsky); *Euschoengastoides neotomae* Loomis; *Fonsecia gurneyi* (Ewing); *Kayella lacerta* (Brennan); *Leptotrombidium panamense* (Ewing); *Pseudoschoengastia farneri* Lipovsky; *Pseudoschoengastia hungerfordi* Lipovsky; *Pseudoschoengastia* whartoni Brennan.

Peromyscus maniculatus. Total chigger species, 1, as follows: *Hexidionis harveyi* Loomis and Lucas.

Peromyscus pectoralis. Total chigger species, 9, as follows: *Sasacarus whartoni* (Hoffmann); *Euschoengastia criceticola* Brennan; *Euschoengastia* n. sp.; *Euschoengastoides loomisi* (Crossley and Lipovsky); *Euschoengastoides neotomae* Loomis; *Euschoengastoides similis* n. sp.; *Fonsecia furneyi* (Ewing); *Leptotrombidium panamense* (Ewing); *Pseudoschoengastia farneri* Lipovsky.

Peromyscus boylii. Total chigger species, 3, as follows: *Euschoengastia criceticola* Brennan; *Kayella lacerta* (Brennan); *Pseudoschoengastia farneri* Lipovsky.

Sigmodon ochrognathus. Total chigger species, 4, as follows: *Euschoengastia criceticola* Brennan; *Fonsecia gurneyi* (Ewing); *Leptotrombidium panamense* (Ewing); *Pseudoschoengastia hungerfordi* Lipovsky.

Neotoma micropus. Total chigger species, 7, as follows: *Euschoengastia criceticola* Brennan; *Euschoengastoides* loomisi (Crossley and Lipovsky); Euschoengastoides similis n. sp.; Eutrombicula alfreddugesi (Oudemans); Hexidionis allredi (Brennan and Beck); Leptotrombidium panamense (Ewing); Pseudoschoengastia whartoni Brennan.

Neotoma albigula. Total chigger species, 13, as follows: Odontacarus morlani Brennan; Sasacarus whartoni (Hoffmann); Euschoengastia criceticola Brennan; Euschoengastoides hoplai (Loomis); Euschoengastoides loomisi (Crossley and Lipovsky); Euschoengastoides similis n. sp.; Fonsecia gurneyi (Ewing); Hexidionis allredi (Brennan and Beck); Hyponeocula arenicola (Loomis); Kayella lacerta (Brennan); Leptotrombidium panamense (Ewing); Pseudoschoengastia farneri Lipovsky; Pseudoschoengastia hungerfordi Lipovsky.

Neotoma mexicana. Total chigger species, 2, as follows: Euschoengastia criceticola Brennan; Kayella lacerta (Brennan).

APPENDIX II

The following is a list of the rodent species studied. No attempt has been made to examine all the specimens collected in Big Bend National Park. Localities, elevations, and number collected are given. Specimens not collected by me, have the institutional names abbreviated and in parentheses. These are Big Bend National Park Mammal Collection (BBNP); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); University of South Tampa (UST); University of Michigan (UM); Texas Technological University (TT).

Spermophilus mexicanus. Specimens examined.--Total, 2, from: Rio Grande Village, 1,850 ft., 2 (BBNP).

Observations. Rio Grande Village, 1,850 ft., 5.

Spermophilus spilosoma. Specimens examined.--Total, 16, from: 5 mi. SW Rio Grande Village, 1,850 ft., 1; 8 mi. SW Rio Grande Village, 1,925 ft., 1; Panther Junction, 3,700 ft., 2; Lower Tornillo Creek Bridge, 1,925 ft., 1; NW Chilicotal Mt., 3,500 ft., 1 (UM); E Burro Mesa, 4,000 ft., 1 (TCWC); Nail Ranch, 3,500 ft., 1 (TCWC); Mouth Santa Elena Canyon, 2,100 ft., 1 (TCWC); NE Panther Junction, 3,700 ft., 7 (BBNP).

Additional records (Borell and Bryant, 1942:20): N End Mariscal Mt., 2,300 ft., 3.

Observations. 12 mi. N Panther Junction, 2,900 ft., 2; Persimmon Gap, 2,900 ft., 1; 1 mi. N Castolon, 2,700 ft., 1.

Spermophilus variegatus. Specimens examined.--Total, 8, from: 3 mi. N Basin, 5,550 ft., 1; Juniper Canyon, 4,500 ft., 1 (TCWC); Basin, 5,400 ft., 1 (TCWC); Casa Grande, 6,000 ft., 1 (TCWC); Boot Springs, 6,900 ft., 2 (TCWC); Upper Green Gulch, 5,300 ft., 2 (BBNP).

Additional records (Borell and Bryant, 1942:20): Juniper Canyon, 4,800 ft., 2; E of Basin, 5,800 ft., 2; Green Gulch, 5,200 ft., 3; (Bailey, 1905:83): Chisos Mts.; (Howell, 1938:141): Chisos Mts.; Boquillas.

Observations. K-Bar, 3,700 ft., 1; N Slope Emory Peak, 6,800 ft., 1; Panther Canyon, 4,300 ft., 1.

Ammospermophilus interpres. Specimens examined.--Total, 10, from: Basin, 5,560 ft., 2; Pine Canyon, 5,100 ft., 1; K-Bar, 3,700 ft., 1; Oak Creek, 4,000 ft., 4 (TCWC); Blue Creek Canyon, 4,500 ft., 1 (TCWC); Wilson Ranch, 4,000 ft., 1 (BBNP).

Additional records (Borell and Bryant, 1942:21): Pine Canyon, 4,700 ft., 1; Green Gulch, 5,200 ft., 2; Basin, 5,200 ft., 1; (Howell, 1938:180): Boquillas.

Observations. Upper Basin, 6,100 ft., 2; Terlingua Abaja, 2,350 ft., 1; 3 mi. SW Rio Grande Village, 1,850 ft., 1; Panther Canyon, 4,500 ft., 1; Basin, 5,500 ft., 4; K-Bar, 3,700 ft., 3.

Thomomys bottae. Specimens examined.--Total, 8, from: Pine Canyon, 5,000 ft., 1; Boot Springs, 6,600 ft., 1 (TCWC); 2 mi. NW Lone Mt., 2,400 ft., 2 (TCWC); Grapevine Hills, 3,500 ft., 1 (TCWC); Panther Junction, 3,700 ft., 1 (TT); Pulliam Canyon, 5,200 ft., 1 (BBNP); Panther Junction, 3,700 ft., 1 (BBNP).

Additional records (Borell and Bryant, 1942:21-22): Green Gulch, 5,200 ft., 2; E Base Burro Mesa, 3,500 ft., 2; Glenn Springs, 2,606 ft., 1; Boquillas, 1,800 ft., 1; (Bailey, 1915:89): Boquillas; (Goldman, 1936:119): Boquillas.

Pappogeomys castanops. Specimens examined.--Total, 6, from: 3 mi. NW Rio Grande Village, 1,900 ft., 1; 5 mi. SW Rio Grande Village, 1,850 ft., 1; 8 mi. SW Rio Grande Village, 1,925 ft., 2; Castolon, 2,100 ft., 1 (UM); Mouth Santa Elena Canyon, 2,100 ft., 1 (TCWC).

Additional records (Borell and Bryant, 1942:22): 1 mi. SW Boquillas, 1,850 ft., 3; Big Bend Rio Grande, 2,000 ft., 6; Johnson Ranch, 2,060 ft., 2; (Nelson and Goldman, 1934: 138): Boquillas.

Perognathus merriami. Specimens examined.--Total, 46, from: 5 mi. NW Panther Junction, 3,523 ft., 1; 1 mi. N Panther Junction, 3,800 ft., 1; 3 mi. SE Panther Junction, 3,700 ft., 15; Green Gulch, 4,200 ft., 5; Lower Tornillo Creek, 1,925 ft., 2; 8 mi. SW Rio Grande Village, 1,925 ft., 1; 13 mi. N Panther Junction, 3,400 ft., 2 (TT): Dugout

Wells, 3,500 ft., 1 (TT); Castolon, 2,700 ft., 3 (UM); Oak Creek, 3,900 ft., 1 (TCWC); Paint Gap Hills, 3,500 ft., 5 (TCWC); Nail Ranch, 3,700 ft., 4 (TCWC); 2 mi. N Lone Mt., 3,400 ft., 2 (TCWC); Green Gulch, 5,600 ft., 1 (BBNP): Rio Grande Village, 1,850 ft., 1 (BBNP); Panther Junction, 3,700 ft., 1 (BBNP).

Additional records (Borell and Bryant, 1942:23): N End Mariscal Mt., 2,300 ft., 4.

Perognathus nelsoni. Specimens examined.--Total, 71, from: Basin Campground, 5,560 ft., 5; Pine Canyon, 5,000 ft., 17; 3 mi. SE Panther Junction, 3,700 ft., 2; Persimmon Gap, 2,875 ft., 2; Park Entrance, 2,835 ft., 1; 7 mi. SE Panther Junction, 3,350 ft., 1; McKinney Springs, 3,100 ft., 1 (TCWC); Oak Creek, 4,000 ft., 3 (TCWC); Oak Creek Springs, 4,200 ft., 1 (TCWC); Blue Creek, 4,250 ft., 3 (TCWC); Pine Canyon, 4,500 ft., 1 (TCWC); Pine Canyon, 5,100 ft., 1 (TCWC); Pine Canyon, 5,300 ft., 1 (TCWC); Green Gulch, 5,000 ft., 2 (TCWC); Grapevine Hills, 3,300 ft., 1 (TCWC); Grapevine Hills, 3,100 ft., 3 (TCWC); Castolon, 2,200 ft., 1 (UM); 3 mi. NE Solis Ranch, 2,100 ft., 1 (UM); NW Slope Chilicotal Mt., 1 (UM); Pine Canyon, 4,700 ft., 4 (UST); Green Gulch, 5,000 ft., 3 (UST); Dagger Flat, 3,450 ft., 7 (TT); Green Gulch, 5,300 ft., 2 (TT); Blue Creek Ranch, 3,900 ft., 5 (TT); Blue Creek Ranch, 3,900 ft., 2 (BBNP).

Additional records (Borell and Bryant, 1942:25): Chisos Mts., 1; Pine Canyon, 4,700 ft., 8; Juniper Canyon, 4,800 ft., 2; Boquillas, 1; Glenn Springs, 2,600 ft., 4; N End Mariscal Mt., 2,300 ft., 3; Pinnacle Springs, 2,800 ft., 9; Smoky Springs, 3,200 ft., 1; (Bailey, 1905:140): Boquillas; E Base Chisos Mts.; (Warner, 1964): Government Springs, 3,958 ft., 1.

Perognathus penicillatus. Specimens examined.--Total, 112, from: 5 mi. NW Panther Junction, 3,523 ft., 1; 4 mi. SE Panther Junction, 3,000 ft., 2; 5 mi. SW Rio Grande Village, 1,850 ft., 1; 8 mi. SW Rio Grande Village, 1,925 ft., 22; Johnson Ranch, 2,020 ft., 9; 6 mi. NW Castolon, 2,344 ft., 14; 10 mi. NE Panther Junction, 2,820 ft., 3; Nine Point Draw, 2,600 ft., 2; 19 mi. SW Panther Junction, 2,250 ft., 3; Lower Tornillo Creek, 1,925 ft., 1; 4 mi. N Rio Grande Village, 1,900 ft., 18; Rio Grande Village, 1,850 ft., 1; Castolon, 2,200 ft., 2 (UM); 3 mi. N Hot Springs, 2,000 ft., 1 (UM); NE Solis Ranch, 2,500 ft., 2 (UM); Dugout Wells, 3,500 ft., 12 (TT); Upper Tornillo Creek, 2,800 ft., 6 (TT); Oak Creek, 4,000 ft., 9 (TCWC); Paint Gap Hills, 3,500 ft., 1 (TCWC); Nail Ranch, 3,500 ft., 1 (TCWC); Tornillo Flat, 2,800 ft., 1 (TCWC).

Additional records (Borell and Bryant, 1942:24): Gano Springs, 3,400 ft., 1; E Base Burro Mesa, 4,400 ft., 4; Boquillas, 1,800 ft., 3; Glenn Springs, 2,060 ft., 3; N End Mariscal Mt., 2,300 ft., 3; Big Bend Rio Grande, 2,000 ft., 28; Mouth Santa Elena Canyon, 2,100 ft., 6; NE Base Mesa de

E Base Chisos Mts.; (Warner, 1964): Mannold Grave, 3,108 ft., 2; Rio Grande Village, 1,873 ft., 9.

Dipodomys merriami. Specimens examined.--Total, 96, from: 5 mi. NW Panther Junction, 3,523 ft., 6; 4 mi. SE Panther Junction, 3,000 ft., 1; Panther Junction, 3,700 ft., 1; 3 mi. SE Panther Junction, 3,700 ft., 1; 8 mi. SW Rio Grande Village, 1,925 ft., 7; 6 mi. NW Castolon, 2,344 ft., 5; 10 mi. NE Panther Junction, 2,820 ft., 19; Nine Point Draw, 2,600 ft., 2; Persimmon Gap, 2,900 ft., 2; Park Entrance, 2,825 ft., 3; 1 mi. S Persimmon Gap, 2,700 ft., 1; Lower Tornillo Creek, 1,925 ft., 7; 19 mi. SW Panther Junction, 2,250 ft., 2; Johnson Ranch, 2,100 ft., 4 (TCWC); McKinney Springs, 3,100 ft., 1 (TCWC); Oak Creek, 3,900 ft., 2 (TCWC); Paint Gap Hills, 3,500 ft., 5 (TCWC); Nail Ranch, 3,700 ft., 4 (TCWC); 2 mi. NW Lone Mt., 3,400 ft., 2 (TCWC); Castolon, 2,150 ft., 1 (UM); 3 mi. N Hot Springs, 3,000 ft., 1 (UM); NE Solis Ranch, 2,200 ft., 1 (UM); Chilicotal, 3,700 ft., 1 (UM); Dagger Flat, 3,450 ft., 6 (TT); 2 mi. N Panther Junction, 3,500 ft., 1 (TT); 12 mi. N Panther Junction, 3,300 ft., 5 (TT); 9 mi. N Panther Junction, 2,800 ft., 3; 4 mi. S Nail Ranch, 3,500 ft., 2 (BBNP).

Additional records (Borell and Bryant, 1942:27): E Base Burro Mesa, 3,500 ft., 3; 1 mi. SW Boquillas, 1,850 ft., 1; N End Mariscal Mt., 2,300 ft., 9; Mouth Santa Elena Canyon, 2,146 ft., 1; N End Mesa de Anguila, 2,300 ft., 1; (Bailey, 1905:150): Boquillas.

Dipodomys ordii. Specimens examined.--Total, 11, from: 10 mi. NE Panther Junction, 2,820 ft., 9; Johnson Ranch, 2,100 ft., 1 (TCWC); Mouth Santa Elena Canyon, 2,100 ft., 1 (TCWC).

Additional records (Borell and Bryant, 1942:27): Mouth Santa Elena Canyon, 2,146 ft., 2; Big Bend Rio Grande, 2,000 ft., 1; Johnson Ranch, 2,100 ft., 2.

Reithrodontomys fulvescens. Specimens examined.--Total, 1, from: Green Gulch, 5,000 ft., 1 (UST).

Additional records (Borell and Bryant, 1942:29): Juniper Canyon, 4,800 ft., 1; Pine Canyon, 4,700 ft., 2.

Reithrodontomys megalotis. Specimens examined.--Total, 37, from: 10 mi. NE Panther Junction, 2,820 ft., 26; Bone Creek Draw, 2,594 ft., 3; Laguna Meadow, 6,700 ft., 4; Green Gulch, 5,000 ft., 2 (UST); Green Gulch, 5,300 ft., 1 (TT); Green Gulch, 5,500 ft., (BBNP).

Peromyscus boylii. Specimens examined.--Total, 58, from: Pine Canyon, 5,000 ft., 1; Pine Canyon, 5,100 ft., 1; Boulder Meadow, 5,700 ft., 11; Laguna Meadow, 6,700 ft., 20; N Base Emory Peak, 7,000 ft., 11; Basin, 5,560 ft., 1; Green Gulch, 5,600 ft., 5; Pine Canyon, 4,700 ft., 8 (UST); Green Gulch, 5,000 ft., 6 (UST); Green Gulch, 5,700 ft., 1 (UST); Boot Springs, 7,100 ft., 3 (TCWC).

Additional records (Borell and Bryant, 1942:32): Pine Canyon, 4,700 ft., 5; Green Gulch, 5,000 ft., 8; Oak Creek, 5,000 ft., 6; Laguna Meadow, 6,500 ft., 2.

Peromyscus difficilis. Specimens examined.--Total, 11, from: Pine Canyon, 5,100 ft., 1; Laguna Meadow, 6,800 ft., 5; N Base Emory Peak, 7,000 ft., 4; Green Gulch, 5,700 ft., 1.

Peromyscus eremicus. Specimens examined.--Total, 78, from: Basin Campground, 5,560 ft., 1; Pine Canyon, 5,000 ft., 1; Pine Canyon, 5,100 ft., 1; 3 mi. SE Panther Junction, 3,700 ft., 7; K-Bar, 3,700 ft., 3; 10 mi. NE Panther Junction, 2,820 ft., 7; Nine Point Draw, 2,600 ft., 2; Park Entrance, 2,600 ft., 1; Persimmon Gap, 2,850 ft., 1; Lower Tornillo Creek, 1,925 ft., 1; 3 mi. SE Panther Junction, 2,100 ft., 1; 7 mi. SE Panther Junction, 3,350 ft., 3; SE Castolon, 2,200 ft., 2 (UM); 1 mi. NE Solis Ranch, 1,900 ft., 5 (UM); Dagger Flat, 3,450 ft., 8 (TT); Panther Junction, 3,700 ft., 6 (TT); 13 mi. N Panther Junction, 3,400 ft., 2 (TT); Sotol Vista, 4,000 ft., 5 (TT); Blue Creek Ranch, 5,000 ft., 1 (TT); Mouth Santa Elena Canyon, 2,100 ft., 1 (TCWC); K-Bar, 3,700 ft., 6 (UST); Mail Ranch, 3,500 ft., 2 (TCWC); Paint Gap Hills, 3,500 ft., 1 (TCWC); Wilson's Ranch, 3,500 ft., 1 (TCWC); Green Gulch, 5,000 ft., 1 (TCWC); Burro Mesa, 3,000 ft., 1 (TCWC); 1 mi. W Grapevine Hills, 3,100 ft., 1 (TCWC); 2 mi. W Lone Mt., 3,400 ft., 1 (TCWC); Mouth Green Gulch, 5,000 ft., 2 (TCWC); Tornillo Flat, 2,900 ft., 2 (TCWC); Government Springs, 4,000 ft., 1 (TCWC).

Additional records (Borell and Bryant, 1942:29-30): NE Chisos Mts., 3,800 ft., 3; Tornillo Flat, 2,800 ft., 2;

N Base Burro Mesa, 3,000 ft., 1; E Base Burro Mesa, 3,600 ft., 4; SW Boquillas, 1,850 ft., 2; Glenn Springs, 2,060 ft., 4; N End Mariscal Mt., 2,300 ft., 2; Big Bend Rio Grande, 2,000 ft., 12; Mesa de Anguila, 2,400 ft., 2; Pinnacle Springs, 2,800 ft., 3; Mouth Santa Elena Canyon, 2,146 ft., 4; (Bailey, 1905:101): Boquillas; (Osgood, 1909:242): Boquillas.

Peromyscus leucopus. Specimens examined.--Total, 11, from: 5 mi. SW Rio Grande Village, 1,850 ft., 11.

Additional records (Borell and Bryant, 1942:31-32): E Base Burro Mesa, 3,500 ft., 1; 1 mi. SW Boquillas, 1,850 ft., 5; Big Bend Rio Grande, 2,000 ft., 2; Johnson Ranch, 2,060 ft., 3.

Peromyscus maniculatus. Specimens examined.--Total, 9, from: Johnson Ranch, 2,020 ft., 2; Bone Creek Draw, 2,594 ft., 4; Big Bend Rio Grande, 2,000 ft., 1 (UM); Mouth Santa Elena Canyon, 2,100 ft., 2 (TCWC).

Additional records (Borell and Bryant, 1942:31): E Base Burro Mesa, 3,500 ft., 5; N End Mariscal Mt., 2,300 ft., 1; Johnson Ranch, 2,060 ft., 1; (Bailey, 1905:97): Bone Springs; (Osgood, 1909:86): Bone Springs.

Peromyscus pectoralis. Specimens examined.--Total, 111, from: Green Gulch, 5,700 ft., 1; Juniper Flat, 5,600 ft., 1; Boulder Meadow, 5,700 ft., 6; Upper Basin, 5,500 ft., 2; Pine Canyon, 5,100 ft., 43; Laguna Meadow, 6,700 ft., 7;

14 (UST); Green Gulch, 5,000 ft., 20 (UST); Green Gulch, 5,300 ft., 1 (TCWC); Boot Springs, 6,800 ft., 11 (TCWC); Pine Canyon, 5,300 ft., 1 (TCWC); Oak Creek, 4,000 ft., 1 (BBNP).

Additional records (Borell and Bryant, 1942:33): Chisos Mts., 5,100 ft., 1; Basin, 5,100 ft., 7; (Osgood, 1909: 165): Chisos Mts.

Onychomys torridus. Record (Borell and Bryant, 1942: 28): Gano Springs, 3,400 ft., 1.

Sigmodon hispidus. Specimens examined.--Total, 34, from: 5 mi. SW Rio Grande Village, 1,850 ft., 2; 10 mi. NE Panther Junction, 2,820 ft., 26; Bone Springs Draw, 2,594 ft., 5; Grapevine Springs, 3,000 ft., 1 (TCWC).

Additional records (Borell and Bryant, 1942:34): Big Bend Rio Grande, 2,000 ft., 3; Johnson Ranch, 2,060 ft., 1.

Sigmodon ochrognathus. Specimens examined.--Total, 58, from: Laguna Meadow, 6,700 ft., 10; Pine Canyon, 5,100 ft., 20; Juniper Flat, 5,600 ft., 3; Boulder Meadow, 5,700 ft., 1; Green Gulch, 5,000 ft., 5 (UST); Green Gulch, 5,600 ft., 6 (TCWC); Laguna Meadow, 6,700 ft., 3 (TCWC); Boot Springs, 6,800 ft., 3 (TCWC); Laguna Meadow, 6,500 ft., 3 (BBNP); Boot Springs, 6,800 ft., 1 (BBNP); Chisos Mts., 3 (UM).

Additional records (Borell and Bryant, 1942:34): Pine Canyon, 4,700 ft., 7; Laguna Meadow, 6,500 ft., 10; (Bailey, 1905:118): Chisos Mts.; (Warner, 1964): Panther Pass, 5,700 ft., 1.

Neotoma albigula. Specimens examined.--Total, 106, from: Green Gulch, 5,200 ft., 1; 1 mi. N Panther Junction, 3,800 ft., 1; Green Gulch, 5,300 ft., 4; Green Gulch, 5,000 ft., 1; Green Gulch, 5,700 ft., 2; Basin Campground, 5,560 ft., 26; Pine Canyon, 5,000 ft., 6; Pine Canyon, 5,100 ft., 3; 3 mi. SE Panther Junction, 3,700 ft., 8; Juniper Flat, 5,600 ft., 9; Boulder Meadow, 5,700 ft., 34; Laguna Meadow, 6,800 ft., 2; Laguna Meadow, 6,700 ft., 2; Panther Junction, 3,700 ft., 2; Boot Springs, 6,700 ft., 1 (TCWC); Pine Canyon, 5,300 ft., 1 (TCWC); Green Gulch, 5,700 ft., 1 (TCWC); Panther Junction, 3,700 ft., 1 (BBNP); Green Gulch, 5,100 ft., 1 (BBNP).

Additional records (Borell and Bryant, 1942:36): E Chisos Mts., 3,800 ft., 1; Green Gulch, 5,200 ft., 1; Basin, 5,200 ft., 2; Oak Creek, 5,000 ft., 1.

Neotoma mexicana. Specimens examined.--Total, 24, from: 5 mi. SW Rio Grande Village, 1,850 ft., 2; 8 mi. SW Rio Grande Village, 1,925 ft., 5; Johnson Ranch, 2,020 ft., 6; 6 mi. NW Castolon, 2,344 ft., 1; 10 mi. NE Panther Junction, 2,820 ft., 4; 13 mi. SE Panther Junction, 2,100 ft., 3; 19 mi. SW Panther Junction, 2,250 ft., 3.

Additional records (Borell and Bryant, 1942:35): N Base Burro Mesa, 3,500 ft., 2; Glenn Springs, 2,060 ft., 1; N End Mariscal Mt., 2,300 ft., 2; Big Bend Rio Grande, 2,000 ft., 2; (Goldman, 1910:29): Chisos Mts.; (Warner, 1964): Rio Grande Village.

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