Exploring a Desert
Experiences of an Ecologist/Naturalist in a New Mexico Desert

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Foreword

Several students suggested that I write a book summarizing what I had learned about the workings of our desert in southern New Mexico. After retiring from the Environmental Protection Agency, I spent the better part of two years writing a hard science book with a global perspective on the ecology of desert ecqsystems. After continuing research for the next ten years on topics and issues of interest for students of the Chihuahuan Desert, I began book that summarizes much of what we have learned about the biota of the Chihuahuan Desert. Working on that book brought back lots of memories of the many students with whom I worked and from whom I learned to see the Chihuahuan Desert through their unique perspectives. It is important to say that I frequently learned as much or more from students than they learned from me, especially from students who worked with me as their graduate advisor. Also, I learned a great deal by serving on graduate committees of students, accompanying them to their field sites and learning about their research. To them I owe a debt that I hope can partially be repaid by summarizing some of their studies in addition to my own that provided fascinating insights into the workings of our local desert environments. My forays into the fascinating world of interactions among animals, plants and soil were frequently in response to questions or suggestions of students. Working with students has allowed me to remain a student for more than 50 years and I hope to be able to continue that association into the future.

My daily interactions with post-doctoral students, graduate students and undergraduate students were largely due to two “big science” programs funded by the National Science Foundation: The International Bological Program’s Desert Biome and the Long Term Ecological Research Program, plus grants from the National Science Foundation and other federal and state agencies. Funds from these programs and agencies supported the educational costs of a large number of undergraduates and graduate students and several graduate students working with other professors who did not have funds to support the students. Students frequently asked for summer jobs or work in the laboratory. Some students were known to say that working with Dr. Whitford often required intimate knowledge of the business end of a shovel. One graduate student commenting on our work said that “honest science” involved lots of digging and hammering. Many of the students who worked with me over the years were not listed as authors on research papers because their contributions consisted of trenching plots, building rain-out shelters, exclosures, etc. However their contributions were important and credited in acknowledgements.

In this book I try to convey my fascination with the natural history of many of the organisms that populate the desert environment with the hope that the reader will be enabled to share some of that fascination. Also there are descriptions of field experiments that provided insights into biological – physical environment interactions that could only be discerned by experimental approaches.

Introduction

This book summarizes more than 50 years of work in the northern Chihuahuan Desert. Most of the experiments and field studies were done on the New Mexico State University's Chihuahuan Desert Rangeland Research Station and the U. S. D. A. Agricultural Research Service's Jornada Experimental Range. These research ranches are located approximately 25 - 30 miles north of Las Cruces, New Mexico and include close to 500,000 acres. These properties include the Dona Ana mountain range on the southern boundary and the western slopes of the San Andres mountains on the eastern boundary. The Chihuahuan Desert Nature Park is located at the southern edge of the Jornada Experimental Range and is open to the public. The Nature Park is a good place to see Chihuahuan Desert landscapes, experience creosotebush shrublands, desert grassland, and see some of the animals that were the subject of studies described in this book.

The Chihuahuan Desert in the U. S. is only a small part of that desert. Most of the Chihuahuan Desert is in Mexico. The desert occupies most of the state of Chihuahua, part of the state of Coahuila, and the state of Durango east of the Sierra Madre Occidental. In the U. S., the Chihuahuan Desert occupies most of southern New Mexico, much of west Texas and a small section of eastern Arizona. In New Mexico, it extends as far north as Soccorro along the Rio Grande valley but is bounded by the Mogollon Rim around Silver City, N. M. In eastern New Mexico a finger of this desert extends north to Roswell in areas around the Pecos River but is bounded eastward roughly at the latitude of Carlsbad N. M. In west Texas, the Chihuahuan Desert extends south to Big Bend National Park and east to Pecos, Texas. The Chihuahuan Desert extends into eastern Arizona to the San Simon Valley east of the Chiricahua Mountains.

There are a number of state and federal parks that provide an opportunity to experience some of the unique features of the Chihuahuan Desert as well as the variety of habitats that support a high diversity of plants and animals. White Sands National Monument features extensive gypsum sand dunes. Short hikes into the dunes from the roads allow the visitor to see some of the animals described herein. The most frequently seen are large colonies of harvester ants, termite galleries, darkling beetles/stink beetles and pale side blotch lizards. Carlsbad Caverns National Monument provides an opportunity to see arroyo vegetation along the road into the Caverns from White City. Around sunset sunset, you may see mule deer , jackrabbits, skunks and other mammals and reptiles that inhabit the Chihuahuan Desert. The vegetation on the hills around the Caverns is primarily a creosotebush association. The Living Desert State Park in Carlsbad features a number of the interesting animals of this desert in addition to many of the plants that are important members of the plant communities. The largest national park in the Chihuahuan Desert is Big Bend which gets its name from a big bend in the Rio Grande River. Big Bend Park offers most of the vegetation associations, and landscapes that we studied in the Jornada Basin. Most of the information derived from the studies in the Jornada Basin is generally applicable to the Big Bend region.

Valley of Fires State Park just west of Carrizozo provides an opportunity to explore a lava flow and some of the wildlife that make this unique geological feature home.. The Mesilla Valley Bosque State Park and the Bosque del Apache National Wildlife Refuge provide opportunities to experience some of the pre-industrial agriculture, river valley ecosystems and see many of the wildlife species that winter along the Rio Grande. The newly protected Organ Mountain – Desert Peaks Reserve offers a variety of desert mountains including extinct volcanos, the steep and rugged Organ Mountains, the fossil rich Reblado Mountains and the diverse landscapes of the Uvas Mountains.

Climate and Weather Patterns

Precipitation.-

In deserts all living things owe their existence to their ability to obtain water, conserve water or to survive for long periods with very little water or even no water. The availability of water for most desert organisms is dependent upon rainfall and the characteristics of rainfall in a given geographical area. In basin and range area, air masses moving across the landscape rise, cool and condense as the air mass bumps up against a mountain range. This is referred to as an orographic effect. As the air rises and cools, orographic clouds form and serve as the source of the precipitation, most of which falls upwind of the mountain ridge. For some narrow mountain ranges the cloud build-up and precipitation affects both the upwind and downwind slopes of the mountains. The orographic effect of desert mountains results in higher rainfall on desert mountain slopes than in the flat basins.

The timing or season of rainfall, the amount of rain, and the time interval between rains events govern germination of seeds, flowering of perennials, and reproduction of animals. In the northern Chihuahuan Desert, the average rainfall is around 9 inches per year with about 60% of that amount falling in July through September as convectional thunder storms. This is often referred to as the monsoon season and many of the storms are of short duration and very intense. Intense rainfall at a rate of more than 1 inch per hour results in lots of run-off and low rates of infiltration into the soil. Such rainfall events also result in flows in the arroyos (dry stream beds). Although the average rainfall is around 9 inches, we have recorded annual rainfalls as high as 20 inches and as low as 3 inches. For many of the plants and animals of the Chihuahuan Desert the extremes in rainfall and temperature are more important than average as a determinant of their growth and long-term survival.

Average rainfall is not an accurate measure of effective moisture. Storm depth or amount of rain delivered in an event is an important consideration. During the summer months, a rainfall event of less than 0.15 inches is lost by evaporation before the water can infiltrate into the soil where even shallow roots can access the moisture. There are years when most of the summer rain events produce less than 0.1 inches and even when the sum of the rain events is around 5 inches, there is very little effect on the plants and animals. Winter rainfall is less predictable than summer monsoonal rainfall and sufficient winter rainfall to produce spring flowers occurs sporadically with intervals several years with no spring annual flowers. Winter rainfall in the Chihuahuan Desert is primarily from frontal storms than originate in the Pacific Ocean off the west coast of the U. S.. Because the Chihuahuan Desert is inland and separated from the coast by high mountain ranges (Sierra Nevada in the U. S., Sierra Madre Occidental in Mexico) many of the winter fronts bring only clouds and wind. Even small winter rain events of less than 0.1 inches tend to be effective because lower temperatures result in low evaporation and winter frontal storms are generally very low intensity.

The clear skies of arid regions are the primary reason for large daily fluctuations in temperature. During the day some fraction of the energy of the sun is absorbed by the soil and vegetation. The amount of energy absorbed is a function of the texture of the surface and the color of the surface. After sunset, energy is re-radiated into the black sky and long wave (infra-red) radiation. The rate at which the stored energy is lost by re-radiation depends on the temperature of the surface or object and the clarity of the atmosphere. Because the skies are very clear most of the year, there are large daily fluctuations in temperature. June is usually a dry hot month with frequent daytime peak temperatures exceeding 100 F. However in June, air temperatures at dawn range from the low 60’s F to low 70’s F. Relative humidity of 30-50 % at sunrise frequently falls to 5-10% or less at mid-day. The lower relative humidity in the middle of the day is not the result of less water in the atmosphere. The amount of water required to saturate the atmosphere increases exponentially as atmospheric temperature rises. Since relative humidity is the fraction of the water needed to saturate the atmosphere at a given temperature, the same amount of water results in much lower relative humidity as air temperature rises.

The build-up of convectional clouds July through September results in fewer days than reach or exceed 100 F and early morning temperatures in 70’s F. The large daily temperature fluctuations also characterize the winter months. December through February there are many mornings when temperatures are below freezing. However most days in winter, mid-day temperatures reach the mid-40’s to mid-50’s. Temperatures below freezing for more than a few hours in the early morning are rare. Extreme winter events such as more than 2 days with high temperatures below freezing can result in death of above ground growth of some plants such as mesquite in the intermountain valleys where cold air settles. Cold air is denser than warm air and tends to move down-slope into the valleys. Students were frequently surprised by how much warmer it was at night on the upper piedmont slopes than around the edges of a playa lake at the base of a watershed. The students experienced the variability of temperature environments that occur as a function of the elevation of landscape units relative to nearby mountain ranges. The reason for the colder night-time temperatures at the lowest elevation of a watershed is that cold air is denser than warm air. The air at higher elevations cools rapidly after sundown and that cold air drains down slope and settles in the valley at the lowest elevation of the watershed (or airshed).

Desert Landscapes

The desert southwest is known for its panoramic vistas. The basin and range topography interacting with the climate establishes the patterns of soil and vegetation that characterize the watersheds and landscapes of the desert. Most of the mountain ranges in southern New Mexico are oriented north-south on the long axis. The watersheds of these mountain ranges may drain into large river drainages such as the Rio Grande, Pecos, and Gila or may drain into closed basins with no outlet to the river system. The lowest elevations of internal drainage basins are dry, ephemeral lakes known locally as playas.

From a vantage point on the toe slopes of the mountains, you can get a clear picture of the landscape and see some of the features of the watershed that determine the soils and vegetation patterns. The characteristics of the soils of a watershed are largely determined by the origin and structure of the mountain range that is the source of the alluvium that forms the hill-slopes and valley floor. Alluvium refers to water-born materials that were eroded from mountain slopes. Mountains that form by crustal uplift and warping expose sedimentary rock to weathering. The San Andres mountains on the east side of the Jornada basin are sedimentary rock with layers of gypsum, calcium sulfate, which when eroded forms gypsic soils on the low elevation deposition areas of the basin. This same feature of the San Andres Mountains is the source of the gypsum that forms the dunes of the White Sands National Monument in the Tularosa Basin. Many of the mountains in the deserts of southern New Mexico are volcanic extrusions of granites. The large mountain at the northern edge of the Dona Ana Mountains, Mt. Summerford, is made of a type of monzonite granite. This monzonite weathers and erodes into coarse sandy gravel. The toe slopes of this mountain are sandy soils that support several species of desert grasses. This can be seen in the aerial photo of Mt. Summerford where the toe slope apron is light tan (senescent grass) that merges into the green of creosotebush. Most of the Dona Ana Mountain complex is composed of rhyolites. Rhyolites are igneous, extrusive rock with very high silicon contents. When rhyolites weather, the stone fragments have relatively sharp edges and tend toward rectangular shapes. The rocks of mountain ranges affect the chemical nature of the soils that develop as the weathered products of the rocks. The physical nature of the soils of basin and range desert landscapes is the result of erosional processes.

Virtually all of the landscape features of the northern Chihuahuan Desert have been shaped in part by changes imposed by the livestock industry. For example, the lower slopes of the Dona Ana Mountains and San Andres Mountains were desert grasslands in the late 1850's. The combination of seasonal drought and grazing pressure resulted in loss of grass cover and increase in shrub cover. Loss of grass cover exposed soil on sloping terrain to erosion during intense convectional (thunder storms) storms typical of this region. Intense rainfall produces sheet-flow across the surface. Light weight soil particles such as clay, silt, and fine sand are transported down-slope as suspended sediment. Heavy materials in the soil such as rock fragments remain in place or are moved very short distances. Over time, the heavy fragments known as lag materials form a surface layer that is called a desert pavement. The desert pavements in the northern Chihuahuan Desert are recent features of these landscapes. We know that desert pavements are recent features because the rocks lack the surface patina known as "desert varnish". Desert varnish is a thin red to black coating found on exposed rock surfaces in arid regions. The color of rock varnish depends on the relative amounts of manganese and iron in it: manganese-rich varnishes are black; manganese-poor, iron-rich varnishes are red to orange; those intermediate in composition are usually a shade of brown. Varnish surfaces tend to be shiny when the varnish is smooth and rich in manganese. Desert varnish consists of clays and other particles cemented to rock surfaces by manganese emplaced and oxidized by bacteria living there. These microorganisms are able to take manganese out of the environment, then oxidize and fix it onto rock surfaces: a process that requires several millennia.

In sloping terrain, the velocity of sheet-flow run-off decreases as the slope angle is reduced. When sheet flow velocity is reduced the heavier suspended sediments are deposited. The sand fraction of suspended sediments is deposited first and the silt and some clay fractions are deposited on the lowest slope surfaces. Run-off water that accumulates in a drainage basin retains some of the clay from the run-off water and that clay is deposited as the basin dries.

The soils from the toe slopes of mountain ranges to the drainage basins therefore occur in the general sequence: coarse sands, sands, sandy loams, loamy sands, loams, and basin clays. Loams are soils that generally contain approximately 40% sand, 40% silt and 20% clay. The texture of soils is a primary determinant of water infiltration, resistance to evaporation and water storage. These variables are factors that determine what kinds of plants can grow and survive on the landscape. Soil texture is also a factor in the availability of water to plant roots. In sand and sandy loam soils, free water in the capillary spaces between sand grains moves readily into plant roots because of the favorable diffusion gradient. In soils with relatively high clay content, water molecules are bound tightly to the clay particles because clay particles have electrostatic charges on the surfaces of the particles that bind water molecules. Water molecules are like tiny magnets where the oxygen part of the molecule has a slight negative charge and the hydrogen parts of the molecule have a slight positive charge. The electrostatic charge characteristics of water molecules interact with the electrostatic charged surface of clay particles to bind the water to the clay. Clay bound water does not move into roots of most plants.

The geology of the mountain ranges in the Chihuahuan Desert is a determinant of the kind of soil that develops in the drainage basins or on the alluvial (eroded materials) slopes. One striking example of that relationship is the gypsum sand dunes that are included in the White Sands National Monument in the Tularosa Basin. The white gypsum dunes are formed from gypsum crystals that form in Lake Lucero. Lake Lucero's water originates as run-off from the faulted side of the San Andres Mountains that are west of the White Sands National Monument. Layers of gypsum (calcium sulfate) are part of the exposed sedimentary rocks that are eroded by intense rainfall and the source of gypsum carried by the water into Lake Lucero.

The mountain ranges in the Chihuahuan Desert may have volcanic origins and be mainly granitic rocks or be sedimentary mountains that are sources of sandstones, mud stones, limestones and a variety of other rock developed from buried sediments. On the west side of the San Andres mountains, the layers of sedimentary rock not as obvious as on the fault-block east side. The slopes on the west side of the San Andres Mountains are not steep and water coming off those slopes is not as erosive. As a consequence, there are large accumulations of gypsic (high calcium sulfate content) soils on the east side of the Jornada Basin, but no white sand. The gypsic soils are clay loams that become extremely slick when wet.

An aerial view of a closed basin landscape on the Chihuahuan Desert Rangeland Research Center with Mt. Summerford on the upper left and other peaks in the Dona Ana Mountains at the back of the photo. The dark green areas are dominated by creosotebush, *Larrea tridentata*. The green ring around the ephemeral lake basin is a dense stand of mesquite, *Prosopis glandulosa*. The foreground is grassland with scattered mesquite shrubs and is the southern extension of the Jornada del Muerto plain.

Other important features of the soils of Chihuahuan Desert landscapes are caliche layers. Caliche is a calcium carbonate precipitate that forms from calcium in the soil, carbon dioxide and water. The carbon dioxide from microbial respiration combines with water to form bicarbonate or carbonic acid. When either of these compounds contacts calcium atoms, calcium carbonate is formed. Since the calcium carbonate is not water soluble, it is not carried to the surface as water is moved along an evaporation gradient. Over time the calcium carbonate adheres to small pebbles and stones and eventually forms a cemented layer in the soil. The test for caliche is to break off small pieces of the cemented layer and drop them into a weak acid. The calcium carbonate will immediately begin to fizz as carbon dioxide is released from the caliche flakes.

A soil profile from the Jornada basin showing the variation in depth of the caliche layer. Caliche layers develop at various depths in the soil depending on the average depth of rainfall infiltrating into the soil profile. Variation in the upper surface of caliche is dependent upon the roots of plants like mesquite. Growing root tips can produce weak acids and penetrate into caliche layers.

Other Important/Unique Landforms

There are many lava fields scattered throughout the Chihuahuan Desert. Many of these lava fields are relatively old (250,000 to 750,000 years old. Lava fields may cover hundreds of acres with patches of soil and vegetation within the rough basalt rock terrain. Deep fissures or “islands” within lava walls that are several meters in height provide habitat for native vegetation. Because lava flows are old, animals living in the lava fields tend to be darker or melanistic (black coloration). Examples of animals that have evolved melanistic coloration are several species of rodents, several species of lizards, and one rattlesnake species: the western diamondback.

Mormon tea shrubs (*Ephedra trifurca*), bush muhly grass (*Muhlenbergia porteri*), and annual grama grasses on a basaltic plain in the interior of a lava flow.

Other Important/Unique Landforms

There are several important and somewhat unique landforms in northern Chihuahuan Desert that are different from the typical piedmont (soils derived from material eroded from the mountain slopes) watersheds derived from volcanic granites.. Some valleys within desert mountain ranges tend to have shallow soils and in some areas exposed bed rock. There are a number of extinct volcanic cones some of which have associated solidified lava flows. Voids within lava flows have soils that were present when the lava flowed out across the landscape. Depressions and fissures within the lava accumulate wind transported soils over time which allows for vegetation to establish. In the Tularosa Basin, the high gypsum (calcium sulfate) in water run-off from the San Andres Mountains settles in the basin of Lake Lucero. Evaporation from the lake exposes large gypsum crystalline structures that erode. The granular gypsum from the lake forms pure gypsum dunes. The eastern part of these dunes is the location of White Sands National Monument.

River Basins

River valleys are important features of the Chihuahuan Desert. Two major river systems (the Pecos and the Rio Grande) cut through the United States portion of the Chihuahuan Desert. The Pecos empties into the Rio Grande in west Texas and forms the eastern boundary of the Chihuahuan Desert in the U. S. A. The sources of these rivers are in the southern Rock Mountains in Colorado. Before European colonization, the river valleys were dominated by cottonwood gallery forests, marshes and oxbow lakes and in the north were home to a number of pueblos of Native Americans. These river valleys are now predominately engineered agricultural landscapes with very small patches of cottonwood woodland. Human settlement brought with it non-native trees, some of which have taken over much of the non-tilled lands of the Rio Grande and Pecos valleys. One of these introduced trees, tamarisk or salt cedar has become the scourge of these valleys as it replaces cottonwoods and occupies wet meadows. Efforts to control this plant have proven to be expensive and short term. Because tamarisk concentrates salt in glands on the leaves, the soils under the tree develop salt crusts as the salts are released from the decomposing leaves. In the Chihuahuan Desert region, the small patches of valley floor that are not tilled have a cover of desert salt grass (*Distichilus spicata*.) and salt cedar with few cottonwoods or other native trees.

The vegetation associations that characterized Chihuahuan Desert river valleys prior to European settlement and the construction of dams, were cottonwood gallery forests, marshes and oxbow lakes. Large reservoirs allowed the river valleys to be engineered to facilitate irrigation. The valleys are now criss-crossed with irrigation water delivery canal systems and irrigation water return drains that carried excess irrigation water and salts back to the river. Irrigation return drains held water all year during the 20th century and the banks of the return drains were populated by scattered cottonwoods and Gooding's willows, some tamarisk, and several species of riparian shrubs (coyote willows, wolfberry, arrow-weed, sumac, screwbean mesquite and honey mesquite). The return drains provided habitat for a few medium-size mammals (skunks, rabbits, raccoons and muskrats) and for several species of breeding birds (red-wing blackbirds, snipe, common moorhens, coots, and Gambel quail). During the winter months, the drains were critical habitat for both altitudinal and latitudinal migratory birds. The most abundant winter migrants inhabiting the return drains and associated vegetation were white-crowned sparrows, Brewer's sparrows, savanna sparrows, and song sparrows. Data from Audubon Christmas Bird

Counts regularly recorded 40-50 species of winter migratory birds that used the return drains as their primary habitat.

Racoons in a riparian area. The stems in the background form a dense stand of coyote willow.

During most of the 20th century, most of the irrigated agricultural lands of the desert river valleys were planted in cotton. Minor crops included onions, lettuce, chili, and alfalfa. In the 1980's several large dairy operations moved into the area on the periphery of the valley. The dairies caused significant acreage to be converted to production of fodder for the dairy industry (corn and alfalfa). Also in the 1980's the lower price of cotton on the world market caused many farmers to convert their fields to pecan orchards. In the late 1980's and early 1990's, birds that had been absent or rare in the Christmas bird counts, exhibited explosive increases in populations. White-wing doves went from the occasional bird to the thousands of individuals coincident with the increased acreage of pecan orchards in the valley. White-wing doves nest in trees and produce multiple clutches per year. These characteristics provided the population numbers that led to the Mesilla Valley Christmas bird count (a 5 mile radius circle centered in Las Cruces, N. M.) having the largest number of white-wing doves of any location in the U. S.. The large numbers of white-wing doves is one effect of the changing cropping patterns in the desert river valleys. Another bird species, American Crows, now dominate the winter migrant numbers in the Rio Grande valley. Large flocks of crows in the hundreds and even thousands roost and feed in the pecan orchards much to the dismay of growers. The shift in cropping pattern from annual crops to perennial orchards has resulted in major changes in the avifauna of the desert river valleys.

A decade of low snow pack years in the southern Rockies, has contributed to declines in abundance of most native fauna that inhabit the desert river valleys and marked declines in the abundance of most of the winter migrant birds. When water releases from the dams on the rivers is reduced to one or two months, farmers have to pump ground water to keep their orchards and other crops alive. This pumping has resulted in dropping ground water levels. Depletion of ground water has resulted in dry irrigation return drains, dry ox-bow lakes, and dry river beds. In the years before extensive ground water pumping, the river beds retained at least some pools of water during the non-irrigation season. Now the only source of water in the river is the treated water from the Las Cruces waste water treatment plant. If dry conditions continue in the southern Rockies for another decade or two, the face of agriculture in these desert valleys is certainly going to change and that has important implications for all of the wildlife that depends on these valleys for winter migrant habitat and for breeding populations.

River valley marshland with cottonwoods in the background plus small cottonwoods and interspersed in the reddish salt cedar (*Tamarisk* spp.) in winter with sandhill cranes in the center of the photo.

Tamarisk flowering (photo by Al Krueger)

Screwbean Mesquite in flower with the screwbean fruits. (Photo by Al Krueger)

Vegetation Associations

Intermountain basins in the U. S. Chihuahuan Desert have several component grassland associations. Some of these grasslands, like tobosa grass (*Pleuraphis mutica*) remain as relatively intact associations because of the coarse nature of the dominant grass. Tobosa grass has high silicon contents and is generally only grazed by livestock when there is new green growth. The senescent stems of the tussocks protect most of the green growth from being eaten. Tobosa grass swales are generally found in the lower locations of watersheds where there is higher soil moisture from run-on and on fine textured soils. Some shrubs found in tobosa grass swales include a few mesquite and in some locations small leaf sumac (*Rhus microphyllum*) and Mormon Tea (*Ephedra trifurca*) establish at the edges of the swales. Another grassland association, alkali sacaton (*Sporobolus airoides*) found in low lying areas where the run-on water originates on hillslopes with gypsum or other high mineral content outcrops. Soils of alkali sacaton swales are also fine textured with relatively high clay content.

A tobosa grassland on fine textured soils of a run-on area at the base of a desert watershed. Note the ring of shrubs at the horizon and a soap tree yucca at distant edge of the grassland

Sandy soils on lower piedmont slopes and in the intermountain basins have desert grassland associations that consist of a mix of grasses dominated by black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.) and three-awns (*Aristida* spp.). The percent cover of these grasses varies considerably depending upon the abundance of mesquite and other shrubs within the grassland matrix, position on the landscape and soil type Soaptree yucca (*Yucca* *elata*) is a typical component of Chihuahuan desert grasslands. Soaptree yucca abundance varies from less than 5 plants per acre to more than 100 plants per acre. In addition to mesquite, some of other shrubs include Mormon tea, and snakeweed. One shrub species that has been reduced to mere skeletons in areas that were grassland that are now mesquite or tarbush shrubland is Torrey Ephedra (*Ephedra torreyana*) a species of Ephedra that is palatable to livestock and rabbits. In studies where we protected Torrey Ephedra plants from rabbit browsers and cattle, the heavily pruned plants that were essentially woody stems with very sparse green leaves and were four inches or less in diameter before protection, increased in size to between twenty inches and thirty five inches in diameter and more than twenty inches tall within two years.

A desert grassland in a basin. The dominant grass is black grama (*Bouteloua eriopoda*) with mesa dropseed (*Sporobolus flexulosus*) the bright yellow thick stemmed grass in the lower left. Soaptree Yucca (*Yucca elata*) and Mormon tea (*Ephedra trifurca*) are the green plants within the grassland.

Desert zinnia (*Zinnia acerosa*) a common small woody plant on hillslopes in the northern Chihuahuan Desert.

Tobosa grass – burro grass (*Scleropogon brevifolia*) association with tarbush (*Flourensia cernua*) shrubs in the foreground.

Tarbush (*Flourensia cernua*) is another shrub that is characteristic of the Chihuahuan Desert. Tarbush is found on valley plains and mesas at elevations from 2500 feet to 6000 feet. Tarbush is a multistemmed shrub that varies between 1 foot and 7 feet in height. Tarbush plants in the northern Chihuahuan Desert are rarely taller than 4 feet. In the Mexican Chihuahuan Desert there are areas dominated by large tarbush that average around 7 feet in height. Tarbush is evergreen in years when there are no hard winter freezes. Tarbush loses its leaves following hard freezes with temperatures of 5 F or lower. After hard freezes, several stems of each plant may die and fail to produce leaves in subsequent growing seasons (see the tarbush shrubs in the photograph).

Tarbush occurs in low numbers in creosotebush shrublands on shallow well-drained soils. In creosotebush shrublands tarbush is frequently associated with small to large drainage channels. On lower piedmont slopes where there are deeper finer textured soils, tarbush can account for between 10% and 39% of the shrubs.

Mesquite coppice dunes are recent landscape features of the northern Chihuahuan Desert. A coppice is defined a grove or thicket of trees or shrubs. Mesquite dunes are called coppice dunes because of the thicket of stems protruding from the crest of the dune. Dunes form around one or more small mesquite shrubs with dense branches. Winds erode sand from downwind areas. The moving sand is captured by the branch network of the mesquite and is deposited around the base of the shrub(s). As more and more sand is accumulated, the buried mesquite branches form adventitious roots that produce a root network within the dune. Because only the terminal sections of the branches are above the crest of the dune, these branches form a relatively short, uniform height, coppice.

A mesquite coppice dune with a Mormon tea on the left, mesa dropseed grasses in the foreground and the coppiced mesquite with flowers.

Valleys within mountain ranges support a mixture of desert grasslands plus some small trees and shrubs. One-seeded Juniper (*Juniperus monosperma*) is the most common tree in montane valley grasslands. In some desert mountain areas there are Arizona oak (*Quercus arizonica*) and Emery oak trees (*Quercus emeryi*) in addition to junipers. Shrubs that are limited to higher elevation montane areas include grey oak (*Quercus grisea*) and turbinella oak (*Quercus turbinella*).

Arroyos (dry stream channels) are characterized by several plant species that are only found in or at the edges of arroyos but other more widely distributed species contribute to the vegetation association on the margins of the channels. Many channels support dense thickets of Apache Plume (*Fallugia paradoxa*), some small trees such as desert willow (*Chilopsis linearus*) and netleaf hackberry (*Celtis reticulata*). Chihuahuan Desert arroyos support one tree, the desert willow, and one shrub, brickell bush (*Brickellia lancinita*) that are obligate arroyo species. Obligate arroyo species are found only in arroyos and may establish in the middle of a dry stream bed channel. The other species of shrubs found at the margins of the arroyos we studied were: Apache Plume, honey mesquite, tarbush, creosotebush and small leaf sumac (*Rhus microphylla*). Arroyos are dynamic features of desert landscapes. The force of flowing water erodes banks and changes channel locations. During flash floods some of the plants growing at the edges of the channels may be uprooted and carried down-stream and deposited on the lower slopes where the velocity of the flood waters are reduced. When arroyos change channel locations, the new channel cuts may incorporate non-obligate plant species into the arroyo margin vegetation

Apache plume flowers. Note the dense stems and small leaves of Apache plume.

Several other plant species dominate specific patches in Chihuahuan Desert landscapes. Some of these patches may result from human activities. For example, cane cholla (*Opuntia imbricata*) forms dense patches in some locations where cattle "camp" near a water source. Cane cholla can establish from joints that are knocked from the stems of this cacti by cattle brushing up against the plant. If the joints fall on bare soil, roots will develop on the underside of the broken joint and produce another plant. I have seen cane cholla joints sticking to the hide of cow by the thorns on the cactus joint. When such cholla joints become dislodged, it is probable that this joint will produce another cane cholla plant.

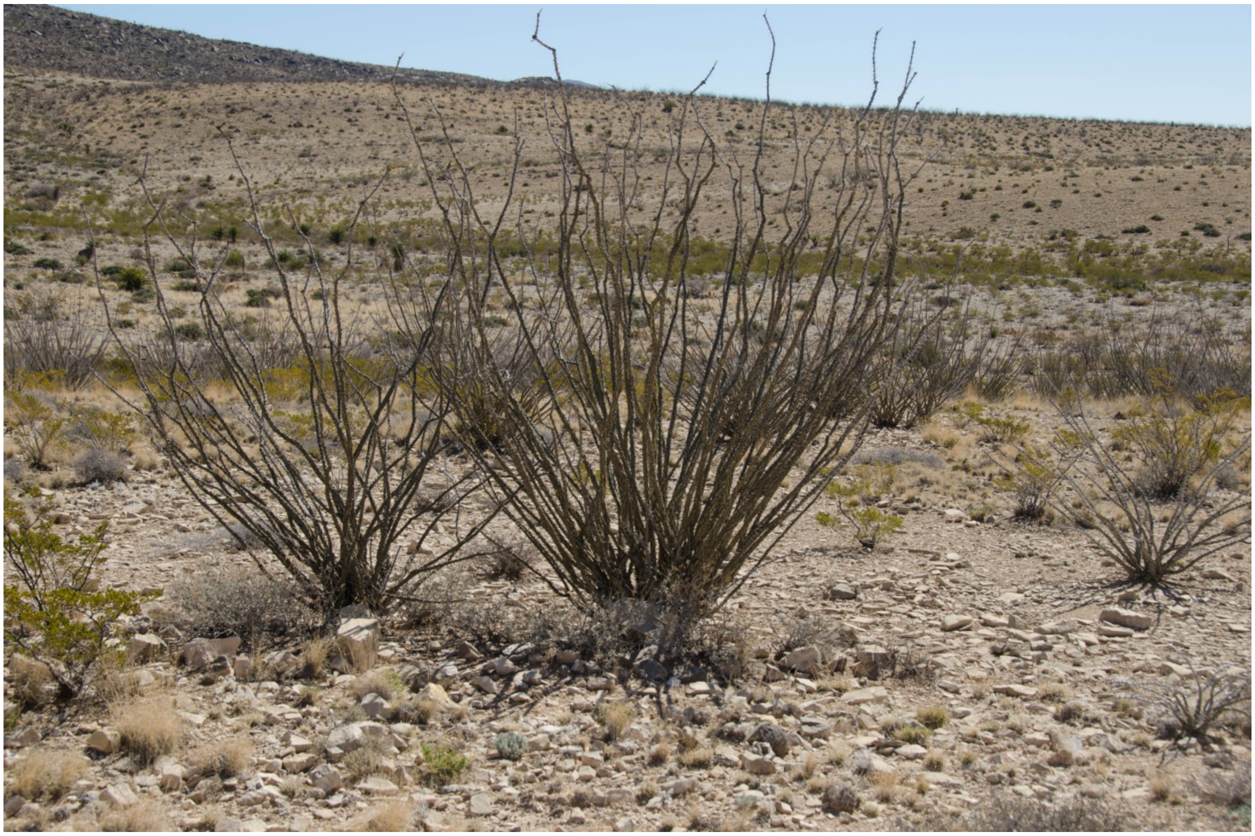
Sotol (*Dasylirion Wheeleri*) with Resin-leaf white thorn (*Acacia neovernicosa*) behind the sotols on the left of the picture. These plants are large components of the sparse grassland on toe slopes of desert mountains.

Higher elevation foothills of desert mountains have several vegetation associations that differ from the lower piedmonts. In some areas, there are dense stands of sotols along with one or two species of *Acacias*. The understory in such areas tends to be a grassland with several of the desert grasses plus blue grama, hairy grama, and side oats grama. These grama grasses tend to be the most abundant grasses along with three awns and annual grasses.

Resin-leaf white thorn (*Acacia neovernicosa*) in flower following monsoon summer rains.

Two species of white thorn acacias (*Acacia nevernicosa* and *Acacia constricta*) form dense thickets on some ridges in the Chihuahuan Desert. However, in most areas white thorn acacias are sparse and generally associated with rills and small drainages.

Patches of ocotillo are scattered throughout the Chihuahuan Desert. Much of the year this plant is leafless. Grooves in the bark on the stems of ocotillo are green which allows this plant to carry on photosynthesis in the absence of leaves. Ocotillo responds rapidly to summer rain events by producing leaves at each spine node. The leaves remain on the plant while there is sufficient soil moisture. As the soil dries out, ocotillo leaves abciss and fall off. If summer rains are scattered with intervals of no rainfall, ocotillo may produce several cohorts of leaves in a single growing season. Dr. Keith Killingbeck has studied this enigmatic plant for thirty years and has learned some surprising things about ocotillo. Ocotillo stem segements that had no connection to roots produced leaves when wet. None of the stem segments produced roots in the entire three years of the experimental study. In addition, stems that were defoliated five times still produced leaves at ninety percent of the nodes.



Octillos in winter. Location on a hill crest with scattered limestone rocks

Ocotillos in May after a wet winter season. Note ocotillo leaves and some flowers and seed pods.

In the Chihuahuan Desert, Ocotillo produces flowers and fruits in mid-April to mid May regardless of the amount and distribution of winter rainfall. In years with adequate winter rainfall, Ocotillo may produce leaves and flowers at the same time whereas in years with less rainfall, Ocotillo flowers without producing leaves.

Succulents

Succulents are plants that store water in stem or leaf tissues. Prominent among the succulents in the Chihuahuan Desert are cacti and agaves. Prickly pear cacti are relatively abundant on well drained soils (gravelly to sandy soils). In some places the green prickly pear cactus (*Opuntia phaeacantha*) is so dense that it appears as a monoculture. One location where green prickly pear cacti occur as a monoculture is on a south facing slope on a stony-gravel soil. Another prickly pear, the purple prickly pear, is fairly common in creosotebush uplands. In creosotebush habitats large clumps of green prickly pear are established at the edges of small arroyos and provide suitable habitat for pack rat middens.

Agaves are important succulents in the Chihuahuan Desert. *Agave lechuguilla* is a common succulent of the Chihuahuan Desert. It grows on most soils and forms thickets or dense stands because it spreads by shoot from shallow stoloniferous roots. *Agave lechuguilla* needs to grow for fifteen years or longer in order to store sufficient starch reserves in the core to produce a flowering stalk. Dense stands of *Agave lechuguilla* grow on the slopes of the Franklin Mountains north of El Paso, Texas where it forms large clumps among scattered creosotebushes. Another common agave in the Chihuahuan Desert is *Agave parryi*. This agave grows as solitary plants or clumps generally on hillslopes. Clumps of *Agave parryi* develop by vegetative growth from sprouts that develop on the stoloniferous roots.

Agave parryi growing among dead creosotebush stems. (Photo by Al Krueger),

Some succulent cacti are chewed off and eaten by rabbits or rodents soon after germinating or in early growth stages where the plant is less protected by spines. The Desert Christmas Cactus is an example of such a plant. However, if Christmas cacti germinate under creosotebushes they may escape being chewed off by herbivores. The creosotebush shrub acts as a "nurse plant" providing a nutrient enriched, higher water content soil, and shade that enhances the growth of the cactus. The down-side of this relationship is that after attaining some growth, the cactus and creosotebush are competing for limited resources, especially water. The creosotebush "nurse plant" relationship is not limited to succulents. In the Jornada Basin, most bush muhly grasses grow under creosotebush. There are several examples of areas where after creosotebushes were killed by herbicide treatment, the bush muhly grew rapidly to more than twice the diameter of bush muhly tussocks under live creosotebushes.

A Pencil Cholla or Desert Christmas Cactus that exhibited expansive growth following death of the “nurse plant” creosotebush that was killed by herbicide. Note the tussocks of bush muhly in the background. Bush muhly exhibit expansive growth after the creosotebush “nurse plant” is killed. See bush muhly in a live creosotebush (photos by Amilee Pasco and Al Krueger)

A Desert Christmas Cactus growing within the canopy of a live creosotebush “nurse plant”.

Yucca torreyana on a creosotebush piedmont slope.

Mountain slopes that are arid because the structure of the mountains do not intercept moisture laden clouds to generate a significant orographic effect, support small trees such as grey oak (*Quercus grisea*) and turbinella oak (*Quercus turbinella*) plus one-seed junipers (*Juniperus monosperma*) plus small shrubs and sotols (*Dasylirion wheeleri*). These vegetation associations are found on the slopes of many mountains in the Chihuahuan Desert.

Creosotebush-grass bajada transitioning to a mountain slope with Junipers (*Juniperus monosperma*) and stools (*Dasylirion wheeleri*) plus grass tussocks in areas with some soil interspersed among the rocks.

The Remarkable Creosotebush

Many areas in the northern Chihuahuan Desert are dominated by an evergreen shrub called creosotebush (*Larrea tridentata*). This remarkable plant is found in all of the hot deserts of North America. It is a dominant plant in the Mojave Desert of Nevada and California where it thrives on less than three inches of winter rainfall. Compare this to the widespread and abundant creosotebush in the northern Chihuahuan Desert where most of the annual rainfall is in the form of thunder storms during the months of July, August and September and you begin to have an appreciation for the adaptive plasticity of this plant. The common name, creosotebush, was probably applied to this plant because of the distinctive odor of the leaves when crushed. The odor is derived from a large number of volatile oils on the leaves. The importance of these chemicals to the creosotebush as deterrents to insects that chew on leaves is an important adaptation for an evergreen desert shrub.

In the Chihuahaun Desert of southern New Mexico, creosotebush densities (number of shrubs per acre) range from as few as 100 per acre to more than 3400 per acre. The density of creosotebush shrubs is related to the depth of soil to the caliche layer and other soil factors that modify the distribution of water and nutrients. A caliche or calcrete layer is a cement-like hard pan that is composed of calcium carbonate (the stuff of limestone). Soil depth to the hardened caliche is related to the average depth of water infiltration into the soil. The caliche acts as a barrier to water movement and the roots of plants like creosotebush tend to grow laterally at the surface of the caliche. However the roots of some plants find voids in the calcrete and grow into the soil below the cemented barrier.

Creosotebushes are cool-season evergreen shrubs. Cool-season refers to the characteristics of shrubs that use the C_3 photosynthetic pathway which is characterized biochemically by the fixation of CO_2 into a three carbon compound. While the biochemical details of photosynthesis are not necessary to appreciate the adaptations of creosotebush, the physiological traits of C_3 shrubs are important in understanding the adaptations of the shrubs. Individual creosotebush shrubs are a conglomerate of mixed-age stems that grow and die at different rates. Stems of different ages are frequently physiologically isolated from other stems of the same plant.

The optimal temperature for photosynthesis and growth for C_3 shrubs is around 25^oC or approximately 75^oF and their photosynthetic apparatus reaches light saturation at one fourth of full sunlight. These physiological characteristics allow for early spring growth and flowering of creosotebushes. The relatively low optimal growth temperatures and low light saturation cause creosotebushes to “face” the southeast. By facing southeast the largest surface area of the leaves are intercepting maximum sunlight during the early morning hours when environmental temperatures are conducive to photosynthesis. Also during mid-day when ambient temperatures are highest and solar radiation most intense, the leaves of the southeast facing creosotebushes are exposing the smallest leaf surface to direct sunlight. Another advantage of catching the early morning light for photosynthesis is that the stomates (small pores in the leaf epidermis) are open during the time of highest humidity for the day. Stomates are opened and closed by the action of guard cells which surround the stomata. Stomates must remain open for carbon dioxide to diffuse into the cellular structures in the middle of the leaves. When stomates are open, water diffuses from the leaf into the atmosphere. The rate at which water is lost through the stomates is directly related to the relative humidity of the air at the leaf surface. By facing southeast, creosotebushes not only optimize photosynthesis, they reduce water losses.

Rainfall Patterns, Nitrogen, and Growth

Creosotebush shrubs exhibit variable growth patterns. Early spring growth and flowering varies with the distribution and amount of winter precipitation. We found that growth patterns in summer were not as clearly related to rainfall distribution and amounts of rainfall. When creosotebushes were fertilized with ammonium nitrate, stem elongation and foliage production was significantly higher in fertilized shrubs than unfertilized shrubs. We concluded that Chihuahuan Desert creostebush shrub growth was limited by nitrogen as well as by soil moisture. Also the growth responses were very variable among shrubs and we concluded that this variability was a function of the interaction between rainfall and soil fertility.

In order to examine the effects of the interaction between rainfall patterns and nitrogen availability on growth, we set up a field experiment in which we applied sprinkler irrigation to simulate rainfall and applied ammonium nitrate to shrubs in half of each plot. We applied simulated rainfall in two patterns: relatively frequent small applications of 0.25 inches each week, and large applications of 1.0 inches per month. We measured increases in length of marked stems to evaluate growth of the shrubs. Stem elongation is only a measure of increase in size of the canopy but does not account for the increase in diameter of stems, hence is only partial indicator of change in biomass. Changes in stem diameters of this shrub were too small for accurate measurements, therefore we concentrated on measuring increase in canopy size.

Canopies of shrubs receiving simulated weekly small storms were much larger than the canopies of shrubs receiving the same amount of water in a single event and the shrub canopies of both of these treatments exhibited more growth than the shrubs receiving only natural rainfall. Stem elongation of shrubs that were fertilized with nitrogen were larger by the same amount in each of the rainfall simulations. The results of this study together with reports of root distribution of creosotebush shrubs in the Chihuahuan Desert help to explain the variability in growth responses during the summer growing season. Creosotebush has extensive lateral roots in addition to deep roots that extend more than 6 feet into the soil. The lateral roots take advantage of the more frequent small storms. Large infrequent storms provide moisture to the lateral roots for much shorter time periods than frequent small storms. Water from large storms may infiltrate to deeper layers of soil and be available to the deep roots of creosotebush in the spring. Infiltration from large storms varies with the intensity of the rain (rate at which the rain falls) and a number of soil factors. Our rainfall simulations provided water at a rate of 0.25 inches in twenty minutes. At that rate, the application of 1.0 inches in one hour and twenty minutes was low enough that there was little run-off and most of the simulated rainfall water infiltrated to deep soil layers.

Creosotebushes, Water and Soil Nutrients

Not only do creosotebushes “face” in a direction that optimizes sunlight interception, these shrubs develop different shapes with age and on different soils. Bushes with relatively erect shapes, (where the external branches are greater than 45^o from the soil surface) are more efficient at channeling rain water down the stems and into the soil to the roots off the root crown. Rainfall intercepted by the leaves runs down along the stems, a process known as stemflow. Stemflow water is collected from the area of foliage of the canopy supported by a single main stem. Thus stemflow a larger volume of water than rain falling directly on the root crown.

Stemflow water on creosotebushes runs down the root crown and thence along the surfaces of root emerging from the root crown. Stemflow water channeled along the roots moves much deeper into the soil than rainfall that breaks up as it moves through the leafy canopy to the soil surface. When you examine a creosotebush with steep exterior branch angles (cone shaped), you will note that the soil surface under that shrub is practically devoid of litter (senesced or dead leaves, and small dead stems). . The ice-cream cone shaped shrubs provide little resistance to wind at the soil surface, therefore leaves, twigs, and fruits are rarely found under cone shaped creosotebushes unless there are grasses or other plants growing around or near the root crown. Even light wind can move leaves, small stems, and fruits of creosotebush. Wind tunnel studies demonstrated that the threshold wind velocity necessary to move leaves, stems and fruits was less than 5 mph. Winds more than 5 mph occur frequently in the northern Chihuahuan Desert providing the force necessary to move plant litter from under the canopy of cone shaped creosotebushes.

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Creosotebush with leaf bearing branches “facing” southeast.

Stem flow not only contributes water moving to a greater depth in the soil by root channelization, stem-flow water is enriched in several mineral nutrients. Minerals that we measured included: sulfate, potassium, sodium, magnesium, calcium, ammonium, nitrate, total nitrogen and total phosphorus. When we compared the concentrations of nutrients in rainfall with the concentrations in stemflow and through fall, the concentrations of most of these nutrients in stemflow water were 9 to 16 times higher in stemflow than in bulk rainfall with the exception of ammonium and sodium. Concentrations of ammonium and sodium were essentially the same as in bulk rainfall. Nitrogen and phosphorus are nutrients that frequently limit plant growth. We have experimental evidence that nitrogen limits the growth of creosotebush. Total nitrogen was 16 times higher and total phosphorus was 9 times higher in stemflow water than in rainfall.

Rain-water falling from and through the leaves of the canopy to the soil surface is called throughfall. The only chemicals enriched in throughfall in comparison to bulk rainfall were sulfate (by 2X), potassium (by 1.4X) and total nitrogen (by 3.4X). These chemicals are high in both atmospheric dry-fall deposition and rainfall. Minerals and chemical deposited on leaf surfaces as atmospheric dry-fall contribute to the chemical composition of throughfall water. The atmospheric dry-fall chemicals accumulating on leaf surfaces between rainfalls are chemicals that increase in the atmosphere as a result of burning of fossil fuels.

The pattern of nutrient enrichment of stemflow water is more than simple washing of dry-fall accumulations on the leaves. Careful examination of the branches of creosotebush reveals that some parts of many stems are covered with a dark-black, rough layer on the smooth gray bark. This is a black, crustose, microbial layer, dominated by fungi of the genus *Coleophoma* but which also may contain algae, bacteria, and cyanobacteria (blue-green algae). Water flowing down the stems washes over this layer picking up particulates and soluble organics that produces a reddish-brown colour of the stem flow water. Nutrients provided to the roots of creosotebush as a result of stemflow may be very important for vigorous growth and recovery from stress.

Creosotebushes that are more hemispherical in shape while less efficient at moving intercepted rainfall to root channels, represent an obstacle to wind and retain leaves, stems and fruits at the soil surface under the canopy. Development of a litter layer under a shrub provides the organic carbon energy source for soil biota that breakdown the plant litter. When the plant litter is decomposed, the essential soil nutrients such as nitrogen, phosphorus, and potassium are released to the soil. Following rains, these nutrients are dissolved in the soil water and can be absorbed by the roots of the shrub and made available to annual plants growing under creosotebushes. The nutrient rich soils under the canopies of cresotebushes and other desert shrubs have been called “islands of fertility” in a sea of low nutrient soils.

Historical Expanded Distribution

Creosotebush had a limited distribution in the late 1800’s. The pre-cattle industry distribution of creosotebush was on rocky or gravelly areas that were well drained and that supported only sparse grass cover. Today, creosotebush is widely distributed on sloping piedmont landforms and on most soils except for clay pans. Creosotebushes are found as widely scattered individuals in the grassy basins. Creosotebush fruits are primarily dispersed by surface run-off and sheet flow or by wind. The fuzzy nature of the fruits may allow some fruits to be attached to the hair or fur of large herbivores.

On the Armendariz Ranch east of Truth or Consequences, N. M. there are two isolated populations of creosotebush on small hills in the middle of the basin grassland. Both hills are near small playa lakes. The ranch manager, Mr. Tom Waddell speculated that these shrubs were from creosotebush seeds transported to the area by flocks of sheep that were moved by early shepherds into the waterless Jornada del Muerto plain during the monsoon season when the small playas had water for the sheep. The early settlers on the Armendariz land grant lived near the Rio Grande River some 20 miles from the creosotebush populations on the grassland hills. The hills were probably chosen for encampment with the sheep because the shepherds could see approaching bands of Apache from those vantage points. Their sheep could easily have transported creosotebush fruits adhering to the wool when they passed through bands of shrubs on the trek from the river to the basin grasslands.

The fungal-algal crust on a branch of a creosotebush. Note the contrast between the gray stems with no crust and the black of the crusted central stem.

Large hemispherical creosotebushes with dense growth of spring annuals (pepperweeds – *Lepidium lasiocarpum*) under the shrubs. Note the absence of the bright green pepperweeds in the barren areas between the shrubs.

The landscape distribution of creosotebush on the piedmont slopes. The creosotebush shrublands are the dark band of vegetation between the mountains and the basin grasslands. The shrubs in the foreground are mesquite. There are two mule deer in the center of the picture.

Creosote Bush Establishment

Considering the expansion of creosotebushes from bands of shrubs on the upper piedmont slopes of desert mountains into the grasslands of the lower slopes, we set up a study that examined the survival of creosotebush seedlings in three different vegetation associations on a watershed. The three different vegetation associations were: (1) a black grama grassland that had not been grazed by livestock, (2) a section of watershed that was dominated by creosotebushes on sandy soils, and (3) a mixed grass grassland that had been intensely grazed by livestock until 2 years before the study. The plots were fenced with fine mesh chicken fence to keep rabbits from eating the seedlings. We followed the fate of seventy five seedlings in each vegetation association. By the end of the first summer, most of the seedlings in the ugrazed grassland and creosotebush shrubland had died. Some of the mortality appeared to be the result of herbivory by some insect or small mammal. Most of the mortality appeared to result from unknown agents that caused atrophy of the stem just above the soil line. In the historically grazed plots, there was very little seedling mortality. By the end of the second growing season, there were no seedlings that survived in the ungrazed grassland or in the creosotebush shrubland but in the historically grazed plots approximately half of the seedlings were still alive. Fifteen years after the seedlings were planted, we returned to measure the surviving shrubs and to evaluate their effect on the environment around the newly established shrubs. The shrubs ranged in size from approximately one-half meter in height and diameter to more than one meter in height and diameter. The soils under the shrubs were bare but there was more than thirty percent grass cover in the half of each plot with no creosotebush. When we tested the aggregate stability of the soils of each half plot, the shrub-free half plots had high aggregate stability but the shrub plots had little or no aggregate stability. Aggregate stability is a measure of how the soil fungi hold soil particles together to form tiny ball-like aggregates and is an indirect measure of the status of the soil microbial community. The bare soil under the shrubs was a condition reported by research scientists in the early 1900’s in areas of recent creosotebush expansion. These scientists attributed the bare soil to allelopathic compounds (toxic to other plants) produced by creosotebush foliage that washed onto the soil. However in the same areas studied by the earlier scientists, we found that the soils under well established creosotebush shrubs supported abundant annual plants. There were no annual plant remains under the creosotebush shrubs in our establishment plots. There were lots of annual plant remains and some live annuals under the shrubs in the creosotebush shrubland upslope from the grazed grassland establishment plots and there were abundant annual plants and remains of spring annuals in the grass (no creosotebushes) halves of the plots.

In more than forty years of studying an ungrazed watershed dominated by creosotebushes, I recorded high numbers of creosotebush seedlings germinating in July and early August four times. Creosotebush germinants appeared during years of frequent rains that were between 1/4 and 1/2 inches. The area was revisited every one or two weeks and by late autumn, there were no surviving creosotebush seedlings. These observations seemed to confirm the idea that creosotebush establishment is a rare event in creosotebush communities. Creosotebush establishment in grassland requires bare patches between grass tussocks. Intensely grazed grassland is characterized by such bare patches.

One of the creosotebush establishment plots in the grazed grassland. Note the bare soil under the creosotebushes and the grass in the foreground and background.

Honey Mesquite

Two hundred years ago, honey mesquites (*Prosopis glandulosa*) were restricted in distribution to the margins of playas (ephemeral or dry lakes) and along the margins of arroyos (dry washes). Most of those mesquite were single stem, large diameter bole, trees. Mesquite began to expand into the desert grasslands soon after the Spanish introduced horses and cattle into Chihuahua and New Mexico and expansion of mesquite into the desert grasslands began when the local Native Americans gained access to horses. They carried mesquite pods as fodder for their horses. When the southwestern U. S. was surveyed in the 1850's, surveyors noted mesquite thickets in locations that were traditional encampments of Native Americans. The mesquite thickets developed from the seeds that passed through the digestive tract of horses and germinated in the dung. The mesquite shrubs that developed around Native American encampments were multi-stemmed and similar in shape to the mesquite of Chihuahuan Desert landscapes today.

Rapid expansion of honey mesquite into the desert grassland coincided with the development of windmills and deep wells. Deep wells and windmills pumped water to the surface which opened up waterless grasslands to commercial livestock operations. For example, the number of cattle on the desert grasslands of southern New Mexico increased rapidly from approximately 158,000 in 1870 to more than a million in 1886. During that same time period, the acreage covered by mesquite on the Jornada Experimental Range northeast of Las Cruces, NM increased from 4.8% to 50.3% while grassland declined from 90% to 25%. The expansion of mesquite into the grasslands is thought to have occurred because of the coincidence of overgrazing and drought. Overgrazing increased the size of bare patches in the grasslands where mesquite germinants could gain a foot-hold and mesquite establishment was high following drought periods.

The fleshy, sweet pods of honey mesquite are an attractive food for many animals ranging from ants and seed weevils to rodents and domestic livestock. In feeding trials with horses, cows and sheep, 91%, 71%, and 16% of the seeds respectively passed undamaged through the digestive tract of these animals. Germination of mesquite seeds that passed through the digestive systems of domestic livestock was high: 82% through horses, 69% through cows and 25% for seeds passing through the digestive tracts of sheep.

In a study of germination and survival of honey mesquite in a lightly grazed black grama (*Bouteloua eriopoda*), we placed dung pats with mesquite seeds at the edges of banner-tail kangaroo rat mounds and in bare patches between grama grass tussocks. We examined the germination and survival of mesquite on the edges of banner-tail kangaroo rat (*Dipodomys spectabilis*) mounds. We wanted to determine if banner-tail kangaroo rats chose to dig their deep burrow systems under the canopy of mesquite or if mesquite germinated,established, and grew faster on the mounds. In each location, we had paired dung pats with seeds, one covered by a small mesh chicken wire dome to exclude birds and rodents and the other open to all herbivores. Germination and establishment of mesquite was nearly zero in both herbivore protected and herbivore exposed dung pats on the banner-tail kangaroo rat mounds. Unprotected germinants in the grassland were cut down by rodents or rabbits. Germinants under the mesh domes stopped growing at the 3-4 leaf stage. At that stage the seedlings were probably transferring the energy from photosynthesis to the roots. Mesquite seedlings are known to put most of their energy into root growth. Greenhouse studies showed that mesquite seedling roots increased in length 10 times that of the increase in stem length.

We examined the depth of roots of mesquite in a variety of habitats: arroyo margins, dry lake margins, mesquite coppice dunes, and grassland mesquite. Multistem mesquites growing at the margins of an ephemeral lake were the tallest mesquite that we sampled (2-4 meters) and had the deepest root system. We recorded roots from drill cores of these plants at depths of more than 30 meters (more than 100 feet). Mesquite in grassland environments and at the arroyo margins had identifiable roots at depths of 10 meters (approximately 30 feet). Roots of mesquite in coppice dunes extended to unknown depths because of sand-gravel layers at 2.5-3.0 meters below the soil surface. The sand-gravel layer could not be retrieved by the hollow core drill and we were unable to evaluate the true depth of the dune mesquite roots. While rooting depth is important for mesquite, this plant also has extensive lateral roots. Excavation of mequite root systems in a grassland and in coppice dunes documented lateral roots extending 3-15 feet from the main plant. Extensive lateral roots of mesquite are common in the soil profile above the caliche layers. These shallow, lateral roots allow the plant to exploit soil moisture from summer monsoon rains. The rooting patterns of mesquite are important characteristics that allowed this species to occupy many different habitats and survive in a variety of soils and soil depths.

Coppice dunes form around mesquite plants that capture wind blown sand that is dropped under the plant. As the mound of sand builds around and over the stems of the mesquite, the buried stems produce adventitious roots (roots that develop from tissues other than the root primordial). The term coppice refers to the uniform height of the stems that protrude from the surface of the dune.

Stem Girdlers and Compensatory Growth

One of the more impressive insects of the Chihauhan Desert is the mesquite stem girdler beetle (*Oncideres rhodostica*). The stem girdler belongs to a family of beetles known as long-horn beetles (Cerambycidae). The long-horn beetles get their name from the long antennae that are characteristic of members of this family. Most members of this family are wood boring in the larval stages. The larvae are elongate, cylindrical, whitish and almost legless. The larvae of stem girdlers are round-headed borers which makes them different from other wood borers that have flat heads.

Although the adult stem-girdlers are small and not easily seen, they leave ample evidence of their presence in the form of dying branches on mesquite plants. The leaves on the stem above the girdle turn yellowish brown after the water and nutrient supply is disrupted by the girdle. The mesquite stem-girdler utilizes mesquite stems for oviposition (lay eggs) and larval development sites. Female beetles chew girdles around mesquite stems severing the phloem and xylem, disrupting water and nutrient transport, and killing the affected stem above the girdle. The beetle then oviposits distally from the girdle, which protects its egg from being coated in sap flowing up the stem in response to the girdle. Mesquite is known to produce a viscous (thick sticky liquid) sap that exudes from a wound when the stem tissue is disturbed. Female beetles girdle and oviposit in only one branch, and have been reported to lay 8.1 eggs per stem.

It has been reported that the mesquite stem girdler occurs at an average density of 4.7 beetles per mesquite plant in the Trans-Pecos region of Texas. Adult beetles kept in field cages lived only 20-30 days. The eggs hatch within one month of oviposition and the larvae over-winter by feeding on the dying mesquite stem. The larvae pupate within the stem and the adults emerge in early autumn, mate, and the females girdle fresh mesquite stems prior to the onset of freezing temperatures.

Mesquite stem girdlers are insects that have benefitted from the expansion of mesquite into the Chihuahuan Desert grasslands in the past century. The abundance of multi-stem mesquite provides an ample resource base for this beetle. While we have no density estimates of stem girdler beetles on mesquite in southern New Mexico, the high levels of stem death from girdling beetles on mesquite suggests that densities of this beetle may be as high or higher than those reported from Texas. Our early studies of mesquite stem girdlers revealed that the beetles killed stems on approximately 45% of the mesquite plants on the upper slopes of a desert watershed. More recent studies have found that in some areas, girdled stems occur on more than 70% of the mesquite shrubs in a basin grassland area.

The first detailed studies of mesquite stem girdlers focused on the potential of this insect to control mesquite. The early studies examined characteristics of the insect and its reproductive potential but provided no information on the responses of the plant to the death of stems that were girdled. We designed studies to examine the responses of mesquite plants to different levels of girdling. Our studies in the early 1970’s documented the resilience of mesquite to stem death produced by mesquite girdlers. That resilience (ability to bounce back) was the result of compensatory growth of stems from nodes below the girdle during the growing season following the girdling. Compensatory growth is the ability of a plant to make up for or more than make up for the loss foliage. The girdled stem was replaced by between 2 and 5 new branches developing below the girdle. The effect of the stem girdler on mesquite is similar to the effect of pruning orchard trees: an increase in the number of new stems which increases leaf area. Increased leaf area increases photosynthesis and increases numbers of flowers and fruits. Clearly the activity of mesquite stem girdlers is of benefit to the plant and increases its viability.

In a recent study, we examined the abundance of girdled stems on small and medium size multistem mesquites in an area where grass cover became sparser and density of mesquite increased. The girdled stems produced 3-4 new stems from nodes below the girdles. This produced plants with a high density of small stems less than two tenths of a meter above the soil surface. The dense small stems contributed to the deposition of sand at the base of mesquite plants that had evidence of high levels of stem girdling in the past. It had been well documented in earlier studies of wind transported dust and sand that wind velocity was reduced in proportion to the density of stems of plants. We concluded that girdling of mesquite stems by cerambycid beetles contributed to the formation of mesquite coppice dunes. In addition, beetles also girdle stems that form the coppice on the mesquite dunes. This contributes to the stability and growth of the dunes and the density of the coppiced stems emerging from the dunes.

Unfortunately it may be several years or decades before the cerambycid mesquite girdlers return to the Chihuahuan Desert areas of southern New Mexico and west Texas. In early February 2011, there was an extreme freezing event with temperatures as low as -25C and below freezing daytime temperatures for 3-4 consecutive days. When we revisited all of the study sites where we had recorded an abundance of girdled stems, we found no girdled stems in the time period late August through early October when most of the girdling by cerambycids occurred. During the girdling period for the next two years, we revisited the study sites and surveyed other areas in southwestern and central New Mexico with the same result. The nearest population of mesquite girdlers was located in the San Simon valley in southeastern Arizona. If the predictions of an increase in temperature extremes resulting from climate change do occur with some irregular frequency, we may find other populations of vulnerable insects experience local extinctions.

Biological control of mesquite was only one of several avenues of research designed to control mesquite in order to restore grassland productivity for the livestock industry. Much of the work by the USDA Agricultural Research Service at the Jornada Experimental Range in southern New Mexico from the 1940’s through the 1980’s focused on use of herbicides to kill or reduce mesquite on desert rangelands. None of the herbicide treatments provided long-term reduction in mesquite abundance.

A mesquite shrub with girdled branches in late September

Tell-tale yellowed leaves indicating stem that has been girdled within during the current year growing season.

A stem that was girdled one or two years before the photo was taken.

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An old girdled mesquite stem that broke open after the wood boring insects had consumed most of the wood.

Multistem Honey Mesquite as Nurse Plants

Honey mesquite appears to serve as a nurse plant for the grass (*Setaria leucophila*). In a study of seasonal grazing by livestock, we found most Setaria plants under or within the branches of multistem honey mesquite in the grazed plots and some Setaria plants not under mesquite in the ungrazed plots. In that study there were other grasses such as dropseeds *(Sporobolus* spp.) and three awns (*Aristida* spp.) that appeared to be larger and more abundant under or within the canopy of the multistem mesquite. However since mesquite are known to fix nitrogen and the leaf litter under mesquite is rich in nitrogen, it is not possible to state unequivocally that the grasses are larger and more abundant because of the “nurse” plant effect or the fertilizer effect of the decomposing leaves.

Mesquite shrub serves as a nurse plant for a grass species that is preferentially grazed by domestic livestock. The grass, *Setaria leucopila*, is primarily found on sandy loam soils in mesquite dominated grassland.

Rainfall and Wildflowers

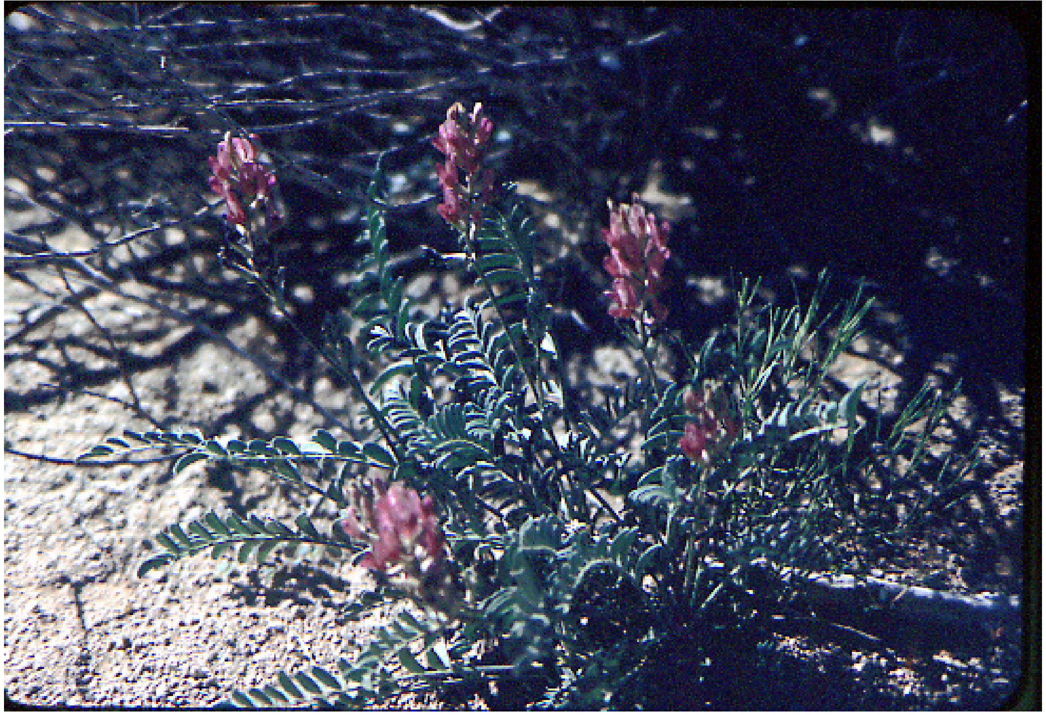
Wildflowers occasionally produce spectacular displays following rains that occur with the appropriate timing and frequency to provide the conditions for certain species that germinate and grow in abundance. Most years the wildflower displays are more subdued and the showy flowers are confined to small patches of habitat that provide the right combination of soil moisture and soil nutrients for the individual species. Since the establishment of the Long Term Ecological Research Program in the 1980's, the list of native plants includes fifty seven species of winter-spring annuals and one hundred species of summer annual plants. Many of these annual plants would hardly qualify as wildflowers because the flowers are tiny and not readily evident with the vegetative growth.

The first good winter rains in late November and December, transform the dry desert into a flower garden from mid-March through April. A trip around the Jornada Experimental Range and the College Ranch in spring reveal a sometimes spectacular display of wildflowers. Some of the most spectacular are Mexican poppies in a Chihuahuan Desert grassland on the New Mexico State University Chihuahuan Desert Rangeland Research Ranch. However most of the spring ephemeral or annual herbaceous plants do not produce large showy blossoms or the monoculture abundance of Mexican poppies. The dominant species of spring annuals vary with landscape position, soils, and the dominant vegetation. The most striking assemblage of annuals is often located on a piedmont on the College Ranch where Mexican poppies produced an eye-popping splash of color and produced the appearance of a cultivated garden. Other spring annuals that are relatively are bladder pod (*Lesquerella gordoni*), four species of locoweed (*Astragalus* spp.), two species of buckwheats (*Eriogonum* spp.) and two species of peppergrasses (*Lepidium* spp.). With the exception of locoweeds and bladder pods, the other spring annuals would not be

characterized as wildflowers. There were a number of other annual plant species that are part of the spring flora following adequate winter rainfall. Tansy mustard (*Descurainia pinnata*) occurs in all of the grasslands, tarbush shrublands, creosotebush shrublands but is most abundant in the mesquite coppice dune areas. The buckwheats are relatively abundant in the creosotebush shrublands, tarbush shrublands and in grasslands on sandy loam soils. A small, white aster like flower, the lazy daisy, (*Aphenostephus ramosissimus*) emerges in the middle of tussocks of tobosa grass or black grama grass and occasionally in other grassland areas.

A display of Mexican Poppies located on a lower piedmont near the NMSU Chihuahuan Desert Rangeland Research Center north of Las Cruces, N. M.

Bladder-pod, *Lesquerella gordoni*, an early spring dominant that germinates in December and flowers in late March through April.



A locoweed, *Astragalus nuttallianus*, is a frequent member of the spring annual flora of the Chihuahuan Desert.

A yellow, desert wild buckwheat (*Eriogonum trichopes*) held by a tall (more than 6 feet) student in order to show the length of the root of this spring annual. Yellow desert wild buckwheat plants germinate in December or January and remain as small green rosettes until late spring. During the rosette stage, the plant is carrying on photosynthesis and using that fixed energy to produce a deep tap-root. There are some lateral roots that develop at the top of the tap root that probably access shallow soil moisture and nutrients for the plant to "bolt". This buckwheat has photosynthetic green stems produces flowers on small branches of the main stem. The only leaves are the early leaf rosettes that die during the flowering stage of the plant..

Such spectacular displays do not occur every year and re-occur only when there are adequate winter rains. We had made sufficient quantitative measurements of the spring and summer annual plant communities to develop some hypotheses about factors that determined the species composition, growth, and habitat relationships of the various assemblages. One of the variables that we identified as a factor affecting species composition and growth of annual flowers was soil nitrogen. Nitrogen is one of the nutrients required by plants; makes up seventy percent of the atmosphere (atmospheric nitrogen (N_2); but atmospheric nitrogen must be converted to ammonium or nitrate to be available to plants. Soil nitrogen varies with weather patterns that regulate decomposition of dead plant material and/or produces soil conditions that allow the soil bacteria to reduce atmospheric nitrogen to ammonium. We tested the relationship between nitrogen availability and species composition and growth of annual plants by applying nitrogen fertilizer to plots plus applying irrigation water during different seasons.

In nitrogen fertilization studies, tansy mustard was one of the species that grew best in high nitrogen soils. Mesquite dunes are nitrogen rich sites because mesquite foliage is high in nitrogen and mesquite leaf litter is trapped by the stems of the coppice and decomposes in place resulting in a nitrogen enriched soil. Tansy mustard is one of several species that make up the spring annual flora that do not produce showy flowers. The flowers of tansy mustard are tiny and the fruits are oval-wing like with the seed at the base. The fruits are wind dispersed which probably accounts for the widespread distribution of tansy mustard in creosotebush shrublands, tarbush shrublands, most grasslands and even mesquite coppice dunes.

Early spring growth of Tansy Mustard (*Descurainia pinnata*) on a mesquite coppice dune prior to leaf growth of the mesquite.

Irrigation and Fertilization

The widely accepted view of germination, growth and production of desert plants is that water drives these processes. Annuals occur as live plants only during short periods that are favorable for germination and growth. They survive as seeds during periods when soil moisture and soil temperatures are not suitable for germination and growth. Desert annual plants are classified as summer annuals if they germinate after summer or early autumn rains when mid-day temperatures are above 68^{o}F and as winter annuals if they germinate after late autumn or early winter rains when mid-day temperatures are below 68^{o}F. In the northern Chihuahuan Desert, winter annuals that germinate in late autumn remain as rosettes of leaves, survive freezing temperatures and don't begin to grow until soils warm in March and April. Herbaceous perennials also grow in response to rainfall but the amounts and timing of rainfall required for growth of these plants is not understood.

In years following summer rains that fill playa lakes, adequate winter rain stimulates extensive growth of a yellow flower aster, (*Hymenoxys odorata*) Bitterweed or Stinkweed. Walking into a patch of Bitterweed provides adequate evidence that the species name, *odorata* is well deserved. These pretty yellow asters produce a scent that is unforgettable.

Because we had observed large differences among years in species composition and biomass production of both spring and summer herbaceous annual wildflowers, we conducted experiments using above canopy sprinkler irrigation and nitrogen fertilization to develop insights into the environmental variables causing this variation. Most of the experimental studies were conducted on a creosotebush dominated piedmont slope. First, we conducted studies to examine size and frequency of rainfalls on annual plants. We hypothesized that most of the spring herbaceous annuals would produce more plants and grow larger in the weekly watered plots because the shallow roots of the germinants would have a constant supply of moisture. We measured species composition and biomass production on plots receiving one inch of simulated rainfall every four weeks; on plots receiving one fourth inch of rainfall each week; and on plots receiving no supplemental water. Soil temperatures did not vary among treatments, but soil moisture was much higher on the supplemental rainfall (irrigated) plots than on the not-irrigated plots. We were completely surprised by the results of the study. The summer annuals essentially did not respond to the irrigation treatments. There were no differences in abundance and/or biomass of summer annuals in the irrigated and not irrigated plots. One species of spring-summer annual, a locoweed (*Astragalus tephrodes*) was most abundant and grew larger plants on the plots receiving one inch of rainfall every four weeks. Several spring annuals produced smaller plants on the plots receiving one fourth inch of supplemental water each week than on plots with no irrigation or one inch per month irrigation. There were no differences in species composition of spring annuals among treatments but the diversity (number of species) of summer annuals was higher on plots receiving one fourth inch per week irrigation. We learned from this experiment that the responses of herbaceous annual plant or wildflowers to rainfall patterns is complex; varies among species; and may involve environmental variables other than rainfall.

Spring annuals around a small creosotebush subjected to summer rain-out.

Spring annuals around a large creosotebush subjected to summer rain-out.
Note the high density of annuals within the trenched plot.

One of the most interesting experiments that provided insights into the factors affecting the abundance and size of annual herbaceous plants was the result of an experiment designed to examine the effects of summer and winter drought on creosotebushes of different sizes. Experimental plots were trenched to the depth of caliche layer, lined with a double layer of plastic sheeting to separate the soil inside the plot from that outside the trenched plot. The sheeting kept the roots from accessing moisture or nutrients from the soil outside the trench. The plots that were subjected to summer drought had rain-out shelters constructed with a steel frame and a clear plastic roof placed over the plots. The shelters were constructed after the plots were trenched in order to have the shelter large enough to prevent most of the rainfall from reaching the trenched plots.

The plots centered on large creosotebushes that were subjected to summer drought exhibited luxurious growth of spring annuals after good winter rains. However the plots centered on small creosotebushes had very few spring annuals. Analysis of soil samples showed that there were high levels of available nitrogen under the large creosotebushes exposed to summer drought but the available nitrogen levels under the small creosotebushes remained low and nearly the same as soils not exposed to summer drought. The large creosotebushes had litter layers and higher organic matter in the sub-canopy soils than the small creosotebushes which had little litter and very low organic matter in the sub-canopy soils. We attribute the high productivity of spring annuals under large creosotebushes that had been subjected to intense summer drought, to the mineralization of organic nitrogen which produced the increased ammonium and nitrate levels in the soils.

We examined the effects of the irrigation-nitrogen fertilization regime on three species of perennial wild flowers. Wild onion, *Allium macropetalum*, failed to establish in plots receiving one inch per month simulated rainfall. The perennial composite, *Bahia absinthifolia*, occurred at higher densities in plots that were not irrigated but there were no differences in the size of these plants in any of the irrigation or fertilization treatments. Desert holly, *Perezia nana*, failed to establish in plots fertilized with nitrogen. Desert holly were more abundant and grew to larger size receiving one inch of irrigation per month. Nitrogen fertilization had either no effect or an adverse effect on the perennial wildflowers in this experiment.

Summer Wildflowers

Summer wildflowers include a variety of annual and perennial species. Depending upon the frequency of rain events in May and June, some buckwheat species species like *Nama hispidum*, survive and continue to produce flowers during the summer months. A number of perennial species are part of the summer wildflower display. One of the most widely distributed summer wildflowers, is the desert marigold (*Baileya multiradiata*). Desert marigolds occur in creosotebush shrubland, tarbush shrubland, mesquite grassland, mesquite coppice dunes and in the foothills of desert mountains. Desert marigolds produce large numbers of seeds and most plants survive for one or two years. Another widely distributed summer perennial is the bull nettle (*Solanum elaeagnifolium*). The bull nettle is in the tomato family, produces purple flowers with yellow stamens, and a fruit that looks like a green tomato. Bull nettles are found in all of the same vegetation associations as desert marigolds. Summer wildflowers are more diverse on sandy loam soils of intermountain basins and lower slopes of piedmonts. Some of the larger and showy summer wildflowers include the common sunflower (*Helianthus annuus*), Cowpen Daiseys (*Verbesina encelioides*), Globe Mallows (*Sphaeralcea subhastata*, *S. angustifolia*, *S.incana*) and Scarlet Globe Mallow (*Sphaeralcea coccinea*). The small, prostrate, spurges (*Euphorbia* sp.) are relatively abundant and often found with the perennial Rattlesnake Weed, *Euphorbia albomarginata* on sandy loam soils.

Summer wildflowers are more diverse on sandy loam soils Of a spring-summer annual, *Nama hispidum*, (no common name)

A dense stand of Globe Mallow, *Sphaeralcea subhastata*, a common summer perennial wildflower that is widely distributed in the Chihuahuan Desert on a variety of soils and vegetation associations.

Cowpen Daiseys, *Verbesina encelioides*, Cowpen Daiseys growing in a low area that experiences standing water following intense summer rainfall. The white flowers in the foreground are a perennial peppergrass (*Lepidium montanum*).

A white summer daisy or fleabane, *Erigeron* spp., growing in a black grama grassland

Desert marigold (*Baileya multiradiata*)

At any time during the growing season it is possible to see dense stands of annuals forming rings or circular patches on the landscape. We recorded greater abundance and larger plants of spring annuals in rings around the nest discs of large harvester ant (*Pogonomyrmex rugosus*). Harvester ants deposit items rejected by nests mates at the margins of the nest discs. These materials decompose and add nutrients and organic matter to the soil. The rings of soil at harvester ant nest margins allow higher water infiltration plus higher nitrogen and other plant nutrients in comparison to soils a few feet from the edges of the harvester ant nests. Rings of abundant, large size, Mexican Poppies are obvious in areas where the poppies and ants co-occur. Another single species ring recorded around *P. rugosus* nests on a burro-grass-tobosa grass flat was Storks-bill (*Erodium texanum*). On harvester ant nests on basin grassland on sandy loam, the most abundant annual in the nest margin ring was tansy mustard (*Descurainia pinnata*). The annual plants that develop high abundance and large plants on the margins of harvester ant nests are species that grow best in high nitrogen soils. In other locations on watersheds and in valley grasslands, the large harvester ant colonies may not have the same effect on water infiltration and soil nutrients. *P. rugosus* nests in a mixed grass site on silt-loam soils had more, larger spring annual plants than reference sites ten feet away from the nest margins. On gravelly or sandy soils on creostebush slopes of the same watershed, the spring annual plants at the nest margins were equal in abundance and size. With the exception of tansy mustard, the harvester ant nests in basin grasslands on sandy soils did not have an effect on the abundance and size of wildflower species.

Another patch of abundant annual plants of one or two species are found on banner-tail kangaroo rat (*Dipodomys spectabilis*) mounds. Banner-tail kangaroo rats produce large mounds with several tunnels that open at the surface. The mounds are composed of soils transported to the surface from depths of up to 10 feet. A nest mound is generally inhabited by a single kangaroo rat unless the occupant is a female with pups. Banner-tail kangaroo rat nests are long-term features of Chihuahuan Desert grasslands and continue to persist for more than 50 years after the grassland has been converted to a shrub dominated community. The soils of nests that have been occupied by successive generations of kangaroo rats develop relatively high concentrations of plant available nitrogen from the breakdown of fecal pellets and uneaten plant materials. The nest soils also have higher water infiltration rates than surrounding undisturbed soils. The water and soil nitrogen regime of the nest soils appear to be the primary factors involved in the development of annual plant cover on the nest mounds. We recorded almost total cover of banner-tail mounds by prostrate pig weed (*Amaranthus blitoides*) and of silver-grey leafed *Tidestromia lanuginosa*. On some of the mounds there were not only prostrate pig weed but other pigweeds (*Amaranthus* spp.).

The clearly showy patches of spring and summer annuals appear to result from the activities of animals that live in the soil. Animals such as termites are widely distributed in the Chihuahuan Desert and their foraging galleries are nitrogen enriched. When the foraging galleries are destroyed by wind and water, the materials are transported down-wind or down slope and contribute to the patchiness of annuals and wildflowers in the desert landscape.

A profusion of a silver- grey leaf summer annual (*Tidestromia languinosa*) growing on a collapsed banner-tail kangaroo rat mound. The person in the photo is a post-doctoral student, Hoeng Tae Mun, who was studying factors affecting the distribution of summer annual plants. The yellow flowers in the background are Desert Marigolds (*Baileya multiradiata*).

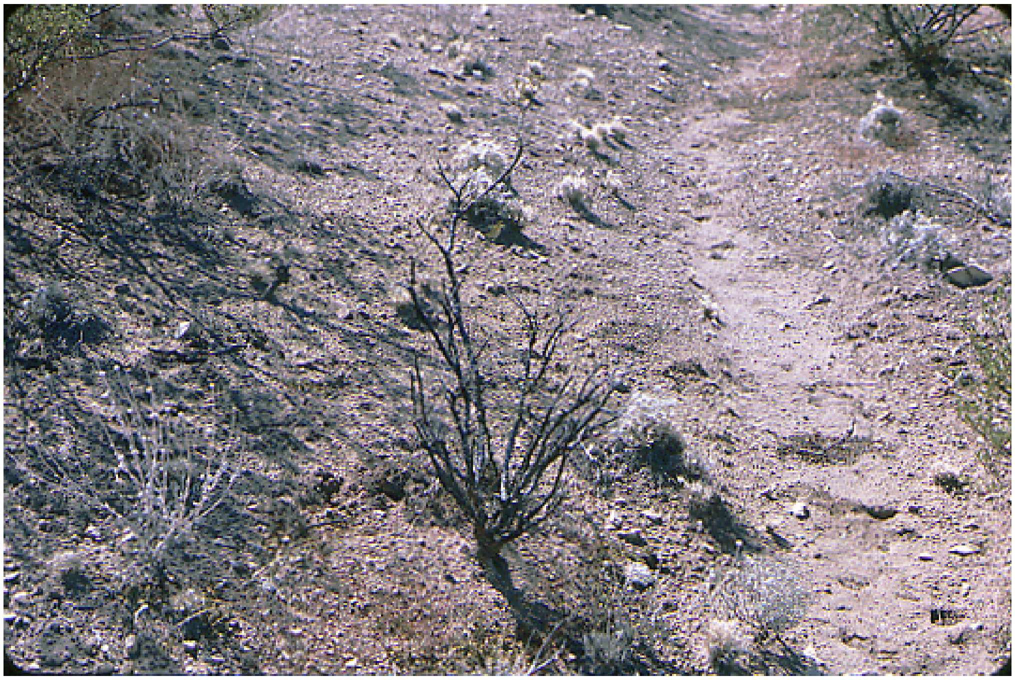
The Browsers: Rabbits and Pack-rats

Jackrabbits (*Lepus californicus*) are now the largest native herbivore living in the shrub dominated landscapes of the northern Chihuahuan Desert. The large ears of jackrabbits allow them to radiate heat to areas with lower temperatures, essentially shaded vegetation and soil. During the summer, jackrabbits dig shallow depressions or "forms" under shrubs with dense canopies that produce deep shade. A jackrabbit will typically dig three forms under a suitable shrub, one on the east side, one on the north side, and one on the west side. The jackrabbit will spend the morning hours lying in the form on the west side, then move to the form on the north side during the middle of the day and finally to the form on the east side in the mid-afternoon. Using this behavior, the animal reduces the heat load from direct solar radiation by maximizing the shading from the shrub canopy and can unload heat by conduction from its belly to the cool soil of the form. During the hottest days of summer, it is possible to walk within 2-3 meters of a jackrabbit hunkered down in its form. If forced to move when conditions are hot, a jackrabbit will only move a few meters and return to its' form as soon as the intruder moves away.

Jackrabbits feed on a variety of plants: annual plants when available, grasses and some perennial herbaceous plants. Because of the low density of jackrabbits (2-6 animals per square mile) it is rare to find evidence of jackrabbit feeding on vegetation during the growing season. During the winter season, jackrabbits tend to need a source of water to allow them to utilize the dry grasses as a source of energy and nutrients. During the winter we frequently see evidence of jackrabbits browsing on shrubs because of the wastage that accumulates around the base of the shrubs that are browsed or by the presence of freshly cut stems. We made observations of jackrabbits browsing on creosotebushes while we were perched atop a military surplus radar van that served as an equipment storage shed. With binoculars, we were provided with a view of several hundred creosotebushes in the vicinity of the van. Jackrabbits bite through the stems and eat the small branches. As a jackrabbit chews off the stems, the leaves and other branching stems fall to the ground. When a jackrabbit locates a suitable plant, it chews off all of the stems that it can reach. Although jackrabbits usually browse on only one plant in several hundred, they completely pruned all of the creosotebushes that were located around the fenced plots that were irrigated during the previous growing season. The stem water content of creosotebush plants that were browsed were higher than the stem water contents of neighboring creosotebushes that were not browsed by jackrabbits. We concluded that the jackrabbits were selecting high water status creosotebushes for browsing in order to obtain water in addition to energy and nutrients.

A black-tail jackrabbit sitting in its resting form under a dense shrub. Note the pruned soaptree yucca in the foreground. Yucca elata are pruned by jackrabbits and by wood rats (*Neotoma* spp.)

A black-tail jackrabbit (*Lepus californicus*) moving away from it resting form.



A creosotebush that has been completely pruned by jackrabbits. Note the location at the edge of a rill where the water content of the soil is elevated relative to sites more distant from the rill.

Branches of creosotebush dropped by a jackrabbit while feeding on the stems.

A creosotebush that has been pruned several times. Note the large stems and short stature plus the dense canopy produced from the browsed stems.

We conducted studies of the effects of jackrabbit browsing on creosotebush shrubs and tarbush shrubs (*Flourensia cernua*) on an upper piedmont slope, on a low slope area dominated by a mix of creosotebushes and tarbushes, on a tarbush monoculture site. We made numerous measurements of plant size and stem diameters. We found that the sum of the stem diameters at the base of the plant were the best predictor of the size of shrubs that exhibited little or no sign of browsing by rabbits. We assigned shrubs to one of three categories: (1) negligible signs of previous browsing to less than ten percent of the branches that had been severed by rabbits, (2) moderate browsing between 10% and 50% of the branches being chewed off by rabbits, and (3) heavy browsing with more than half of the branches being chewed off by rabbits.

On the lower piedmont site, nearly one half of the tarbush shrubs were dead while less than five percent of the creosotebush shrubs were dead. More than sixty percent of the dead tarbush shrubs had been heavily browsed and those plants were less than half of the size predicted by the basal stem diameters. Less than ten percent of the creosotebush shrubs were in the heavily browsed category. Tarbush shrubs that were classified as moderately browsed grew to only 55% of the predicted volume and those that were heavily browsed grew to only 36% of the predicted volume. Heavily browsed creosotebush shrubs were only 62% of the predicted volume but those shrubs that were moderately browsed grew to approximately 130% of the predicted volume. While jackrabbit browsing reduced the canopy size and therefore the foliage area for photosynthesis of tarbush, negligible to moderate browsing on creosotebush shrubs actually resulted in greater growth and increased photosynthetic area.

On the upper piedmont most of the tarbush shrubs grew along the edges of drainage channels and tarbush shrubs were sparse on the gravelly ridges. Jackrabbits preferentially pruned tarbush shrubs at this location where creosotebushes were ten times more abundant than tarbush. Less than three percent of the creosotebush shrubs exhibited signs of heavy browsing by jackrabbits whereas between twenty-one percent and thirty-five percent of the tarbush were heavily browsed by jackrabbits.

At the tarbush monoculture area there were twenty nine hundred tarbushes per acre and only nine percent of these were dead. None of the dead shrubs showed signs of having been browsed by jackrabbits. Only fifteen percent of the shrubs had stems that had been severed by jackrabbits and these shrubs had grown to an average of thirty-one percent of the predicted volume.

Creosotebush shrubs exhibit compensatory growth in response to loss of stems by jackrabbit pruning. However, tarbush does not exhibit compensatory growth in response to browsing. Indeed, jackrabbit browsing on tarbush contributes to the death of these shrubs. Creosotebush may benefit from the preference of jackrabbits for tarbush. In a study of more than 50 years, tarbush canopy cover on plots from which rabbits were excluded by rabbit-proof fencing was much higher than on plots where jackrabbits had access to the creosotebush and tarbush shrubs.

The preferential browsing exhibited by jackrabbits may represent avoidance behavior motivated by the digestibility or toxicity of the food material rather than its palatability or nutritional quality. It has been reported that the concentration of phenolic compounds (toxic chemicals) is two times higher in creosotebush foliage than in tarbush foliage. That study also reported that the concentration of condensed tannins was twelve times higher in creosotebush foliage than in tarbush foliage. Tannins are chemicals that affect the digestive systems of animals that ingest them. It is not surprising that jackrabbits would prefer to browse on tarbush stems to obtain water and nutrients.

Creosotebush and tarbush are not the only plants that are affected by browsing by rabbits. One of the abundant prickly-pear cacti, the reddish *Opuntia violacea*, is used as a food-water source by both jackrabbits and the desert cottontail rabbit. Cottontails remove only the epidermis (skin layer) between the tufts of hair-like spines called glochids. Cottontail feeding on prickly-pear cacti leaves a distinctive scar on the surface of the pad. In contrast, jackrabbits bite through the skin and the underlying fibrous internal pad tissues producing a semi-circular hole from the edge of the pad toward the center of the pad. The chewed surface of the cactus pad forms a kind of scar tissue that prevents moisture loss from the damaged pad surface and keeps the remainder of the pad alive.

We measured the seasonal use of prickly-pear by rabbits by recording the amount of rabbit dung pellets around the prickly-pear plants that were chewed on by rabbits. When rabbits spend time feeding on plants, they defecate as they are biting and chewing the plant material thereby leaving evidence of the level of feeding on a plant. Rabbit dung pellet accumulations provided evidence of the rabbit species feeding on several species of plants.

Rabbit feeding on prickly-pear increased between January and March, was less in April and May and increased again in June. There was little evidence of rabbit browsing on prickly-pear July through November during and following the summer monsoon rainy season. Both jackrabbits and desert cottontail rabbits utilized prickly-pear when there was little or no other vegetation containing water available as a food source. When there are sufficient winter rains to produce spring annuals, rabbits use these plants and reduce their browsing on prickly-pear. Rabbits probably browse on prickly-pear cacti for water more than for the food value of the cactus tissues eaten by the animals.

We found that rabbits did not browse on small prickly-pear plants: that is on prickly pear with fewer than 5 pads and browsed very infrequently on cacti with fewer than 10 pads. Rabbit browsing had little or no effect on the production of new pads, flowers or fruits of large cacti with more than 30 pads per plant. Also the rabbits grazed preferentially on the older pads at the edges of the large plants. There was no evidence that rabbit browsing on the large prickly-pear cacti had any effect on the production of new pads, flowers and fruits. However, production of new pads, flowers and fruits were reduced on heavily grazed plants in the size range between 10 pads and 30 pads per plant.

Rabbits also browse on small soaptree yucca plants but that browsing is not limited to the dry winter season. In a study of prescribed fire in a black grama grassland, forty-three percent of the re-sprouts of burned soaptree yucca were pruned to some extent. The measurements of rabbit browsing were made at the end of the second summer after the prescribed burn. Based on observations of fecal-pellet deposition and aggregation near pruned leaves, all of the browsing of soaptree yucca resprouts was attributed to black-tailed jackrabbits (*Lepus californicus*). Rabbit browsing removed an average of 25% - 50% and consumed all of the leaves of two of the small re-sprouts in the area that had been burned. Jackrabbits browsed 24% of the yucca in the unburned grassland removed an average of 26% of the leaf crown area of the browsed plants. In the unburned grassland small soaptree yucca were browsed. Rabbit browsing was limited to small yucca with leaf crowns less than 24 inches in diameter and leaves that were less than 24 inches long.

Browsing by jackrabbits was also found to modify the morphology of young- small honey mesquites. Jackrabbits bite off the small stems and appear not to eat much of the severed stem (see photo below). Young mesquite plants that had not been browsed by jackrabbits were characterized by a few (five or six) elongate stems. Browsed young mesquite had numerous stems that formed a tight matrix of stems. The stems in that matrix had many spines and those spines were longer than the spines on un-browsed young mesquite. The dense matrix of spiny stems of young mesquite that have been browsed by jackrabbits become focal plants for the deposition of wind-blown sand and the formation of coppice dunes.

A small mesquite with three stems that were browsed by rabbits.

Pack rats/wood rats

In North American deserts, several species of rodents known as pack rats or wood rats, *Neotoma* spp., build houses or middens of sticks plus other plant materials, dried dung, and frequently include shiny man-made objects in their middens. This behavior has earned members of this genus the common name pack rats. *Neotoma* spp. are widely distributed in North American deserts and the nest midden structures have been shown to vary considerably depending upon the availability of suitable shelter of rock or vegetation for the location of the nests. Two pack-rat species inhabit the Chihuahuan Desert areas of southern New Mexico: the white-throated woodrat, *Neotoma albigula*, and the plains woodrat, *Neotoma micropus*. The white-throated woodrat has expanded its range from the rocky slopes of mountains and rocky drainages into the desert grasslands, which are the historical habitats of the plains woodrat, and into the shrub dominated plant communities that have replaced desert grasslands over the past one and a half centuries. The plains woodrat continues to occupy some of the shrublands that were grasslands in the past. Plains woodrat middens in shrubland habitats are similar to those of the white-throated woodrat.

A packrat (wood rat) emerging from its midden constructed primarily of banana yucca leaves.

We conducted a series of studies of the middens (houses) of pack rats to examine the selection of materials for midden construction, the environmental conditions within the middens and the other animals that occupy the middens. The highest density of *Neotoma* spp. middens was in the creosote-bush bajada habitat (3 per acre) where most of the nests were within large banana yucca (*Yucca baccata*) patches or large Engleman's prickly pear (*Opuntia phaecantha*) patches at the edges of small drainage channels. The lowest abundance of pack-rat middens was in the tarbush shrubland (0.8 middens per acre). Pack-rat middens were most abundant in the mesquite thickets at the margins of a dry lake (10 middens per acre). The size distribution of pack-rat middens varies among the plant communities in which they occur. For example pack-rat middens in the creosote-bush shrubland (average of 50 lbs of material per midden) are larger than the middens in the tarbush shrubland and in grasslands at the base of a mountain (average of 10 lbs. of material per midden). The largest middens are in the mesquite thicket areas at the margins of a dry lake (70 lbs. of material per midden).

The materials used in the construction of the middens represent the materials available within a 160 foot radius of the midden site. Seven of nine middens in a toe-slope grassland were built within large clumps of Engleman's prickly-pear cacti. The pads of Engleman's prickly-pear accounted for between 30% and 50% of weight of the materials in those structures. Other woody species: morman-tea (*Ephedra trifurca*), snakeweed (*Gutierrezia sarothrae*), soaptree yucca (*Yucca elata*) and creosotebush stems plus unidentifiable sticks accounted for most of the remaining materials in the nest structure in toe-slope grassland. In tarbush shrubland, no plant species were represented in all of the middens sampled. Stems of several shrub species accounted for more than half of the materials in the nest structures of different nests (tarbush, *Flourensia cernua*, crucifixion thorn, *Koeberlinia spinosa*, wolfberry, *Lycium pallidum*, and pencil cholla, *Opuntia leptocaulis*). The three largest middens in the tarbush shrubland were under large crucifixion thorn bushes and the smaller middens were located in old badger, *Taxidea taxus*, excavations. The middens in the creosote-bush shrubland were located at the edges of small washes under mesquite shrubs or within large patches of banana yucca, or Engleman's prickly-pear. These middens were constructed primarily of stems and branches of creosotebush, mesquite, snakeweed, and desert willow (*Chilopsis linearis*). The average diameter of sticks from the outer layer of a midden are nearly twice that of sticks from the middle layer of the midden.

In early September, when air temperatures reached a maximum of the upper 90's the difference between the relative humidity in the middle of the midden and the external air relative humidity ranged from no difference to 39% higher than the outside air. The interior of the nest midden was slightly cooler than the outside air temperature in the early morning but was 20 degrees cooler by late afternoon when the outside air temperature was more than 90 F. In mid-October, when maximum ambient temperature remained below 80 F, the average relative humidity of the interior of the middens was 15% higher than the humidity of the outside air.

Pack-rat middens provide refuge microhabitat for more than 40 different species of arthropods. The pack-rat middens are an important microhabitat for crickets (Gryllus sp.), wolf spiders (*Lycosa* spp and *Geolycosa* spp.), and lycid beetle larvae (Lycidae) in all of the shrub habitats. More arthropods (479) were captured from the pack-rat middens in the tarbush area than in the creosote-bush area (338 arthropods). Although middens in the tarbush shrubland are smaller than those in the creosote-bush shrubland, middens in the tarbush area provide habitat for more individuals and for more species that may be obligate residents than middens in the creosotebush shrubland.

Above, a packrat nest midden constructed with crucifixion thorn segments. Below thorn segments cut from the branches of a tall crucifixion thorn by a packrat.

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Pack-rats are acrobatic climbers. Somehow they manage to clamber up the trunks of soap-tree yucca stalks to access the green leaves at the top of the caudex (main stem). Pack-rats browse the green leaves of yucca during the winter as seen in the photo probably to obtain water since few of the yucca leaves are incorporated into the midden structure of pack rat nests that are close to intensely browsed yucca.

A soaptree yucca that has been browsed by pack-rats, Neotoma spp.

A crucifixion thorn shrub from which most of the smaller thorny foliage has been removed. Pack rats eat the bark of this plant as evidenced by the skinned branches in the photo.

Mammal Communities

Soon after arriving in New Mexico, I began studies of the physiological and behavioral adaptations of desert rodents that allowed these animals to survive in the harsh environment of the Chihuahuan Desert. My interest in this topic was the result of a fascinating study of water balance in Merriam's kangaroo rat (*Dipodomys merriami*). That study showed that Merriam's kangaroo rat could survive on a diet of dry seeds. The metabolism of the seeds produced sufficient water to meet the animal's needs. Merriams kangaroo rat conserved water by producing dry feces, concentrating urine in its kidneys, and capturing most of the water in the respiratory exhaled air by cooling the air in its long nose. The kidneys of kangaroo rats remove more water from the urine than kidneys of other mammals because of longer loops in the kidney tubules. That publication stimulated us to examine the physiology and behavior of other species of Chihuahuan Desert rodents. My students and I examined grasshopper mice (*Onychomys torridus*) and concluded that this small predator survived by living in underground burrows where the temperature and humidity were moderate and by eating insects and other arthropods which provided adequate water to support the mouse. However, in winter when arthropods were scarce, grasshopper mice would eat seeds and other mice. For grasshopper mice, survival in the desert was primarily behavioral adaptation with less physiological adaptations than documented for kangaroo rats. When we reviewed the literature on desert rodents, we knew that we needed to learn as much as possible about how the variations in desert weather patterns affected the reproduction and survival of all of the desert rodents in the community.

We initiated studies of Chihuahuan Desert rodent communities as part of the Desert Biome of the U. S. International Biological Program. These studies were focused on a Chihuahuan Desert watershed. The rodent communities were studied on a creosotebush shrubland on a sloping gravelly-sandy alluvial piedmont on the upper slopes of the watershed and at the base of the watershed on a mesquite shrub association that formed the circumference of a dry lake (playa). The playa bottom was essentially bare soil with some large patches of tobosa grass (*Pleuraphis mutica*) and vine mesquite (*Panicum obtusum*) at the margins of the lake bed . We trapped rodents in the three vegetation associations at regular intervals for five years.

Checking traps in winter produced a unique teaching moments. I gave students the choice of checking traps around the dry lake or on the upper slopes of the watershed. Most chose the dry lake because they thought it would be warmer than the upper slopes. The next night, I had that group of student switch locations with the group of the previous night. In two nights, I had demonstrated to the students the phenomenon of cold air drainage to the low elevation site and the relatively pleasant conditions of the mid-slope. One winter night when I was checking a line of traps that crossed the arroyo, I picked up a trap that was very heavy. That trap held an adult pack rat (*Neotoma* spp.) that filled the entire box trap. Adult pack rats weigh between 10 and 12 ounces. When I reached in to extricate the rat from the trap, the rat bit my finger producing a wound that exposed the bone. Needless to say, I dropped the rat in order to nurse my finger and cursed loudly at my stupidity for attempting to pull a large live animal from a box trap that was nearly too small for the rat. The following night, the students made sure that I would check the same line of traps and when I reached the edge of the arroyo and picked up a trap, it was as heavy as the pack-rat trap from the previous night. When I yelled for help with the trap, there was loud laughter that echoed across the desert. I then pushed down the trap door and found that the students had placed a rock in the trap that weighed as much as the pack-rat. This was a way that the students hazed the professor who thereafter had everyone carry cloth bags in which to empty traps containing large rodents.

The most important factor affecting rodent species composition and population dynamics was amount of rainfall and distribution pattern of the rainfall. Rainfall amounts and frequency affected vegetation growth, seed crop, and insects. The study area was in a drought (below the long-term average of ten inches) for the first two years of the study. The drought was followed by above average rainfall not only during the mid-summer monsoon season but with average to above average rainfall in the autumn, winter, and spring.

There were only two species that were residents in the grass covered margins of the playa basin: the western harvest mouse (*Reithrodontomys megalotis*) and the cotton rat (*Sigmodon hispidus*). The population size of these two species remained very low at one or two per hectare (2.47 acres) during the drought period. They increased to 6 per hectare during the first wet year. The western harvest mouse and cotton rat populations exploded to more than 40 animals per hectare during the second wet year. During the dry years, the only tall grass cover was in the mixed tobosa grass-vine mesquite patches at the edges of the lake bottom. During the wet years there was high productivity of vine mesquite grass that covered the playa bottom. That grass matured at a height of more than two feet. Because of the vine mesquite grass, the suitable habitat for the western harvest mouse and the cotton rat expanded from approximately 1.5 hectares to more than 25 hectares. Harvest mice build nests in tall grass and cotton rats are known to prefer dense undergrowth and tall protective grass habitat. The favorable weather conditions converted the dry lake bottom from marginal habitat for these two species to excellent habitat.

Four other rodents were trapped occasionally on the lake bottom: silky pocket mouse (*Perognathus flavus*), deer mouse (*Peromyscus maniculatus*), white footed mouse (*Peromyscus leucopus*) and house mouse (*Mus musculus*). The silky pocket mouse was found on the playa bottom before the growth of vine mesquite grass. The other rodents appeared on the dry lake bottom in the third spring and summer following the drought breaking rains. These species were classified as immigrants from other habitats or from the ranch buildings that were less than 0.25 miles from the dry lake basin..

We recorded fourteen species of rodents from the mesquite association around the dry lake. Six species were trapped all five years of the study: Merriam’s and Ord’s kangaroo rats, banner-tail kangaroo rats, white-throated wood rats, desert pocket mice, and spotted ground squirrels. Desert wood rats are commonly called pack rats because of their attraction to shiny objects which are often added to their dens. We frequently found the aluminum tags that we used to identify plants or ant mounds flashing in the bright sunlight from the sticks of the pack rat dens..

The most abundant species in this habitat were Merriam’s kangaroo rat (*Dipodomys merriami*) and Ord’s kangaroo rat (*Dipodomys ordii*) that were estimated at populations of more than 60 per hectare following drought breaking rains. In the drought years, numbers of Merriam’s kangaroo rats ranged between 10 and 15 per hectare and the numbers of Ord’s kangaroo rats ranged between 2 and 8 animals per hectare. Meriam’s and Ord’s kangaroo rats are medium size animals that weigh approximately one ounce. Ord’s kangaroo rats are normally a grassland species but they reached equal abundance with Merriam’s kangaroo rats in at the dry lake margin. In that area there were patches of grassland with black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.), and three awns (*Aristida* spp.). During years of adequate summer rainfall this habitat produced abundant annual grasses: needle grama (*Bouteloua aristoides*) and six week grama (*Bouteloua barbata*). The annual grasses produce large quantities of seeds and also provide an abundant source of green vegetation that many of the rodents need to produce young and for lactation. Lactation (milk production) requires more water and nutrients than can be obtained from dry seeds. Both Merriam’s and Ord’s kangaroo rats were reported to consume green plants and insects when lactating. Ord’s kangaroo rats were taken occasionally in the creosotebush shrubland and even following two years of above average rainfall, their estimated abundance in that habitat remained at less than one per acre.

Banner-tailed kangaroo rats were estimated at three or four animals per hectare during the five years of study. The large banner-tail kangaroo rat has an average weight of 4 ounces and probably because of their size cannot survive on a diet of only dry seeds. Banner-tails construct large burrow mounds that are more than ten feet in diameter and up to 3 feet higher than the surrounding land. These burrows are inhabited by successive generations of banner-tails. Burrows are occupied by a single banner-tail except when females have young. They store large quantities of seeds and plant parts in these burrows.

The white-throated wood rat (*Neotoma albigula*) and the southern plains wood rat (*N. micropus*) live in large dens (5 feet in diameter and up to 4 feet high) located at the base of large multi-stem mesquite. The dens are constructed of sticks, dried dung pats, and joints of cholla cacti. Dens provide a moist, moderate temperature environment that is safe from most predators. The numbers of pack rats remained constant at one per hectare in the mesquite around the margins of the dry lake throughout the study. In this habitat, pack rats fed on the green leaves of soaptree yucca (*Yucca elata*) and gnawed on mesquite bark during drought periods removing large patches of bark from many of the mesquite stems that were within 100 meters (300 feet) of a den. Enough bark was removed from some of the stems to induce death of individual stems.

The mesquite shrubland adjacent to the playa lake was the only part of the watershed where we found the diurnal, spotted ground squirrel (*Spermophilus spilosoma*). Spotted ground squirrels feed on green vegetation, seeds and insects. We trapped spotted ground squirrels in the spring and autumn when moderate temperatures allowed us to open traps in the early afternoon and check the traps several hours after sunrise. All of the spotted ground squirrels trapped in April were in breeding condition and the females were lactating. Spotted ground squirrels maintained densities of two per hectare until the second wet year when densities increased to three per hectare. The other resident species in the mesquite shrub-land was the desert pocket mouse (*Perognathus penicillatus*). During the drought years the numbers of desert pocket mice were highest in early summer (between 10 and 15 per hectare) and dropped to less than one per hectare in the winter months. During the years of above average rainfall, the numbers of desert pocket mice increased from less than one per hectare to 20 per hectare in the autumn of the first wet year and from 5 per hectare in the spring of the second wet year to 20 per hectare in the autumn of that year. The silky pocket mouse exhibited a very different abundance pattern than that of most of the rodents in the mesquite shrub-land. Silky pocket mice occurred at densities of less than one per hectare during the first drought year and then exhibited explosive population increase in the second drought year to 25 per hectare in late summer..

The southern grasshopper mouse (*Onychomys torridus*) was trapped in the mesquite shrubland only during the drought years. Although grasshopper mice are established and breed in most habitats in the Chihuahuan Desert, they tend not to be trapped with grain baits during periods when there are abundant insect prey. We are confident that southern grasshopper mice were present in the mesquite shrub-land at the margins of the dry lake during all seasons and years of the study.

Seven additional rodent species moved into the mesquite shrub-land habitat during years with above average rainfall and some of these species exhibited rapid population increases by the third year of above average rainfall. Several of the species were also found on the dry lake bottom when the lake was no longer flooded. These were the silky pocket mouse, the deer mouse, the house mouse, the western harvest mouse, and the white footed mouse. The deer mouse reached population density averaged 5 per hectare during the drought years and increased to an estimated population of 14 per hectare in the last of the wet years. The white footed mouse did not appear in this habitat until the second wet year and reached a population size of 5 per hectare. The cactus mouse (*Peromyscus eremicus*) and the rock pocket mouse (*Perognathus intermedius*) were absent from the mesquite shrub-land habitat until the second wet year. The cactus mice and rock pocket mice trapped in this habitat were probably dispersing from high population densities in the upslope creosotebush shrub-lands.

The populations of small mice of the family Cricetidae, genus *Peromyscus* exhibited the largest fluctuations in abundance. Species that were absent or in low densities during drought years increased rapidly during periods of average or above average precipitation. Rapid changes in population size were primarily a function of breeding periods and reproductive potentials of the species. The kangaroo rats typically reproduced once a year and in wet years produced two litters of approximately two pups per female. The records in our study showed that white footed mice were in breeding condition throughout the year and young were recruited into the population throughout the year. The average number of young produced by crecitid mice was 5.7 per litter. These reproductive characteristics allow these mice to increase population size very rapidly when rainfall stimulated growth of many annual weeds and grasses. As numbers of crecitid mice increase, many of the young are forced to disperse and move into marginal habitats. If suitable weather patterns persist for several years, crecitid mice may be more abundant in desert habitats than the kangaroo rats. On a geographic scale, the crecitids, *Peromyscus* spp. and harvest mice, *Reithrodontomys* spp., are only present in desert habitats where productivity is high and/or potentially competitive pocket mice are absent because of geographic barriers to their dispersal.

The rodent community of the creosotebush shrub-land on the upper slopes of the watershed was less diverse than the rodent community in the mesquite shrub-land at the base of the watershed. This habitat did not provide the necessary resources or habitat for banner tail kangaroo rats, cotton rats, or spotted ground squirrels. Merriam's kangaroo rat, two pocket mice (rock pocket mouse and desert pocket mouse), the cactus mouse, the white throated wood rat or pack rat (*Neotoma albigula*) and the southern grasshopper mouse were found in this habitat throughout the study.

Density estimates for white throated wood rats in the creosotebush shrubland fluctuated more than in the mesquite shrubland. In the creosotebush shrubland, sub-adult pack rats remained in the trappable population for as long as two to three months. After two years of above average rainfall, the estimated numbers of white throated wood rats increased from one per acre to four per acre as a number of sub-adults entered the population. During the first three years of the study, most pack rat middens were found in large clumps of banana yuccas (*Yucca baccata*). Banana yucca produced large clumps on small side channels that fed into the large wash that bisected the study site. The increase in abundance of white throated wood rats was the result of young animals building new nests (middens) in the apache plume (*Fallugia paradoxa*) thickets at the edges of the large dry wash. During the wet years, there was considerable new growth and expansion of apache plume thickets which increased the suitability of this vegetation as potential nest sites. White throated wood rats are dependent upon limited habitats that provide protection for the nest middens and food during drought periods. Banana yucca and apache plume provide thick or spiny deterrents to predators attempting to raid a midden. Banana yucca also provides spiny materials for midden construction. Yucca leaves and small stems of apache plume provide food and water even during dry winter months.

In a separate study over several additional years, the rock pocket mouse (*Perognaths intermedius*) expanded its range into the creosotebush habitat during moist conditions but retreated to the more mesic mountain slopes during drought periods. This expansion and contraction followed the productivity of perennial grasses, forbs, and annuals. The desert pocket mouse (*Perognathus penicillatus*) occurred in this habitat throughout the study. The transient nature of suitable habitat affects competition between similar species and allows the coexistence of competing species because species do not occupy the same area all of the time. Populations of deer mice, white footed mice, western harvest mice, silky pocket mice and Ord's kangaroo rats were more transient and entered the trappable population when rainfall produced suitable islands of habitat within the creosotebush shrubland. These animals probably represented dispersing young animals. Young rodents disperse when their population numbers increased to levels where there were conflicts for space and resources between individuals of the same species.

Livestock Grazing and Mesquite Removal

We conducted a five year study of small mammal populations in a black grama (*Bouteloua eriopoda*) grassland with scattered mesquite as part of a study on vegetation alteration by livestock grazing and mesquite removal. Trapping was conducted on eighteen one acre plots. Mesquite shrubs were removed from nine plots; six plots were grazed in summer; six plots were grazed in winter, and six plots were not grazed. Stocking rates of livestock on the grazed plots were adjusted to remove approximately fifty percent of the available forage.

Pretreatment trapping of small mammals was conducted in the autumn following two years of above average precipitation. There were a large number of cotton rats (*Sigmodon hispidus*) in the pretreatment period but cotton rats were not recorded during the following five years of study. Cotton rats present a real enigma for a desert ecologist. Why do these animals exhibit explosive population growth during some years and then disappear from the trappable population for a decade or more. We tried trapping cotton rats on north facing boulder slopes of a mountain where grasses and cooler temperatures might have provided a suitable refuge during drier conditions but never trapped a single cotton rat. Other spot checking in grasslands near water wells and other "potentially suitable" habitat yielded no cotton rats. The sudden appearance and disappearance of cotton rats in the Northern Chihuahuan Desert remains one of the great mysteries of this desert.

The cricetid deer mouse was relatively abundant in the pretreatment trapping with very few surviving to the next spring. Deer mice were not present during the remainder of the study. Ord's kangaroo rats (*Dipodomys ordii*) were the most abundant rodent on all of the plots throughout the study period. Ord's kangaroo rat populations decreased during two years of below average rainfall but increased to more than double the numbers in two subsequent years of average rainfall. Numbers of pack rats (*Neotoma* spp.) remained relatively constant over the years of the study as did the populations of grasshopper mice (*Onychomys* spp.) and spotted ground squirrels (*Spermophilus spilosoma*). There were no differences in numbers of small mammals that were attributed to either shrub removal or grazing by livestock with the exception of the silky pocket mouse (*Perognathus flavus*). Silky pocket mice arrived on the livestock grazed plots after two years of grazing had increased the amount of bare soil in the grazed plots.

Fire and Rodent Communities

Since fire suppression had been suggested as one of the factors leading to the spread of shrubs into Chihuahuan Desert grasslands, we conducted a fire study on a black grama grassland with scattered mesquite shrubs. The prescribed fire burned large patches of grassland and there were large patches of grassland that were not burned allowing us to trap rodents in burned patches and unburned patches. There was only one species in the pre-burn trapping: Ord’s kangaroo rat (*Dipodomys ordii*). Ord’s kangaroo rats were present on both the burned and unburned plots over the duration of the study. One month after the prescribed fire, silky pocket mice (*Perognathus flavus*) were captured on the burned plots but not on the unburned grassland. Four months after the prescribed fire, the numbers of pocket mice on the burned plots were more than double the numbers on the unburned plots. In addition to Ord’s kangaroo rats and silky pocket mice, we captured pack rats (*Neotoma micropus*), spotted ground squirrels, and grasshopper mice four months after the prescribed burn in burned and unburned grassland. We concluded that fire had a positive effect on silky pocket mice by increasing the size of bare patches between grass tussocks but had little effect on the other rodent species. This study provided additional evidence that the rodent communities in desert grasslands are much less diverse than rodent communities in desert shrublands.

Rodents as Herbivores

Kangaroo rats are not exclusively seed eaters; they consume significant amounts of green foliage especially in the breeding season. We observed large quantities of freshly cut tillers of several species of grasses in the desert grasslands of southern New Mexico. Close examination of the soil around the tussocks from which the cuttings originated revealed “tail drags” characteristic of kangaroo rats. These observations led us to hypothesize that kangaroo rats were responsible for these cuttings. In order to test this hypothesis, we did field studies in plots that were designed to exclude all mammals larger than Ord’s kangaroo rats and forage preference studies of Ord’s kangaroo rats in an outdoor laboratory setting.

We used large outdoor chambers filled with soil and provided with an artificial burrow for our experiments. Ord’s kangaroo rats were released into the chamber and quickly moved inot the artificial burrow. Into each chamber we buried pots with tussock forming grasses that were in good condition, green leaves and growing tillers and seed heads. The three species of grasses that were in the pots were common grasses in the desert grassland: black grama (*Bouteloua eriopoda*), mesa dropseed (*Sporobolus flexuosus*) and silver bluestem (*Bothriochloa saccaroides*). The rodents were provided with a excess amount of rolled sorghum in order to provide a choice of a preferred grain or the green grass plant with flowering tillers. We checked the chambers each morning, counted the number of cut green tillers and collected all cut pieces of the plant for drying and weighing. Ord’s kangaroo rats cut most of the tillers of each grass plant placed in the chamber and ate a portion of the each tiller. The kangaroo rats ate a larger percentage (70%) of the cut silver bluestem tillers than of the black grama (54%) and mesa dropseed (34%). Only small amounts of grass and sorghum were cached in the burrow. We found that the kangaroo rats consumed very little of the grain sorghum unless they were deprived of grass plants for one or more nights.

We were allowed to examine grass cuttings in plots that allowed access by rodents the size of Ord's kangaroo rats and smaller and plots that excluded all rodents. These plots located on a lower piedmont near Portal, Arizona were established by J. H. Brown for long term studies on seed consumption by ants and rodents. On the rodent exclusion plots less than 0.5% of the grass tussocks had cuttings around the base of the tussock whereas in plots accessible to Ord's kangaroo rats almost 60% of the grass tussocks had clippings around the base. We attributed the small amount of clipping in the kangaroo rat exclusion plots to insects.

We measured the mass of grass clippings in the four major plant communities in the Jornada Basin. In the black grama grassland we estimated that the clippings accounted for approximately seven percent of the grass production. In the mesquite coppice dune habitat, clippings accounted for approximately five percent of the grass production. In the creosotebush and tarbush shrublands, clippings accounted for between one and two percent of the grass production.

The outdoor chamber showing the grass clippings by Ord's kangaroo rats and the rolled grain sorghum provided for the rats.

The field studies demonstrated that the flowering tillers cut by kangaroo rats represent a considerable amount of the reproductive effort of the grasses are lost to herbivory by these rodents. Kangaroo rats cut-off and consume only the lower portions of the green stems of the grasses. The rats select the plant parts with high soluble carbohydrate content. Both Ord's and Merriam's kangaroo rats have been reported to consume green vegetation which can make up as much as thirty five percent of the diet.. Consumption of green vegetation is correlated with reproduction in kangaroo rats. Green vegetation provides water as well as nutrients. Since reproduction and lactation require more water than the rodents can obtain from dry seeds, consumption of the lower segments of flowering tillers provides that need. The cutting of grass tillers also provides evidence of why the population dynamics of kangaroo rats are tied to precipitation and production of green grasses.

Kangaroo rats cut tillers of almost all of the tall tussock grasses that occur in the northern Chihuahuan Desert. The only grass species with no evidence of stems severed by kangaroo rats was bush muhly (*Muhlenbergia porteri*). Bush muhly grows under creosotebushes and develops a dense hemispherical shaped tussock of fine stems. Kangaroo rats may avoid cutting stems of this grass because of the nature of the stems or because the grass is "protected" by the creosotebush that serves as a nurse plant. In addition to cutting perennial grasses, kangaroo rats cut and consumed parts of stems of annual grama grasses and Mexican witchgrass (*Panicum herticaule*). Kangaroo rats also cut stems of several herbaceous perennials and annuals. These included summer annual buckwheats (*Eriogonum* spp.), and two other summer annuals: spiderling (*Boerhaavia spicata*) and wooly tidestromia (*Tidestromia lanuginosa*). The perennial herbaceous plants with stems cut and eaten by kangaroo rats were: leatherweed (*Croton pottsii*), two-leaf senna (*Cassia bauhinoides*), and hairy seed bahia (*Bahia absinthifolia*). These herbaceous plants are relatively abundant and produce new growth following summer monsoon rains.

We conducted additional studies of grass cutting by kangaroo rats to test the hypothesis that kangaroo rat herbivory reduces grass tussock growth and seed production. We predicted that grasses protected from kangaroo rat herbivory would have elevated growth, tiller production, and seed production. We used individual rodent exclosures constructed of welded mesh topped with aluminum flashing to prevent rodents from climbing into the exclosures to eliminate the possibility of rodents cutting stems of the enclosed grass tussocks. These cages were buried three inches into the soil around the selected grass tussocks. We selected tussocks of mesa dropseed (*Sporobolus flexuosus*) that varied between 20 centimeters and 90 centimeters in diameter and assigned tussocks at random to rodent exclusion or available to rodents. We measured leaf and tiller lengths monthly and recorded leaf and tiller loss to kangaroo rats by collecting the severed stem segments from the unprotected grasses.

There was little grass growth during the first four months of the experiment because of very little rainfall during that period. Following a large rain event in July, leaf growth was rapid. Plants that were exposed to kangaroo rat herbivory, leaf length peaked in July and declined thereafter. Leaf lengths of plants within the rodent exclosures continued to increase through August. The length of tillers exhibited a similar pattern. Tillers of mesa dropseed tussocks exposed to kangaroo rat herbivory were relatively short whereas the tillers of protected tussocks were up to six times greater in the exclosures.

Grasses from which kangaroo rats were excluded exhibited no loss of tillers characteristic of kangaroo rat cutting. Plants exposed to kangaroo rats lost an average of thirty eight tillers per plant and less than two percent of the tillers had flowers or seeds. Grass tussocks protected from kangaroo rats produced 65 times more inflorescences than those tussocks accessible to kangaroo rats. The mesa dropseed grasses subjected to defoliation by kangaroo rats had significantly reduced leaf and tiller growth. Because a large fraction of the photosynthesis in grasses is known to occur in the distal portion of tillers, loss of tillers cut near the base of the tussock by kangaroo rats results in loss vigor of those plants. These results provide an alternative explanation for the marked increase in cover and biomass of grasses in the long-term rodent exclusion plots near Portal, Arizona. The protection of tillers from kangaroo rat herbivory may have been more responsible for the grass increase in the rodent exclusion plots than the lack of seed harvesting by kangaroo rats.

In a separate study, we tested the hypothesis that kangaroo rats cut more tillers from grasses in open patches than from grasses that were adjacent to other tussocks. We experimentally removed tussocks of Lehmann's lovegrass (*Eragrostis lehmanniana*) to increase the space around individual tussocks. We found that tiller cutting from Lehmann's lovegrass was a function of both the size of the tussock and the density of surrounding vegetation. None of the tussocks that had other tussocks a few centimeters from the edge of the test tussock that provided total cover suffered any kangaroo cutting. The extent of tiller cutting increased with increasing exposure (percent of tussock periphery exposed to open space of more than fourty centimeters). Small tussocks in an open space had the highest number of tillers cut by kangaroo rats. The importance of space around a grass plant for access by kangaroo rats was confirmed by measurements on the annual Mexican witchgrass (*Panicum hirticaule*). Mexican withgrass plants growing in patches with less than 30 percent cover by adjacent plants loss all of the flowering tillers to cutting by kangaroo rats. Tiller loss declined with an increase in other plants growing around the Mexican witchgrass plants. Mexican witchgrass plants growing under other plants suffered no loss of tillers to kangaroo rats. These studies clearly show that grasses growing in open patches are more likely to suffer tiller loss to kangaroo rat herbivory than grasses growing in high density patches.

Mammalian Predators on Rodents

The most important rodent predator is undoubtedly coyotes. In one of our rodent population studies when we were checking traps at dawn, we found several traps that had been sprung and closed on the first two lines of a ten line grid. We then heard a trap snap shut from about two lines away from our position. We immediately suspected that a coyote had been "running" our trap line. When we examined the soil around sprung traps, our suspicions were confirmed. There were distinct coyote tracks around the sprung traps. The coyote(s) had learned how to place a paw on the trap and use the other paw push the trap door open. When the kangaroo rat or other rodent tried to escape through the opening, the coyote would snap up his breakfast. From this experience, we learned to appreciate the brain power and versatility of this important rodent predator.

A pair of coyotes searching a tobosa grass area for rodents. (Photo by Amilee Pasco)

Kit foxes (*Vulpes macrotis*) are well adapted desert animals. Kit foxes hunt primarily at night but may hunt during the early morning and late afternoon when light intensity is low. They typically occupy multiple dens which the either dig themselves or modify burrows of other animals. We had the good fortune to watch a family of kit foxes that modified a banner tail kangaroo rat burrow for a natal den. That kit fox pair produced four young. We were able to watch the young foxes play at the edge of the den and were able to photograph the young. That was the only year that we had a kit fox den at that location. Kit foxes prey primarily on rodents and rabbits but are known to eat birds, amphibians, carrion and some fruits.

Bobcats (*Lynx rufus*) are widely distributed in the Chihuahuan Desert occupying a variety of desert habitats plus riparian woodland and shrubland. Critter cameras at the Mesilla Valley Bosque Park have documented the presence of this predator in the Rio Grande river valley habitat. We have seen bobcats on several occasions in the early morning or late evening hours while working in the Jornada Basin research sites. While jackrabbits and desert cottontails are the primary prey of bobcats, they prey on rodents and birds in the northern Chihuahuan Desert. Bobcats have large home ranges and cover long distances in their hunting forays.

Badgers (*Taxidea taxus*) are primarily nocturnal predators that are adapted for digging prey from their underground burrows and nests. We have seen badgers on several occasions when traveling to the Jornada research sites in the early morning. Once when I was taking an ecology class to the Jornada to teach field sampling techniques, we spotted a badger a few yards off the road. The students tried to surround the badger but they quickly ran off when the badger came at them in an attack mode. We frequently found evidence of badger predation where rodent burrows had been excavated by large pits and the tell-tale piles of fresh soil. We also found where badgers had excavated honey pot ants (*Myrmecocystus* spp.) apparently to raid the honey pot chambers. Badger excavation of honey pot ant nests did not always destroy the colony because we frequently found new nest entrances at the edge of the pit or in the pile of excavated soil at one side of the pit. Badgers have been reported to prey primarily on pocket gophers (Geomyidae), spotted ground squirrels (*Spermophilus spilosoma*), kangaroo rats (*Dipodomys* spp.), woodrats/pack rats (*Neotoma* spp.)

A family of kit foxes occupied a banner tail kangaroo rat burrow near a soaptree yucca. The playa lake where the rodent trapping grids were located is the background.

Larger Herbivores

The Chihuahuan Desert is home to two medium size herbivores, black tail jack rabbits (*Lepus californicus*) and the desert cottontail (*Sylvilagus auduboni*). These rabbits dig out oval shallow pits, called forms, under dense foliage shrubs. Rabbits lie in these shallow pits to unload heat to the cooler soil. This is an important behavior in mid-summer when sunlight is intense and air temperatures are higher than 85^{O}F. Even in midsummer when disturbed by an approaching person, desert cottontails bolt from their shaded shelter, run off, and disappear from sight. However when it is hot, jack rabbits appear to be reluctant to leave their cool environment and remain on their shaded form until nearly touched by the approaching person. Only then will the jackrabbit get up and move slowly to a nearby shade. If the person does not make threatening moves and retreats a few yards, the jack rabbit will return to its form. In summer jack rabbits typically use forms on the north, east, and west sides of shrubs. A jack rabbit moves in a sequence, from the west form to the north form and to the east form as the day progresses from morning to evening. The differences in avoidance behavior of jack rabbits and cottontails are probably related to size differences and efficiency of cooling during the heat of the day.

Other than cattle, the only large mammals that we regularly saw were pronghorn antelopes, *Antilocapra americana*. My first encounter with pronghorns really surprised me. A small herd of pronghorn were in a tobosa grass-burro-grass area next to the road into our research site. The herd ran across the road in front of our vehicle which was stopped to get a better look at these beautiful animals. I couldn't believe what I saw next. When the herd got to the three strand barbed wire fence, instead of jumping the four foot fence which I expected, the pronghorn hit the ground; slid under the bottom strand and jumped to their feet on the other side of the fence. After that first encounter, we regularly saw the small herd 12-20 animals in the grassland areas just off the road. The pronghorn were generally in that area in the winter months and early spring. Watching pronghorns led to one of my studies of the effects of harvester ant nests on spring annual plants. We frequently would stop for a few minutes to watch the pronghorns and to try to ascertain their feeding habits. We observed the pronghorn feeding on dark green circles in the tobosa grass flats. When we returned from our research measurements, we trekked out into the tobosa grass flats to see what the pronghorn had been grazing. The dark green circles were stork's bill (*Erodium texanum*) that were essentially a monoculture around the harvester ant colonies. Smaller stork's bill plants were scattered among the tussocks of tobosa grass but the stands around the harvester ant nests were dense, large plants that were approximately double the size of the storks bills in the grassland matrix. We collected soil cores from the areas adjacent to the harvester ant nests and an equal number of soil cores in the surrounding grassland. Analysis of the soil showed that the available nitrogen was nearly ten times higher in the soils around the nests than in soils in the grassland matrix. Those observations led us to a series of studies of the effects of the harvester ant (*Pogonomyrmex rugosus*) nests on the distribution and biomass production of annual plants and on the soil parameters that were affected by the behavior of the ants.

A pair of pronghorn antelope in a grassland area.

Bird Communities

There is a surprising number of breeding bird species in the northern Chihuahuan Desert. Many of these species do not nest every year depending upon the rainfall of the previous year and abundance of insect prey. As part of the Long Term Ecological Research Program, we established one kilometer transects (approximately 0.6 miles) in five of the major habitat types of the northern Chihuahuan Desert in southern New Mexico: creosotebush shrubland plus a large arroyo, tarbush shrubland with a large patch of burro grass an bare soil), a mesquite tall shrub fringe around a dry lake (playa), a mesquite coppice dune site, and a black grama grassland site with few mesquite. The average distance for most of the song birds was 160 feet from the center line. Each transect provided a sample of the birds in approximately 22 acres of the habitat sampled.

Black throated sparrows are the most abundant and widely distributed year long residents of the Chihuahuan Desert. There were black throated sparrows breeding in late spring and early summer in all of the habitats examined except on the mesquite coppice dune in one year. That year followed a low rainfall summer and winter. The numbers of black throated sparrows were reduced to one pair on the grassland and tarbush, only two pairs in the creosotebush shrub-land and three pairs in the playa mesquite shrub-land that year. In subsequent years the numbers of breeding pairs of black throated sparrows ranged from one in the mesquite coppice dunes to ten pairs the creosotebush and tarbush areas. In years with average or above average rainfall, the numbers of black throated sparrows nesting in the mesquite coppice dunes and black grama grassland were low ranging between two and three pairs. Numbers of breeding black throated sparrows were much higher in the creosotebush shrub-land, playa mesquite shrub-land and tarbush shrub-land. In these habitats numbers of breeding pairs ranged between four and ten in years with average or above average rainfall.

Black throated sparrow

Black-throated sparrows are insectivorous during the summer growing season. The number of eggs per clutch varies with prey availability. The most common prey types are grasshoppers and moth or butterfly larvae. Black-throated sparrows exhibit opportunistic foraging. When there was a large emergence of Mydas flies, the sparrows concentrated their feeding effort on these flies. Following rains that initiated termite flights, both male and female sparrows took termites to nests. Black-throated Sparrows took termites to the nests with loads of three to ten termites per trip. During termite mating flights, female termites shed their wings and move around on the soil surface where they are easy prey for birds, lizards and frogs.

Table 1. Numbers of birds recorded in different habitats during the five summer breeding seasons. Number in parenthesis is number of years a bird was recorded in that habitat. Numbers are lowest and highest number of birds recorded.

species	grassland	mesquite	creosotebush	tarbush	Playa shrub
Ash throated flycatcher	1-2 (2)	0	2-4 (2)	0	1-2 (3)
Cassins sparrow	3-4 (2)	0	1-2 (2)	2-4 (3)	
Cactus wren	1-4 (2)	1-4 (3)	1-4 (5)	0	1-2 (2)
Chihuahuan raven	6 (1)	2 (1)	6 (1)	2 (1)	0
Crissal thrasher	1 (1)	1 (3)	2-3 (3)	1 (0)	2 (2)
Gambel quail	0	0	1 (1)	0	0
House finch	0	8 (1)	2-10 (4)	0	0
Horned lark	1 (1)	0	0	1-4 (3)	0
Ladderback woodpecker	0	0	0	0	2-4 (2)
Lesser nighthawk	0	1 (1)	2-4 (3)	3 (1)	1-10 (2)
Loggerhead shrike	1-2 (3)	1-4 (2)	1-6 (2)	1-2 (2)	1-4 (3)
Meadowlark	2-6 (2)	6 (1)	1 (1)	1-6 (4)	2 (3)
Mockingbird	2 (2)	1-4 (4)	1-2 (4)	1 (2)	2-4 (5)
Mourning dove	1-2 (4)	1-4 (3)	1-4 (3)	1 (1)	1-3 (3)
Pyrrhuloxia	0	0	1-2 (5)	0	4 (1)
Roadrunner	0	0	1 (2)	0	1 (1)
Scaled quail	0	1-2 (3)	1 (1)	1 (1)	1 (1)
Scotts oriole	1-2 (3)	0	1-4 (4)	3 (1)	1-7 (4)
Says Phoebe	1 (1)	1 (1)	1-3 (4)	1 (1)	1 (1)
Swainsons hawk	1 (2)	0	1 (2)	1 (1)	1 (1)
Verdin	0	0	1-2 (3)	1 (1)	1 (1)

Most of the birds that breed in the Chihuahuan Desert are insectivores. There are few species that are seed feeders: house finches, mourning doves and quail. The house finches were found in areas that were less than 1 mile from ranch buildings and water sources. House finches were seen picking seeds from cattle and horse dung. Roadrunners feed on large insects but feed their young on lizards and snakes. Female roadrunners will not mate until the male brings a lizard as a gift to the female. This behavior assures that lizards are active and available as prey to feed the hatchling chicks.

Scaled quail at the base of a fence post. Scaled quail are seed eaters and also eat insects and green vegetation.

In addition to black throated sparrows, there were two additional bird species that were recorded in all five years at one of the sites: cactus wren and Pyrrhuloxia on the creosotebush transect. Both species were present and singing from tall mesquite along the margin of the large arroyo. There are other species that are known to have breeding populations most if not every year regardless of the rainfall. These include cactus wrens, crissal thrashers, lesser nighthawks, meadowlarks, scaled quail, and Swainsons hawks. Cactus wrens, crissal thrashers, meadowlarks and scaled quail are yearlong residents. Lesser nighthawks and Swainsons hawks migrate south in the winter. Swainsons hawks leave in late September to early October and fly to Patagonia in Argentina. Adult Swainsons hawks may occupy the same nest for up to five successive years after their return from Argentina in April.

A Swainson's Hawk on a nest in a large mesquite. These hawks will improve an old nest each spring and use the same platform for several consecutive nesting seasons.

A turkey vulture soaring over the Chihuahuan Desert in summer looking for carrion.

Nesting sites

. On several occasions we recorded ladder-back woodpeckers on fence posts of the perimeter fence of the playa pasture. Ladderback woodpecker nest holes were located in one or two of the fence posts and those nesting birds foraged for insects in the tall mesquite at the playa fringe. Ash throated fly catchers were associated with tall mesquite in the grassland and playa shrub habitats and with small trees on the edge of the arroyo in the creosotebush habitat. Cassins sparrow is described as a grassland specialist and was recorded on only during average or above average rainfall yeas. Chihuahuan ravens are known to use man-made structures for nesting sites. We found Chihuahuan raven nests on power line tower structures, on windmill platforms and in tall mesquite. Chihuahuan ravens are feeding young from late April to early June depending upon the year. Some of the ravens recorded in Table 1 could have been young of the year. Since ravens fly up to six miles from the nest to feed, ravens nesting in the Rio Grande drainage basin may travel to the agricultural areas in the river valley to get band-wing grasshoppers and other large insects. Most of the kingbird nests that we have found have been located in the dry flowering stalks of soaptree yucca that had a caudex (stem/trunk) that was more than seven feet to the base of the leaves.

A western kingbird

A roadrunner (photo by Al Krueger)

A Say’s Phoebe perched on a mesquite branch.

more than 7 feet high. Crissal thrasher nests were found in tall mesquite at the edges of a large arroyo. Says phoebes preferred man-made structures as nesting sites. Says phoebes regularly nested at a weather station or equipment storage structure that provided shade for the nest and the chicks.

Hawk or raven nest in a mesquite tree in a black grama grassland with scattered mormon tea shrubs. (Photo by Vic Crane)

Winter Birds

Walking the LTER bird transect in black grama grassland, provided a most memorable moment in my life. I was walking the transect in late spring and was concentrating on birds that were flying in and out of the few large mesquite in the grassland. Suddenly a huge bird took off from almost under foot. The tips of the primary wing feathers brushed my face and my heart nearly stopped from the rush of adrenalin. The shadow of the bird was immense, adding to my fright. I didn’t need binoculars to tell me that I had nearly trod on a mature golden eagle which was so large that I felt like a prey item. I was frozen in space and when I recovered my composure sufficiently to look around, I realized why the eagle had not flushed when I approached. The eagle had been feeding on pronghorn fawn. A few pronghorn (herd of 6-10 individuals) were seen occasionally in the grassland areas on the Jornada especially in the winter and spring. One of the young pronghorn from that small herd was probably the victim of the golden eagle. The eagle continued to soar within visual range and undoubtedly went back to its kill when I departed. That was the only golden eagle recorded that year on the LTER transects.

The northern Chihuahuan Desert provides important winter habitats for a number of western North American birds. Several raptor species winter in grassland or shrubland habitats.

These include Prairie Falcon, Northern Harrier, Red-Tail Hawk, and Golden Eagle. The number of raptors varies considerably among years depending upon the availability of prey i.e. rabbits, rodents, and birds.

Three habitats provided resources for large numbers of winter migrants: mesquite coppice dunes, tall mesquite playa fringe, and black grama grassland. The winter migrants were mostly sage sparrows, Brewers sparrows, and white-crowned sparrows. Sage sparrows were most abundant in the mesquite coppice dune habitat ranging in abundance from one to three per acre. In the grassland and tall mesquite fringe habitats sage sparrows occurred at densities of less than one per acre to two per acre. Brewers sparrows were found in the black-grama grassland only one winter. Brewers sparrows were most abundant in the mesquite coppice dune habitat with densities ranging from one per acre to three per acre. In the playa habitat, Brewers sparrows were at lower abundance ranging from less than one per acre to two per acre in the five winters of the study. Wintering white-crowned sparrows occurred at less than one per acre and were absent from the grassland during three of the winters and from the playa fringe habitat during two of the winters. During the years of this study, large numbers of wintering white crowned sparrows were reported from the brushy irrigation return drains and willow thickets along the Rio Grande river by the Audubon Christmas Bird Counts. Other winter birds that were found some years were dark-eyed juncos and lark buntings. The flocks of these birds move frequently and therefore are not adequately sampled using transects.

Wintering grassland birds were studied on the Armendariz Ranch northeast of Truth or Consequences, N. M., the Uvas valley grasslands west of Hatch N. M. and the Otero Mesa grasslands southeast of Alamogordo. The most abundant bird in these grasslands was horned larks. In winter, horned larks form flocks of ten to forty birds and are widely distributed in the grassland. In grasslands with tall mesquite, Chihuahuan Ravens are relatively common. Ravens, red tail hawks and kestrels frequent perch on power line structures in Chihuahuan Desert,

An American Kestrel in flight.

Horned lark on a mesquite stem in a black grama grassland (Photo by Vic Crane).

Reptiles

Habitat, seasonal and daily activity patterns of lizards

During the warm summer months, the most frequently encountered vertebrate animals are lizards. The Chihuahuan Desert is home to many species of lizards and lizards utilize the full range of available habitats in this region. The most common lizard is the side-blotched lizard, *Uta stansburiana*, which may even be seen on warm, sunny days in mid-winter. Soon after arriving in New Mexico, I began studies of the physiology of side-blotch lizards. A graduate student and I captured these lizards by hand or by noosing. Side-blotch lizards were easily kept in aquaria in the laboratory and were kept healthy by feeding them crickets. Side-blotch lizards are essentially an annual turnover species because most live less than one year. They mate in the late spring and young hatch in May and June.

A male side-blotch lizard, *Uta stansburiana.*

We used several techniques to study habitat use, daily activity patterns and interactions among lizard species. Initially we used pit-fall traps to census lizard species in various habitats and to obtain estimates of relative abundance. However we quickly learned that the results of pit-fall trapping must be interpreted with care because lizards that are active hunters are captured more frequently than are lizards like side-blotch lizards that are "sit and wait" hunters.

In order to add a "correction" to the pit-fall traps, we established two additional sampling methods for population estimates and to study the behavior of lizards. We established walking transects across study plots of approximately 2 acres in size. These paths were walked early to mid-morning and late afternoon when most of the lizards were active. The lizards that were either flushed from hiding or seen foraging were recorded by species and by location. The most effective method for studying the activity patterns of the lizard species the use of towers on which an observer could observe lizards up to 200 feet from the tower.

Using these techniques, we examined the lizard communities on a Chihuahuan Desert watershed. The lizard communities were studied on a piedmont creosote bush area (bajada) and associated arroyo; a mesquite-mormon tea, soaptree yucca vegetation around the perimeter of the playa lake, and the playa lake grassland basin. Rainfall patterns were very different in each of the five years of the study. Effective rainfall during the first year of the study was limited to one event of 2.3 inches at the end of July that resulted in flooding of the barren playa lake. However by mid-August, the playa bottom was dry and vegetated with vine mesquite grass (*Panicum obtusum*). Rain events during the second year were small, providing very little effective moisture and very little vegetative growth. Abundant rainfall in the next two years resulted in growth of both perennials and annuals. The summer rainfall in the last year of the study was close to the long term average. The abundance of insects that are the prey base for lizards was correlated with the amount and distribution of rainfall. The abundance of grasshoppers and crickets was highest during the second and third year of the study.

Seven lizard species were permanent residents of the mesquite, mormon tea, soaptree yucca area: western whiptail (*Cnemidophorus tigris*), checkered whiptail (*Cnemidophorus tesselatus*), side-blotch lizard (*Uta stansburiana*), desert spiny lizard (*Sceloporus magister*), leopard lizard, (*Crotophytus wislizenii*), roundtail horned lizard (*Phynosoma modestum*) and Texas horned lizard (*P. texanum*). There were four permanent resident lizards in the creosotebush shrubland: western whiptail, checkered whiptail, round tail horned lizard, and leopard lizard. In the arroyo shrub association the permanent residents included: greater earless lizard (*Cophosaurus texana*), side blotch lizard, desert spiny lizard, and leopard lizard. Before the development of vine mesquite grass on the playa basin, the basin was essentially devoid of lizards. After the basin was vegetated there were many lizards trapped or caught on the playa basin that were transients from nearby habitats: all of the lizards from the mesquite- mormon tea-soaptree yucca area plus the little striped whiptail (*Cnemidophorus inornatus*). In addition there were two species that were classified as immigrants from grassland, Chihuahua whiptail (*Cnemidophorus exsanguis*) and little striped whiptail and one immigrant from the mountain boulder slope: the great plains skink, (*Eumeces obsoletus*).

A male side-blotch lizard sunning on a bare patch (photo by Al Krueger)

There was a relationship between abundance of adults of most species and the rainfall of the two previous years. The abundance of western whiptails doubled in the fourth year of this study in comparison to the two previous years. This increase in abundance was attributed to larger clutch size in the third year of the study and to the rapid growth of juveniles in the third year as a result of abundant insects. Overwinter survival of most lizards is dependent upon size and fat storage. Years with abundant food resources are followed by years of increased populations of adult breeding lizards. The numbers of adult western whiptails per acre on the creosotebush plots returned to the numbers recorded in the first three years of the study in the last year. However the western whiptails in the mesquite, mormon tea, soaptree yucca area remained at the high numbers of the previous year in the last year of the study. Few hatchlings of western whiptails were seen in the year with little effective moisture which accounts for the low recruitment of adults the following year.

Western whiptails were observed feeding on termites. These lizards used their nose to flip through leaf litter under shrubs and pick up termites and other small insects exposed by this behavior. After watching this species hunt through leaf litter for termites, we found active termites in the leaf litter when the lizards were disrupted by us. These observations led us to examine the morphological differences in shrub structure that resulted in sufficient litter accumulation under shrub canopies for termite foraging.

There were fewer adult checkered whiptails (approximately two per acre) than adult western whiptails (approximately fifteen per acre) on the study areas. Checkered whiptail population size changed little during most years. Numbers of checkered whiptails were lowest in the year following the year with little effective rainfall.

In order to examine the factors affecting the population size of desert spiny lizards, it was necessary to mark and map the distribution because of their largely aboreal behavior. Adult desert spiny lizards exhibited high fidelity to large multi-stemmed mesquite (more than 12 feet in diameter and more than 8 feet in height). Large mesquites with large pack-rat mounds built within the outer circle of stems were preferred habitat for this lizard. The only desert spiny lizards seen that were more than 3 feet from the "home plant" were hatchlings and some females during late June and early July. The number of adult desert spiny lizards was predictable from the number of large mesquite clumps which had packrat nests at the base. Four of the adult desert spiny lizards marked during the first year were found in their original mesquite plants three years later. The territorial fidelity of desert spiny lizards accounts for the stable population size of this species among drought years and years of abundant rainfall. Desert spiny lizards feed on ants and other insects that live on mesquite. Honey-pot ants, *Dorymyrmex* spp., *Formica perpilosa,* and *Iridomyrmex* spp. are ant species that are found on mesquite throughout the growing season. Some of these ants are active in mesquite even during severe drought conditions and they provide a stable food supply for desert spiny lizards.

The changes in population size of the greater earless lizards in the arroyo habitat were similar to those recorded for the western whiptails. Peak numbers of greater earless lizards occurred in the fourth and fifth years of the study as a result of above average rainfall in the third and fourth years.

Side blotch lizards have been classified as an annual turnover species meaning that the average life span of adults is one year. We found that by midsummer most of the adults from the previous year had disappeared and the adult size side blotch lizard were the young of the year. Abundance of side blotch lizards was high (10-12 lizards per acre) in the third and fourth years of the study that had abundant winter-rainfall and above average rainfall in the monsoon season. Side blotch lizard's diet in order of importance is beetles, termites, grasshoppers, ants, and insect larvae. The abundance and availability of these insects is rainfall dependen. The abundance and availability of insect prey is the most important predictor of abundance of ground-dwelling lizards and explains the numerical responses of the lizards during the years of above average rainfall.

Lizards on the creosotebush piedmont emerged from winter dormancy more than four weeks before individuals of the same species became active in the mesquite-mormon tea-soaptree yucca area at the lowest elevation of the watershed. Hatchlings were seen on the creosotebush piedmont up to six weeks earlier than the appearance of hatchlings on the mesquite-mormon tea-soaptree yucca area. Juvenile lizards captured on the creosotebush piedmont were approximately twenty-five percent heavier than juveniles of the same species on the low elevation site in September. Nightime temperatures are higher on the creosotebush piedmont than at the playa edge location as a result of cold air drainage. Frost temperatures are three to four weeks later in the spring and up to three weeks earlier in the autumn in the playa area than on the creosotebush piedmont. The lower temperatures at the playa edge account for the later emergence of hatchlings at this location in comparison to the upland creosotebush location.

There are several other species of lizards that are common inhabitants of other habitats in the northern Chihuahuan Desert. On the mountain with monzonite granite boulders on the slopes, the two most common lizards were the ornate tree lizard, *Urosaurus ornata*, and the collared lizard, *Crotaphytus collaris.* These lizards are confined to the slopes of the mountains and small rock outcrops. In some intermountain basin habitats with a mix of shrubs and grasses, eastern fence lizards (*Sceloporus* *undulatus*) are relatively abundant and in some areas approach the abundance of side blotch lizards. The leopard lizard (*Gambelia wislizenii*) can be found in most of the desert habitats but is known to avoid dense grass or brush areas which interfere with running. Leopard lizards are both active and sit and wait predators that feed on large insects such as cicadas, grasshoppers, and crickets; large spiders, lizards and small rodents.

Desert grassland habitats are home to some very interesting whiptails: the desert grassland whiptail (*Cnemidophorus uniparens*) and the New Mexican whiptail (*Cnemidophorus neomexicanus*). The New Mexican whiptail has a very limited distribution in the grasslands west of the Rio Grande in southern New Mexico, and the grasslands of the Rio Grande drainage and the Jornada Basin. These two species of whiptails are female only species. They produce viable eggs and young without sperm from males. This is known as parthenogenesis and is rare in vertebrate animals.

Intensive study of individually marked lizards provided some interesting insights into the activity patterns of western whiptails, greater earless lizards, and side blotch lizards. None of the marked individuals were seen every day. Individual western whiptails were seen on average about one fourth of the days as were most of the greater earless lizards. Three of the large male earless lizards were seen on two thirds of the days. There were thirty western whiptails with sufficient repeated observations to provide reliable data on activity patterns. Eight were active only during early morning hours, five were active during the middle of the day, seven were active only in the afternoon, seven were active both morning and late afternoon, and three were active throughout most of the day. Of the thirteen greater earless lizards, three were active only in the morning, two were active only in the afternoon, three exhibited both morning and afternoon activity and five were active throughout the day. Individual side blotch lizards exhibited variable day time activity patterns with five having morning only activity, four exhibiting bimodal (morning and late afternoon) activity, and four with only late afternoon activity.

When we mapped the movements and locations of the individually marked lizards, we found no overlap in the foraging areas of the side blotch lizards. Male and female western whiptails exhibited almost complete spatial overlap. Individual male western whiptails exhibited spatial overlap ranging from one hundred percent of the foraging area of other males to as little as five percent. Foraging area overlap by two individuals was most common but foraging areas were shared by three or four males in more than half of the mapped foraging areas. The temporal behavior patterns of the lizards reduced the potential competition with others of the same species for prey and hunting space.

Lizard Communities in Different Habitats

As part of the Long-term Ecological Research Program, we established pit-fall trap grids in several different habitat types: creosotebush slopes transected by an arroyo, tarbush flats, upper piedmont grasslands, basin grasslands, mesquite coppice dunes, and mesquite-grass mosaic. Side-blotch lizards (*Uta stansburiana*) were the most abundant lizards in all of these habitats during all eight years of the monitoring study. Side blotch lizard hatchlings were recorded from late June through mid-August. One female side-blotch lizard actually laid eggs in the trap in mid-July. The highest number of juvenile side-blotch lizards was reported in mid-August along with low numbers of juvenile checkered whiptails, western whiptails, and greater earless lizards.

The highest lizard diversity was in the creostebush gravelly to sandy piedmont slopes, piedmont grasslands and basin grasslands with twelve species of lizards in each habitat. The greater earless lizard (*Cophosaurus texana*) was trapped only in the creosotebush shrubland areas near arroyos. Great plains skinks (*Eumeces obsoletus*) were found only in the upper piedmont grasslands and the upper creosotebush slopes. Basin grasslands and upper piedmont grasslands were the domain of desert grassland whiptails (*Cnemidophorus uniparens*) and the New Mexico whiptail (*Cnemidophorus neomexicanus*). Little striped whiptails (*Cnemidophorus inornatus*) were most abundant in the basin grasslands, moderately abundant in the creosotebush and tarbush shrublands, and were found infrequently in the mesquite/grass mosaic and mesquite coppice dunes. The lesser earless lizard (*Holbrookia maculata*) was recorded infrequently in most habitats but fairly frequently in the basin grasslands. The eastern fence lizard (*Sceloporus undulatus*) was most frequently trapped in the tarbush shrubland and infrequently in the basin grasslands and coppice dunes. Horned lizards are not adequately sampled by pit-fall trapping. Neither species of horned lizard were trapped in the coppice dunes or mesquite/grass mosaic but were seen in all of the habitats studied. The harvester ants and honey-pot ants that are the primary prey species of horned lizards are components of all of the habitats studied. (See chapter on horned lizards and ants)

A greater earless lizard sunning on a rock at the edge of an arroyo. (Photo by Al Krueger)

A striped whiptail searching for insects under an annual buckwheat plant. (Photo by Al Krueger)

Habitat Modification

As part of a study designed to examine vegetation changes after shrub cover had been reduced, we compared habitat use by the two most abundant lizards: side blotch lizards and western whiptails. This study was conducted in an area treated with a herbicide that defoliated shrubs and an adjacent area with the same vegetation composition that had not been treated with the herbicide. The study was initiated ten years after the herbicide treatment. The vegetation of the treated area was mostly large tussocks of bush muhly grass (*Muhlenbergia porteri*), mesa dropseed (*Sporobolus flexuosus*), and fluff grass (*Dasyochloa puchella*) with a few surviving creosotebush and tarbush shrubs. The number of mesquite was similar on the two plots but the mesquite were young, small plants on the treatment plot and older, large plants on the untreated plot. The vegetation of the untreated plot was nearly equal numbers of creosotebush, tarbush, and mesquite shrubs. Approximately half of the shrubs in this area had small bush muhly grass tussocks around the basal stems. Small tussocks of mesa dropseed and fluff grass were very sparse.

Lizards were monitored with binoculars from a 7 foot observation tower in the center of each plot. The central observation tower provided clear views of lizards over an area of approximately two acres. The lizards were identified by paint spots or bars at the base of the tail. We captured lizards in pit-fall traps to obtain animals for marking. More side-blotch lizards were captured on the herbicide modified plot (246) than on the natural plot (194). Fewer western whiptails were captured on the herbicide modified plot (117) than on the untreated plot (153).

Side-blotch lizards employed a “sit and wait” predation strategy. These lizards typically sat under the vegetation surveying the surrounding area. When a side-blotch lizard spotted a potential prey (usually a small arthropod), it would dash from its sheltered spot, capture the prey and then return to its original location. Side-blotch lizards occasionally captured insects when moving from one plant to another but this was relatively infrequent. When side-blotch lizards did move to another plant, those movements were usually in a circular area. After visiting several plants, a lizard would return to the area where it was first seen.

Western whiptails are active foragers. They moved from plant to plant and searched through the litter at the base of plants if there was a litter layer present. Western whiptails moved relatively rapidly through the area, traveling as much as 150 feet in ten minutes if the animal did not encounter any plant litter accumulations. Occasionally western whiptails would climb into a bush muhly grass tussock or tarbush shrub and crawl around on the branches or grass strands. Movement through grass tussocks or shrub branches lasted less than a minute and it was not possible to determine if the animal captured any prey. Foraging bouts under the shrubs of the untreated plot were longer than the search bouts under plants of the herbicide treated plots.

The frequency of visits and length of time spent under each plant are good measures of habitat suitability for these lizards. Side-blotch lizards used plants with the same frequency as would be predicted from the cover of the plant species on the plots. This lizard used the plants as cover from potential predators and concealment for its “sit and wait” feeding strategy. The higher grass cover and lower shrub abundance on the herbicide treated plot seemed to provide a marginally better habitat for side-blotch lizards than the more open untreated plot.

The active foraging behavior of western whiptails and the importance of leaf litter accumulations for their preferred prey, accounts for the differences in abundance and foraging behavior in the herbicide treated and untreated plots. Because whiptails spent less time foraging under grass tussocks and small shrubs on the herbicide treated plot, the amount and quality of litter appears to be the most important factor affecting the behavior of this species.

Snakes

Snakes are seldom seen residents of the northern Chihuahuan Desert. With the exception of one study on coachwhip snakes (see below) most of the information that we have gleaned on Chihuahuan Desert snakes is anecdotal. Most Chihuahuan Desert snakes are crepuscular, (active a few hours after dawn and a couple of hour before sunset) or nocturnal. The snake species most frequently encountered in our research activities were gopher snakes (*Pituophis melanoleucus*), western patch-nosed snakes (*Salvadora hexalepis*), coachwhip snakes (*Masticophis flagellum*),western diamondback rattlesnakes (*Crotalus atrox*), and prairie rattlesnakes (*Crotalus viridus*). The boulder strewn slopes of Mt. Summerford in the Dona Ana Mountains were habitat for rock rattlesnakes (*Crotalus lepidus*) and black-tailed rattlesnakes (*Crotalus molossus*). On several occasions when the playa lake flooded, we encountered Mexican hognose snakes

(*Heterodon nasicus*) at the edge of the water or on the drying lake bottom after the water receded to a series of small puddes. Hognose snakes feed on frogs and toads which explains their presence following a flood event.

A gopher snake on a paved road. (Photo by Al Krueger)

There are several memorable encounters with rattlesnakes in the years that I was actively involved in research in the desert north of Las Cruces. While running live traps for rodents I released a kangaroo rat from the aluminum trap. The rat hit the ground and proceeded to hop toward a nearby creosotebush. Neither the kangaroo rat nor I saw the diamondback rattlesnake under that bush. The snake struck the kangaroo rat which took another three hops then fell to the ground with hind legs twitching. The rattlesnake slowly crawled to the dead kangaroo rat and swallowed the rat head first. After the tail of the rat disappeared into the snake's mouth, the snake crawled into the sun and rested. I gave the snake a wide berth to allow him to continue to digest his prey. One morning a few years later when we stopped to work on plots that were fenced with chicken wire mesh, we found a large western diamondback wedged in one of the holes in the fence. The snake was dead probably from overheating. Because the snake was exiting the plot with a large bulge in the stomach area, we surmised that the snake had entered the plot without a problem; had eaten a rat and then was trapped in the fence as it tried to leave. The scales that were depressed when the snake moved forward were pushed up by the wire thereby preventing the snake from reversing out of the fence.

We actually encountered more rattlesnakes while engaged in measuring grass cover or grass production than in any other research activity. The most memorable encounter was nearly putting my hand on a Massasauga or pigmy rattlesnake (*Sistrurus catenatus*). Fortunately for me, it was early in the morning and that little rattlesnake was not moving very fast. Another time when we were measuring grass cover in a fenced plot, the ten year old daughter of one of the students came to me and said very calmly, "there is a small rattlesnake near a rat burrow where you are headed." We stopped our work and stood looking at a small (approximately two feet long) prairie rattlesnake that was coiled up in a slight depression where it looked very much like a dried dung pat. This was in the morning in mid-November and the rattler was probably sunning in order to digest the contents of its stomach.

A western diamondback rattlesnake: Note the black and white bands on the tail below the rattle. (Photo by Al Krueger).

We would see snakes on the road about every third or fourth trip to the Jornada during summer months when we worked from sun-up to midday. When we saw a snake we would stop and try to move the snake off the road. Over the years we probably moved more than fifty snakes off the road(s). There were about equal numbers of gopher snakes and rattlesnakes: western diamondbacks and prairie rattlesnakes. We moved the snakes off the roads because if left to "sun" on the road, there was a high probability that they would end up as "road kills". On the return to the university at midday, it was not unusual to see turkey vultures on the carcass of a dead jackrabbit or dead snake.

Feeding Behavior of Coachwhip snakes (*Masticophis flagellum*)

One of my graduate students, K. Bruce Jones, did a field study of the feeding behavior of coachwhip snakes in two habitats: a creosotebush shrub-land and a mesquite coppice dune site. The creosotebush shrub-land produces a sparse shade – full sun environment. The mesquite dunes are between three feet and seven feet high and between fifteen feet and fifty feet in diameter. Mesquite dunes are coppiced on the crowns of the dunes with up to 100 stems per coppice and an average stem height of less than twelve inches. The coppiced mesquite produces almost continuous shade on the crown of the dunes during daylight hours.

Coachwhip snakes were thought to be active searching predators on lizards. This study was designed to examine the hypothesis that habitat structure has no influence on the feeding behavior of an active search predator. The study was conducted from April through September. Twelve coachwhips were captured and followed in the mesquite dunes and seven coachwhips in the creosotebush shrubland. Individual snakes were captured, marked, and released at the point of capture. After the snakes recovered and returned to normal search behavior, each snake was followed, behaviors recorded, and time spent in each behavior. The behaviors recorded were: inactivity, active pursuit of prey (chasing prey), prey handling, and movement not associated with active pursuit of prey. It was not possible to determine if snakes were thermoregulating or resting, this was recorded as inactivity. Overnight cover sites were marked so that the individual snake could be relocated the following day.

In both habitats in spring and autumn, coachwhip snakes initially exposed only the head outside of the burrow in which the snake spent the night. This head basking behavior varied in time and duration possibly because of wind or other environmental factors. Following head basking, snakes actively searched for lizards and chased prey after visual contact. The time spent in pursuit depended upon the escape behaviors of the lizards and the structure of the habitat. When chased by coachwhips the western whiptails (*Cnemidophorus tigris*) and greater earless lizards (*Cophosaurus texana*) avoided the predator by moving in and out of cover provided by the shrubs. Tiger whiptails and greater earless lizards escaped pursuing coachwhip snakes by “out-running” the snake rather than going into the nearest cover. Side-blotch lizards were normally near a rodent burrow or close to or on a rock. Escape behavior of side-blotch lizards consisted of rapid retreat to shelter under rocks or in burrows. Coachwhip snakes that pursued side-blotch lizards were either immediately successful or lost the prey in their retreats. Therefore pursuit times tiger whiptails and greater earless lizards were much greater than pursuit times for side-blotch lizards.

Coachwhip snakes successfully captured only 17% of the lizards that were pursued. The snakes were able to subdue and eat only 73% of the captured lizards. This snake was most successful at capturing side-blotch lizards and less successful at capturing tiger whiptails and greater earless lizards. After capturing a lizard, the snakes spent several minutes attempting to control and swallow the live prey. Snakes controlled the prey by pinning the lizard to the ground with their neck perpendicular to the ground. Lizards occasionally escaped from the coachwhip snakes during this handling process which accounts for the smaller number eaten than captured.

In spring and early autumn, coachwhip snakes were active during most of the day. In the summer months in the creosotebush shrubland, coachwhips hunted early morning to mid-morning; retreated to burrows during mid-day, and emerged in the late afternoon and hunted until dusk. In the mesquite coppice dune area, the snakes maintained activity throughout the day. In the coppice dune area during summer, coachwhips exhibited a different prey capture behavior than recorded in the spring and autumn. In summer, the early morning hours were spent basking and moving from dune to dune. Although coachwhips encounterd several lizards in the open areas between dunes, they did not give chase during the early morning hours. From late morning to mid-day, coachwhips moved into the shade of the coppiced mesquite on the dunes and coiled around the base of a mesquite stem. Snakes remained inactive with their heads resting on the body coils until a lizard entered the area. The snakes would then extend the body in a strike towards the lizard with the snake's tail firmly around the stem. This resulted in a much higher capture rate (80%) than the free moving pursuit in creosotebush habitats (17%) and also reduced handling time and prey escape. Coachwhips in the creosotebush habitat successfully swallowed only 75% of the lizards captured initially compared to 99% of lizards that were swallowed in the coppice dune habitat.

A mesquite coppice dune with a mormon tea on the crest of the dune

This study clearly demonstrated the behavioral plasticity of coachwhip snakes. The mesquite coppice dunes are a relatively recent (within the past century) landscape component of the Chihuahuan Desert. In order for coppice dunes to develop, mesquite seeds had to be dispersed from the original habitat for this shrub which was margins of large dry washes or dry, playa lakes. Small mesquite shrubs caused the accumulation of sand around the base of the multistemed shrubs. Over time, the terminal stems were the only part of the plant that existed above the crest of the dune. This coppice of stems, with leaves during the growing season, provided a unique habitat for coachwhips. In this habitat in summer, the snakes were able to give up the active pursuit mode of predation in favor of a “sit and wait” strategy. Whiptail lizards that moved from coppice to coppice in search of food became vulnerable to predation by motionless coachwhip snakes that were probably much less visible when motionless in the shade of the coppice. The “sit and wait” predator behavior is a marked shift in the behavior of snake that has been an active pursuit predator for eons prior to the development of the coppice dunes.

Floods and Frogs

One of the most fascinating and exciting things about the Chihuahuan Desert is the occasional, but infrequent, large convectional storm (thunderstorm) that drops enough water in minutes to cause overland flow and flooding of arroyos. Anyone lucky enough to be caught somewhere dry and safe in such a deluge will witness some spectacular events. Once when we were working at the bottom of a watershed, we jumped into the truck to wait out what was usually a brief thunder shower. Soon the rain was so intense that we could not see out the windshield. There were several streaks of lightning that were followed immediately by explosive thunder. One of the lightning streaks traced the barbed wire fence along the edge of the road creating a halo of bright light around the wire. The proximity of the lightning strikes to our vehicle made us very appreciative of our shelter.

Through the side windows we could see several inches of water moving past the vehicle. The moving water had waves that made it look a bit like watching the sea from a breakwater. Then we noticed that there were frogs riding the waves of the moving water while singing loudly. Here we were witnessing an “it’s raining frogs” event. The rain continued for more than 30 minutes and when it ceased, we were treated to a deafening chorus of the mating calls of five species of frogs (Couch’s spadefoot toads, (*Scaphiopus couchi*), little green toads, (*Bufo debilis*) western spadefoot toads, (*Spea hammondi*) plains spadefoot toads, (*Spea bombifrons*) and great plains toad (*Bufo cognatus*) calling from the now-filled dry lake or playa.

The large numbers of frogs calling from the flooded playa caused us to quickly design a study to examine habitat selection or lack thereof by the calling males. We conducted transects across the flooded playa by moving slowly so as not to disturb the frogs, identifying the species and their location with respect to vegetation and depth of water. The males choose the appropriate areas of the flooded playa for their eggs and tadpoles . From this study we learned that the western spadefoot toads were concentrated in open water deeper than five inches. Most of the plains spadefoot toads were calling from areas with sparse vegetation with water deeper than five inches. The Couch’s Spadefoot toads were calling from dense vegetation in shallow water less than 5 inches in depth. The Great Plains Toads selected dense vegetation without regard to water depth and were interspersed with Couch’s spadefoot toads. Most of the Green Toads were calling from areas of sparse vegetation with no apparent preference for water depth. The sonogram (recorded tracings of the breeding calls) records showed that there were large differences in the calls of each species. The Great Plains Toad vocalization was a high pitched trill while the call of the Green Toad was a lower frequency continuously rising pitch call that was almost a whistle. The calls of the spadefoot toads ranged from short bursts of low frequency, short duration (less than 0.1 sec.) trills by Plains Spadefoot Toads, to long duration (2 seconds) low frequency trills by Western Spadefoot Toads. Because of the distinctive vocalizations of the males, females were able to locate males of their own species by responding to their calls. When the males were calling, they would clasp anything that moved close. Male frogs clasp the female abdomen just below the arm pits with their arms (front legs). The clasping of a female frog by a male is called amplexus. We frequently would have a male in amplexus on our finger if we moved it slowly by him. With large numbers of five species of frogs calling all at once, it was inevitable that occasionally a male would clasp another male. When this happened, the clasped male emitted a sharp, distinct call that clearly communicated the mistake made by the amplexing male who quickly released "mistaken identity".

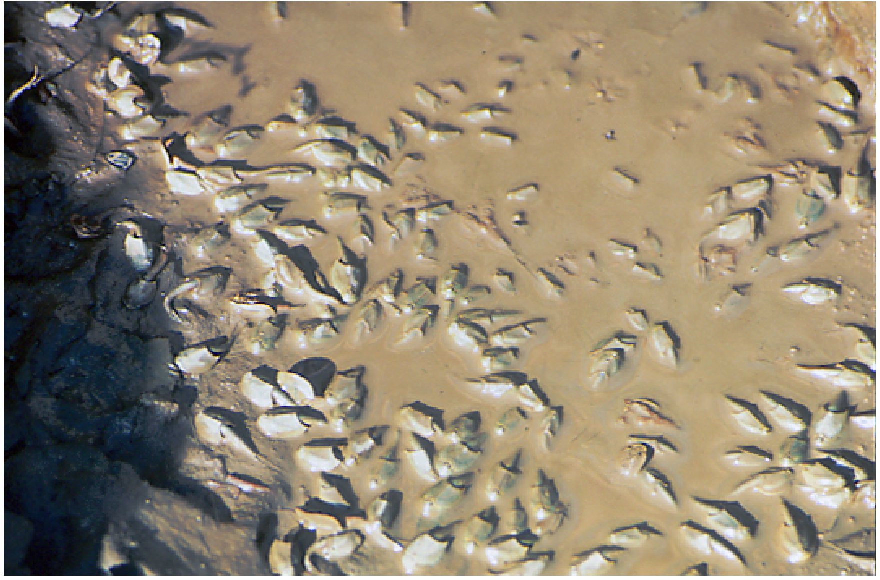
By the next morning, there were hundreds of strings of fertilized eggs floating in the water or attached to grasses, snakeweed, and other plants. However there were also many calling male frogs in all areas of the flooded playa. Our mark-recapture data showed that there were approximately 7000 adult frogs on that 20 acre playa. Using a mark-recapture technique, we estimated 3000 Western Spadefoot Toads, 2500 Plains Spadefoot Toads, 1000 Couch's Spadefoot Toads, 400 Green Toads and 150 Great Plains Toads. Standing at the edge of a flooded dry lake with thousands of simultaneously calling frogs exposes you to an unforgettable sound experience. The breeding chorus continues for several hours after dawn and then resumes at sunset.

Flooded playa (dry lake) with shallow area in the foreground with emergent vegetation.

A western spadefoot toad on the baked clay edge of a playa

A stock tank dug into a playa lake that holds water for several weeks after the rest of the playa dries

As soon as a dry lake floods, the desiccation resistant eggs of several kinds of invertebrates hatch and within a day the lake waters are teeming with this hatch. The life cycle of these organisms is fast onset, immediate development which means that they complete their life cycle within two weeks or often less than two weeks. The invertebrates with this life cycle that were collected by towing a plankton net through the water two days after the playa lake filled included: mosquito larvae (*Aedes* sp.), clam shrimp (*Eulimnadia texana*), and tadpole shrimp (*Triops longicaudatus*). These fast life cycle species utilize organic matter and the microorganisms on the microscopic organic matter fragments as their primary food source. The mosquito larvae pupate and emerge as mosquitos within two weeks. The clam shrimp and tadpole shrimp reach adult size within 7 to 10 days; reproduce and die. After laying eggs, these animals die. Theirs is a single fast life cycle that is completed long before a flooded playa lake dries.



An aggregation of dying tadpole shrimp in a drying puddle at the edge of a playa lake.

Another group of dry lake organisms follows a life cycle described as a fast onset, prolonged development life cycle. This group included two species of fairy shrimp (*Streptocephalus texanus* and *Thamnocephalus platyurus*), water fleas (*Moina wierzejskii*), and spadefoot toad tadpoles. These organisms fed primarily on the unicellular and multicellular algae. Populations of algae built up during the first two weeks after playa flooding. Those algae plus some of the suspended organic matter-microbial particles provide a thin soup of food for filter feeders. Fairy shrimp, water fleas and tadpoles are filter feeders. The fairy shrimp swim with their ventral side up using their feathery gills to sweep through the water pushing food particles into their mouths. The spadefoot tadpoles suck water into their mouths which is forced across their gills where the fine comb-like structures known as gill rakers collect food particles which are then swallowed.

A tadpole with rear legs. Note the swollen area below the eye where the gills and gill rakers are located.

Some of the filter-feeding tadpoles grow more rapidly than their brethren and these become predators. The predatory tadpoles develop a hard, keratinized beak that allows them to kill and tear flesh from smaller filter-feeders. In laboratory aquaria containing fairy shrimp, water fleas, tadpole shrimp and tadpoles, the predatory tadpoles took fairy shrimp and water fleas but were only able to bite chunks of the tails of the filter-feeding tadpoles that were nearly the same size as the predators. As the playa lake receded in size, there were large numbers of recently transformed juvenile toads that took shelter in the cracks of the drying clay bottom and under debris that settled on the drying lake bottom. These juvenile toads varied considerably in size. The predatory tadpoles had a survival advantage because they transformed at a larger size than the filter feeding tadpoles of the same species.

Spadefoot toads and Green Toads transformed relatively quickly but the larvae of the Great Plains Toads moved to the deeper water of the stock water tanks where they continued to feed and increase in size prior to transformation. Great Plains Toads transformed as much as 3-4 weeks after the spadefoot toads and Green Toads.

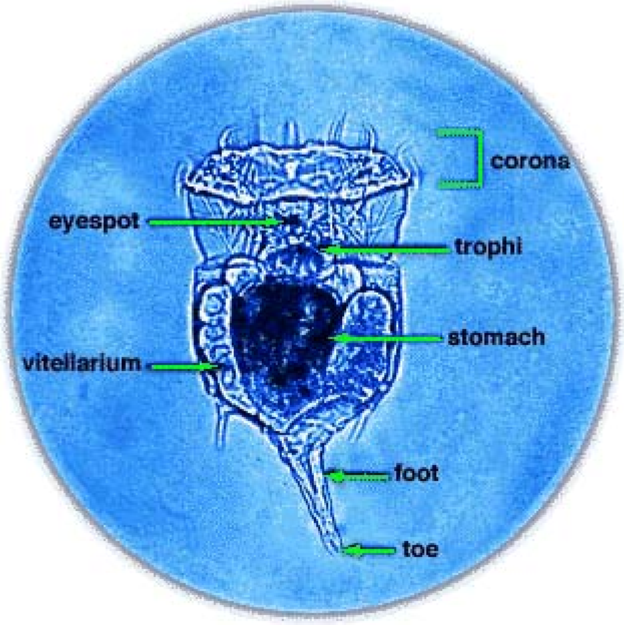
Our studies of the behavior of recently transformed juveniles confirmed the conventional wisdom that the juvenile stage is most critical in the life cycle of desert amphibians. The amount of fat and water stored in the bodies of the juveniles is a direct function of the size of the frog. Recently transformed juvenile frogs must select habitats where there is an abundance of food while also providing shelter from the extreme temperatures and drying conditions typical of summer days. We found that most of the juvenile frogs utilized the shelter of the fissures that developed at the edges of the receding water of a playa. When we excavated fissures, we found that more than 80% of the juvenile frogs were located within 8 inches from the surface. Many of the frogs in a fissure were actually touching another individual of its species or a different species. Also many these juveniles were found to burrow approximately 1-2 inches into the sides of the fissure thereby providing extra protection from desiccation and heat. Juvenile frogs that utilized the sandy habitat that surrounded the clay-pan bottom of the playa were active only one or two days following a rainfall whereas the juveniles from the lake bottom habitat were active every evening for up to 55 consecutive days. These juveniles feeding on insects grew larger and faster than the juvenile frogs that moved to the sandy habitats.

In another study where we were excavating the nests of harvester ants (*Aphenogaster cockerelli*) we found eleven adult Green Toads in or near the chambers of the nest. Juvenile Green Toads were also found burrowed into the sides of rodent burrows.

A juvenile spadefoot toad recently emerged from the water at the edge of a drying playa lake. Note the developing fissures on the right side of the photo and in the upper left corner.

We conducted laboratory studies to examine the relationship between fat storage and overwinter survival. When we placed juvenile toads on sandy loam soil in aquaria or individual flasks, the individuals quickly burrowed into the soil using the spades on their back feet to dig into the soil. We watched the frogs slowly “sink” into the soil finally disappearing as the tip of their nose dropped below the sand. The digging was very intense for 10-15 minute bouts separated by equal time at rest. We compared the weight changes of the burrowed frogs with other juveniles that were kept in flasks with moist paper toweling. These containers were placed in environmental chambers kept at 59°F. The temperature of the environmental chambers was set at the average temperature of the soil at a depth of 12 inches: the average depth at which overwintering toads had been excavated. The stored body fat of the toads that burrowed into the soil accounted for 3.2% of the body weight of which 86% was water. After ten months burrowed in the soil, water accounted for 75% of the body weight and 2% was fat. We concluded that the juvenile frogs had sufficient energy stored as fat that they could have survived another year if burrowed in the soil. Our measurements showed that juveniles burrowed in the soil lower their metabolism which reduces the rate at which stored body fat is used.

A group of microscopic organisms, rotifers, developed measureable populations in the organic soup of a flooded playa lake more than one month after the initial filling of the lake. The name rotifer refers to the cilia around the mouth of the animal. The rapid movement of the cilia (hair-like projections around the mouth) gives the appearance of a wheel that moves the animal through the water.



The general body plan of a rotifer consists of four basic regions: head, neck, trunk (body), and the foot. In most species, the head carries a corona (crown) of cilia that forces a water current of water into the mouth, which the rotifer sifts for food particles. Food particles are ground by the trophi (jaws), which are located below the mouth.

We recorded one species of rotifer, B*rachionus* spp. that reached high numbers between 40 and 60 days after initial flooding. That species was replaced by *Polyarthra* spp. as the most abundant rotifer during the third month of that the playa lake remained flooded. These rotifers belong to a class of rotifers called bdelloids that are known for their remarkable ability to survive drying through a process known as cryptobiosis (hidden life). Rotifers probably develop from desiccation resistant eggs after flooding of a playa lake. The cryptobiotic forms may contribute to the population of rotifers when the playa lake partially dries and then re-fills from subsequent rain events.

Other microscopic animals that appear soon after a playa lake floods include ciliate and flagellate protozoans. These single cell animals feed on bacteria and organic matter particles.

Chihuahuan Desert dry lakes and ponds are ephemeral aquatic environments that exist for one or two weeks to as long as three to four months depending upon the frequency and intensity of summer rainfall. The organisms that depend upon these aquatic habitats for reproduction and maintenance of their populations must of necessity have short life cycles and either some kind of anhydrobiosis (life without water) or desiccation resistant eggs or spores. The appearance of single cell and colonial algae within two days after a flooding event is the result of such adaptations. Fairy shrimp, clam shrimp and tadpole shrimp appear very quickly, grow rapidly reproduce and die within two to three weeks. High evaporation rates during the summer accelerate the loss of water which accounts for the short-term nature of this environment.

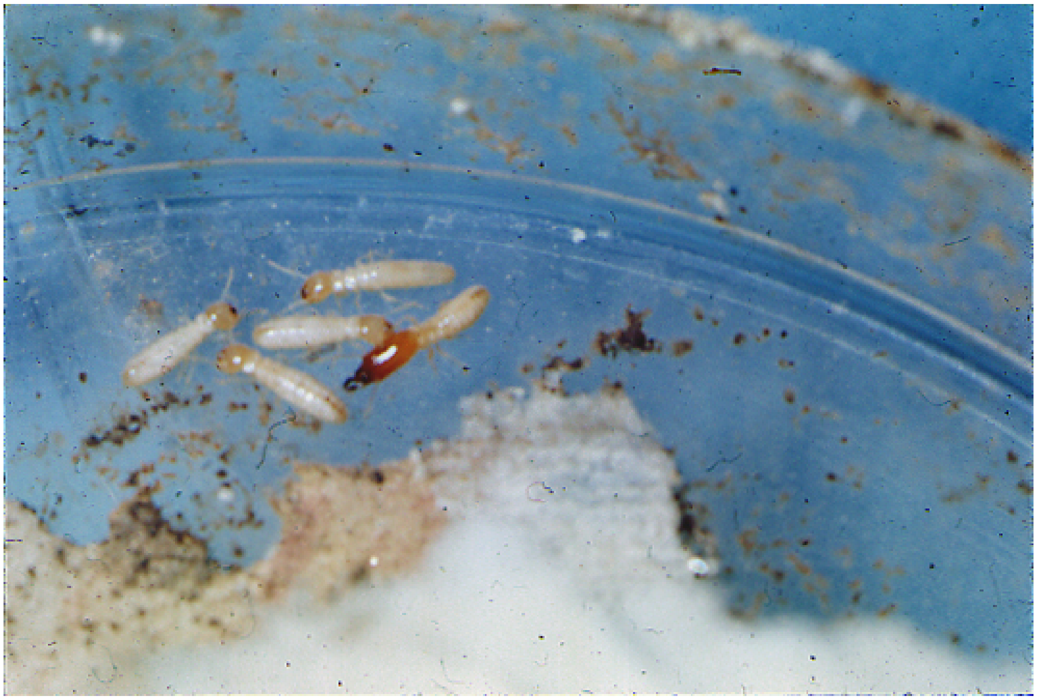
Subterranean Termites

My introduction to the natural history and ecological importance of subterranean termites in the northern Chihuahuan Desert was the result of a conversation with Dr. William Nutting, an entomologist colleague from the University of Arizona who suggested that termites might prove to be the most important invertebrates in Chihuahuan Desert ecosystems. He recommended that I use his toilet paper roll bait technique as a way of assessing the presence of these tiny insects and for obtaining minimum estimates of their numbers.

In order to use toilet paper roll baits, I had to order several cases of toilet paper. When the order came in, we went to the local grocery store to pick up 10 cases of toilet paper. We loaded the cases on shopping carts and took them to the pick-up truck for transport to the research ranch. My wife later informed me that she was in the store at the time that we picked up the toilet paper. Because she did not want people to know that she was married to the nut who purchased all of that toilet paper, she hid behind the aisle farthest from the storeroom. She was not the only person that questioned the sanity of a biologist who planted large numbers of toilet paper rolls in the desert.

At the research ranch, we set up two arrays, 100 rolls per array, in a creosotebush shrubland on a piedmont slope and a grassland with scattered creosotebushes that was grazed by livestock. The results of this simple study were staggering numbers of termites extracted from the toilet roll baits in the thousands per acre in both habitats. Subsequent studies using the toilet paper roll baits have shown these termites are widespread and abundant in every habitat except for those areas of the landscape that are periodically flooded. Termites that are extracted from the baits are the foragers and an occasional soldier.

A toilet paper roll termite bait. Note the gallery carton constructed by the termites on the surface of the roll that is being eaten by the termites. Termites were shaken and scraped from the bait into a pan where they could be counted and returned to the laboratory for weight measurement.



Termites (*Gnathamitermes tubiformans*) extracted from a toilet paper roll bait. The termites with light tan heads and small dark brown mandibles are forager-workers. The larger individual with a brown head and large mandibles is a soldier.

We found three species of subterranean termites: *Gnathamitermes tubiformans*, *Reticulotermes tibialis*, and *Amitermes wheeleri*. We found a small number of *A. wheeleri* in a piece of dead mesquite wood and in some dry cattle dung pats and very few *R. tibialis* in a bait in the grassland. Most of the termites recovered from the baits and from cattle dung pats, were the tube-forming termite, *G. tubiformans*. When soils were moistened by summer monsoon rains and when soil surface temperatures were lower in late summer, *G. tubiformans* announces its presence by constructing sheeting and tubing over and around suitable food items. These food items are as diverse as jackrabbit dung pellets, dead stems of shrubs, accumulations of grass and herbaceous plant parts, standing dead annual herbs and grasses, dead or senesced tillers of perennial grasses, and dead cactus pads. Basically tube forming termites will take any organic material that has no or almost no chemical feeding deterrents.

Based on the data from the numbers of forager termites extracted from the bait rolls, we estimated that there were 1700 foragers per square meter. When that number is converted to biomass, it works out to be 30 lbs of termites per acre! When compared with the average stocking rate for domestic cattle on Chihuahuan Desert rangelands, the biomass of termites is between 2 to 10 times greater than the live mass of domestic livestock that can be supported on these lands. That is based on the fraction of a termite colony that is feeding in baits at the time the bait is emptied! The actual numbers and biomass of termites per unit area is probably several times higher than these estimates. However these estimates do suggest that these organisms are very important in these ecosystems.

Why are subterranean termites so abundant? One probable reason is that they have abundant food and are less dependent upon local weather conditions than animals that live above-ground. In addition, termites have a complex microbial community consisting of bacteria, protozoans, yeasts and other fungi within their gut. Those gut symbionts allow termites to process pure cellulose, lignin and other components of wood, and animal dung. In addition, to the ability to use many different carbon sources, we discovered that the tube forming termites are capable of fixing atmospheric nitrogen. While cattle need protein in their diet in order for their ruminant organisms to digest plant materials, tube-forming termites can happily live on pure or almost pure cellulose because they obtain nitrogen from the atmosphere.

In desert ecosystems, dead plant materials on the soil surface are partially broken down or decomposed by ultraviolet light and high temperatures. Plant litter or detritus is broken down by soil microorganisms during short periods after rain events when these materials are sufficiently moist. Most active soil organisms such as bacteria, protozoans, and nematodes reside in water films on the surfaces of the materials that they metabolize. The soil bacteria and fungi need water to be effective in decomposing and mineralizing organic matter. Therefore organic matter processed by these organisms in a desert environment is an erratic process occurring during brief periods after rains. However this limitation does not apply to termites. Subterranean termites provide a permanent moist environment for their symbiotic gut microorganisms, allowing the gut symbionts to process dead plant materials even when soils are too dry for the activity of free-living soil microbes.

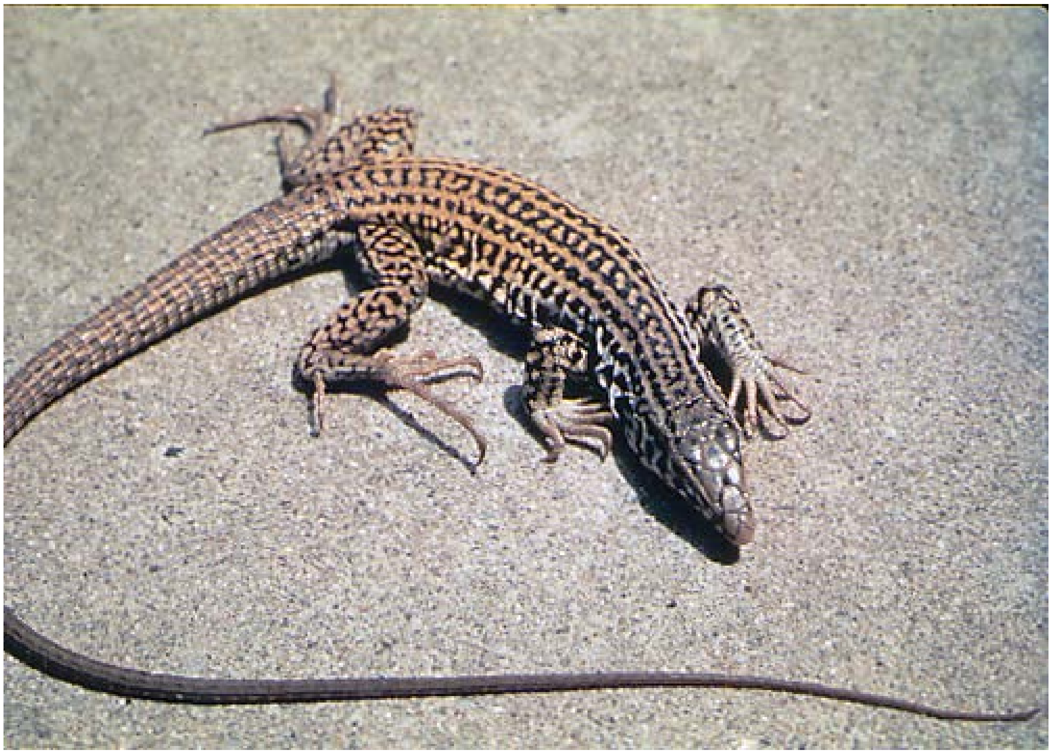
Termites that live belowground lose very little water because they live in an environment where the humidity is close to 100%. When soils are dry, subterranean termites feed on dead roots and other organic materials that may have been buried by wind eroded soil and only venture to the surface to feed in large objects such as cattle dung pats where they are protected from high temperatures and low humidity. We conducted an experiment to determine how termites locate suitable large objects such as cattle dung pats. Our experiment was designed to measure if the movement of the termites to the surface was random or if the termites focused their movements directly toward the object. We established plots with large sheets of saran-wrap plastic sheeting covered with soil. Cattle dung pats and artificial dung pats (styrafoam circles of the same diameter and height as dung pats) were placed at predetermined locations on the soil above the plastic sheeting. When the plastic sheets were removed after three months in the field, the termites had cut hundreds of holes in the sheets under both real and artificial dung pats and virtually no holes in the spaces between the pats. That result convinced us that the termites were not “smelling” the dung or using chemical cues because there were no differences in numbers of attack points between the real and artificial pats. Soil temperatures under dung pats were several degrees lower than open soil at the same depth. We concluded that termites locate large food items by locating thermal shadows and then moving up into the suitable food item.

When there has been sufficient rain to provide a moist layer of clay and silt in the soil profile, the tube forming termites will produce foraging galleries, foraging tubes and sheeting. Building foraging tubes and galleries is a type of chain-gang operation. When a termite reaches the rim of the structure, it empties the wet clay from its buccal cavity (basically a throat pouch) which is deposited by the mandibles over the sand grain(s) left by the previous worker. The termite then sets the sand grain in its mandibles on the clay cement layer. This process is repeated many hundreds of times per hour with a structure appearing and growing during that time period. Coarse sand (500-750 micrometers diameter) accounts for 35% of the mass of gallery material; medium fine sand (100-500 micrometers diameter) makes up 44.5 % of gallery material weight and clay and silt account for 20.6% of the mass of gallery material.

Foraging gallery tubes produced by subterranean termites *G. tubiformans* on dead stems.

Termites building a gallery tube around the stem of a dead annual plant.

While I have seen termite galleries in May, June, and July, in most years, gallery and sheeting construction occurs in late August, September and early October when air temperatures at mid-day are lower than in early summer and when soil moisture tends to be the highest. There is no consensus among termite experts as to the function of the galleries. Do the galleries provide a cooler, moister environment and thereby reduce the potential of desiccation of the foragers or do the galleries provide protection from predators? I have observed whip-tail lizards breaking open gallery sheeting to get at termites so gallery sheeting is not sufficiently robust to deter that predator. However gallery sheeting probably does protect the foraging termites from predation by ants, spiders and other invertebrates.



A whip-tail lizard, (*Cnemidophorus tigris*) one of the main predators of termites.

Whip-tail lizards are very good at locating termites. Termites are preferred prey for these lizards. I have followed whip-tail lizards when there were no galleries to locate termites and watched their foraging behavior. Whip-tail lizards move between patches of litter, using their snout to root around in the litter to find termites which are then swept into the lizard's mouth by its tongue. Following whip-tail lizards gave me the opportunity to evaluate the environmental conditions for surface foraging by subterranean termites.

Studying the behavior of termites has been a happy diversion from the primary focus of our work: the role of termites in the functioning of Chihuahuan Desert ecosystems. We spent several years measuring what and how much of the plant materials produced in a year were removed and consumed by subterranean termites. These studies provided numbers confirming that these animals are responsible for decomposition of most of the dead plant parts that are produced in a year. Termites removed 40%-80% of the above ground parts of annual plants, 50%-70% of the dead roots of annual plants, 60% - 90% of the dead above-ground parts of perennial grasses and 50%-70% of the dead roots of perennial grasses. Tube forming termites do feed on the leaves of some shrub species and that is dependent upon the shrub species and the availability of other foods. For example, *G. tubiformans,* was found to remove creosotebush leaves one year but did not feed on creosotebush leaves in two subsequent years. Therefore we have not been able to calculate a reasonable range of values for temite consumption of shrub leaves in the Chihuahuan Desert. Tube-forming termites do feed on dead wood and frequently build galleries around dead stems within the clumps of mesquite, creosotebush and wood of other species of shrubs in pack-rat nests. Our studies showed that termites scrape off the surface layer of dead wood that has been softened by fungi. They remove between 1% and 5% of the mass of dead stems within a year.

Termites are the primary decomposers of dried cattle dung. When we measured the mass losses from dung placed on termite-free (insecticide treated) areas and on areas with termites, there were huge differences in the loss of mass from the dung pats. Over a three month period, dung pats that were initially attacked by termites were completely broken down and pats which were attacked by termites in the last month of the study lost approximately 20% of the original weight. Mass loss from dung pats that were not attacked by termites was less than 4%. We concluded that if termites were not present in rangelands grazed by cattle, the accumulation of dried dung could potentially cover so much of the soil surface that grass growth would be inhibited.

Because the symbiotic gut organisms of termites are so efficient at breaking down organic matter (even recalcitrant molecules like lignin), they produce very little fecal material. Since there is little fecal material and most of the organic matter ingested by termites is converted to carbon dioxide or methane, where termites are abundant the soils have very little organic matter. When we mapped the abundance of subterranean termites on a 3 km (approximately 2 miles) line with 89 grids of termite baits spaced 100 feet apart and measured the soil organic matter content of the soils of each grid, there was a very strong negative correlation between termite abundance and soil organic matter. Soil organic matter was a fraction of 1 % where termites were most abundant and was highest at the margins of a playa lake (>3.4%) where termites were absent.

Effects on water infiltration

In the northern Chihuahuan Desert, subterranean termites play an important role in the movement of water into the soil. For close to twenty years, we conducted a number of studies on large plots which had been treated with a long-lasting insecticide that eliminated termites. The importance of termites in breaking down dead plant materials and dung led us to consider termites as analogs of earthworms. One important role of earthworms in moist environments is the production of burrow systems that serve as “straws” conducting rainfall down the burrows and deep into the soil. This process is called “bulk flow” and is contrasted with movement of water into the soil via capillary channels. When we measured run-off from the termite exclusion plots and from plots with termites present, we found run-off from the termite exclusion plots to be two times higher than from plots with termites present. Termite foraging tunnels that open at the surface provide the avenues for “bulk flow” and provide soil moisture at greater soil depths than occurs with water infiltration via capillary pores. This feature of termite biology plus the nitrogen in the above ground galleries, produced a soil environment that resulted in higher growth of annual plants and of creosotebush on plots where termites were present than on plots where termites had been eliminated.

Termites and soil formation

In the Chihuahuan Desert the tube forming termites transport large quantities of selected soil particles from subsoil horizons to the surface during the construction of sheeting over foraging runways or foraging galleries. Termite galleries and sheeting are constructed with sand, clay and some silt collected from sub-surface soil layers. The tube forming termites mix the clay with chemical secretions or excretory products to cement the sand grains into a sheet. Clay content and organic carbon contents are higher in termite sheeting and galleries than in surface soils.

Galleries on dead grasses and dead stems of mesquite and a gallery complex in a tussock of dead mesa dropseed grass.

The soil particles incorporated into the sheeting or foraging galleries represent a large turnover of sub-soil that has the effect of natural tillage of the soil. The sheeting and galleries are fragile and easily broken apart by wind and water. Gallery and sheeting turnover is quite high with most structures lasting approximately one week. The quantity of sheeting and galleries varies spatially as does the abundance of termites. When we measured the amount of sub-soil incorporated into galleries and sheeting at one sampling date, we estimated that between 14 and 150 tons of subsoil was brought to the surface by termites in 100 years. This activity of termites is therefore an important factor determining the physical and chemical characteristics of soils.

After learning the importance of termites as agents affecting soil fertility, soil water storage, and organic matter decomposition, we considered tube-forming termites as “keystone” species. It is clear that when termites are eliminated, many ecosystem functions are compromised. That should earn termites the “keystone” role in the northern Chihuahuan Desert. There are many other aspects of termite biology that need to be examined. For example, it is known that termites release methane to the atmosphere as a result of the fermentations in their hind-gut. Since methane is a greenhouse gas many times more potent than carbon dioxide, are termites contributing to global warming?

Ants

We have recorded more than 50 species of ants in our studies of the major ecosystems of the Chihuahuan Desert. Ants are social insects that live in colonies of various sizes. Numbers of ants in colony nests range from around one hundred to several thousand. They are the most frequently seen insects in the Chihuahuan Desert. The Chihuahuan Desert ant fauna is very diverse and these insects are important players in the functioning of the ecosystems of this desert. Large seed harvesting ants have been the subject of numerous studies because of their potential impact on the distribution and abundance of the plants whose seeds these insects collect. Honey-pot ants are known primarily for the workers that become storage "pots" for the honey dew collected by other workers. Honey-pot ants are known to tend and protect aphids and other plant sap sucking insects. However, many species of less conspicuous ants are omnivores. Among those are several species of widely distributed tiny ants that forage on insect produced honey dew or sap exuded from plants. One ant species that attracted our attention is a member of a family of tropical leaf-cutter ants. That ant is *Trachymyrmex smithii neomexicanus* which grows fungal gardens on the leaves that it collects. There is at least one species of "army ants" in the Chihuahuan Desert, *Neivamyrmex nigrescens* but we never had enough time or energy to develop any studies of this species.

Our first studies of ants focused on the feeding behavior of the ants, the average size of workers and their distribution on a watershed. We then estimated the number of colonies on the upper piedmont creosotebush community and on the lower slopes of the watershed in a mesquite-Yucca-grassland at the edge of a dry lake. The ants on this watershed, their feeding guild, size, and relative abundance are shown in Table 1. We also recorded the number of active colonies of ants on two acre plots on the creosotebush piedmont and on the mesquite-Yucca-grassland at the edge of a dry lake. The largest number of colonies were of the small *Iridomyrmex pruinosum* were active in summer after the beginning of the monsoon rains. The colonies of *Dorymyrmex insana* were most active in late summer after late June/early July rains. The peak numbers of active *Dorymyrmex bicolor* nests were in early summer with few colonies active during the monsoon rainy season.

Table 1. Relative abundance of ant species in four feeding guilds in two northern Chihuahuan Desert plant communities. Relative abundance indicated by *** abundant ** moderate abundance, * rare-low abundance

Feeding guild	worker length Range in mm	Creosotebush Piedmont	Mesquite-Yucca Grassland
Granivores (seed feeders)			
Pogonomyrmex rugosus	6.5-9.5	*	***
Pogonomyrmex desertorum	5.0-7.5	*	***
Pogonomyrmex californicus	4.5-6.5	*	**
Pogonomyrmex apache	7.5-8.5		*
Pogonomyrmex imberbiculus	3.8-4.0	*	**
Pheidole desertorum	2.9-3.8	*	*
Pheidole militicida	2.5-4.0	*	**
Pheidole rugulosa	1.5-1.7	**	***
Pheidole xerophila	1.8-2.4	**	***
Honeydew-exudate feeders			
Myrmecocystus mimicus/depilis	3.0-5.5	*	***
Myrmecocystus mexicanus	4.0-8.5	*	**
Myrmecocystus navajo	3.0-4.5		*
Omnivores			
Aphaenogaster cockerelli	8.5-9.8	**	***
Formica perpilosa	5.0-8.5		**
Dorymyrmex bicolor	2.8-4.0	**	***
Dorymyrmex insana	2.5-3.8	**	***
Forelius pruinosum	1.8-2.5	**	***
Solenopsis xyloni	2.5-3.1	*	**
Solenopsis aurea	less than 2.5	*	*
Solenopsis krockowi	less than 2.5	*	*
Crematogaster sp.		*	
Fungus Growers			
Trachymyrmex smithi neomexicanus	8.5-9.8	**	**
Predatory			
Neivamyrmex nigrescens	3.5-5.0	*	

Seed Harvesting Ants

At the beginning of the Desert Biome section of the International Biological Program in 1970, senior scientists encouraged me to initiate studies of large seed-harvesting ants since they are probably among the most abundant invertebrates in the northern Chihuahuan Desert. Few ant species have common names and many of the more cryptic species in the Chihuahuan Desert remained unknown to science until the "Ants of New Mexico" was published by William and Emma MacKay. Here common names are used when available and scientific names of species or genera used when common names are not available.

As we began our studies, we had the good fortune of hosting the sabbatical studies of an Australian biologist, Dr. George Ettershank, who was an ant biologist-guru. Ettershank led us over a steep learning curve and proved to be a great partner in the field and in the laboratory He helped design our studies and taught us the essentials needed to study ants. Our initial studies were focused on the relative abundances of the different species of seed-harvesting ants in the various habitats of a watershed. Estimating the numbers of colonies per unit area was simple. However, the next step, estimating the numbers of individuals in a colony was far more complicated and required considerable physical work. We tried estimating the numbers of workers, by capturing ants leaving the nest using an aspirator. An aspirator is a jar equipped with two tubes: one tube is sucked on like a straw when the other tube is positioned just above an ant. The ant is vacuumed into the jar and with a little practice; a person can aspirate more than 100 workers in a few minutes. The jars with the ants were placed in an ice chest to use cold anesthesia to immobilize the animals. We learned to anesthetize these insects because early encounters with active ants resulted in many stings that were as painful, or more painful, than wasp stings. The sting of a harvester ant produces a hard lump that is painful and burns for several days. A report in the publication Science reported that the venom of this harvester ant has the highest mammalian toxicity of any venom tested. Fortunately these are small insects do not inject a dangerous dose of venom. The stings are not dangerous unless one is allergic to hymenoptera stings or is stung by a large number of ants.

The cold ants were removed one at a time from the aspirator jar and a paint spot placed on the gaster (the large tail segment of an ant). The marked ants were placed in a glass jar and allowed to warm-up before being returned to their nest. On the following day, we would capture foragers by aspirating individuals traveling on the trails originating at the colony. These ants were cold narcotized, and the marked and unmarked workers were counted. Our mark-recapture studies provided variable estimates of numbers of adult workers that were foraging for food items. The estimates ranged from a few hundred to nearly 1000 individuals in a colony. We estimated that there were approximately 90,000 harvester ant foragers per acre during periods when annuals that produced seeds preferred by harvester ants were abundant. Since the foragers represent an unknown fraction of the number of ants in a colony, this method did not provide information on the total population of a colony.

The most reliable way to obtain information on the size of colonies was to excavate a colony and count all of the individuals removed from the colony. When excavating a colony, we also mapped the chambers to determine the locations of food storage chambers and chamber with larvae or pupae.

A nest disk of the large rugose seed harvester ant (*Pogonomyrmex rugosus*). The ants keep the nest disk free of vegetation. The green ring of plants around the nest are large storks-bill (*Erodium texanum*) spring annuals.

Mapping was accomplished by pouring liquid plaster of Paris into sections of the nest, allowing it to set and then carefully excavating the cast. This was a very slow process and produced a huge cast that had to be wired together to transport the structure back to the laboratory. The nest of seed-harvester ants had some chambers that were cut into the calcrete layer more than four feet below the surface. The food storage chambers were within 4-6 inches of the surface to approximately three feet below the surface (see diagram below). In the summer, some larvae and most of the pupae were carried from the deeper nursery chambers to chambers nearer the surface where temperatures were more suitable for faster development into callow (pale or nearly unpigmented) workers. The total number of adults in the large rugose seed-harvester ant colonies ranged from 2,000 to nearly 15,000 individuals.

There are three species of large seed harvesting ants in the northern Chihuahuan Desert: the rugose seed harvester (*Pogonomyrmex rugosus*), the desert seed harvester (*Pogonomyrmex desertorum*) and the California seed harvester (*Pogonomyrmex californicus*). These ants occur in most habitat and all three species frequently occur in the same area. Estimated numbers of foragers from colonies of the desert seed harvester ants ranged from 400 to 600 workers.

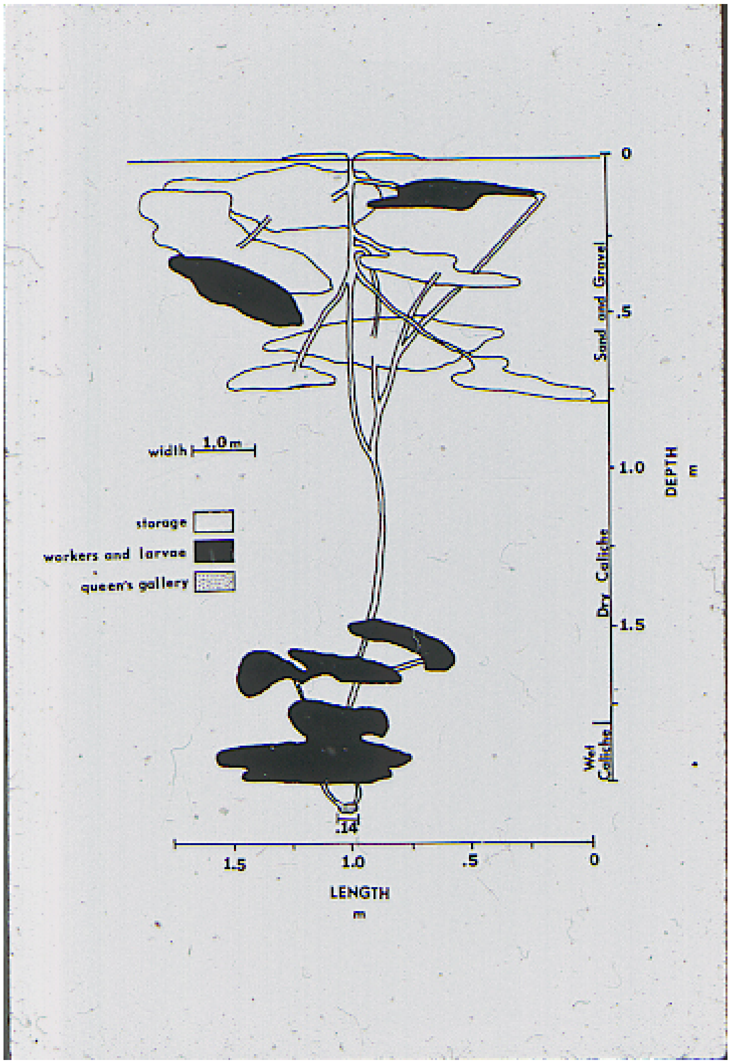


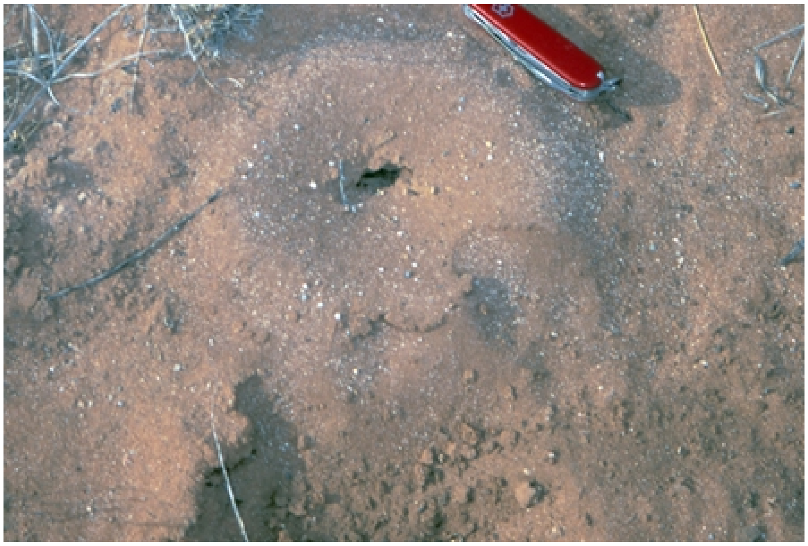
Diagram of an excavated seed harvester ant (*Pogonomyrmex rugosus*) nest. All measurements are metric (1 meter = 39 inches)

Since the presumed ecological impact of these ants on the ecosystems was the reduction of viable seeds in the seed bank, our early studies focused on foraging behavior, environmental factors controlling foraging, and the numbers of foragers leaving the nest. We collected ants returning to the nest with food items and when these ants were subjected to cold narcosis, they dropped the items carried in their mandibles. The collection of items carried by harvester ants allowed us to obtain samples of the species of seeds carried to the nests and other items collected by foragers.

The rugose harvester's activity varies with the availability of preferred seeds and this species is most active in late spring and early summer and in late summer. The rugose seed harvesters may open their nests and begin seed harvesting as early as late March or April and continue foraging activity through mid-October depending upon the timing of rains. The desert seed harvesters open their nests in June or July and exhibit peak foraging activity in July and August.

The rugose seed harvester is a column foraging species. Column foragers emerge from the nest and follow scent marked trails (trunk trails) to the edges of patches with high densities of seed-producing annuals where the foragers disperse until they locate a suitable forage item. There may be as many as ten trunk trails from a single rugose harvester ant nest but there are usually only two or three trunk trails that are used at one time. When rugose harvesters are intensively foraging there is rather frenetic two-way traffic on the active trunk trails. Rugose seed harvesters will also forage at night during periods when there is a large seed rain.

The desert seed harvester and the California seed harvester forage as individuals. A forager emerging from the nest may go in any direction away from the nest and travel in a random movement, changing direction frequently in search for a forage item. The rate of return of forage items to the colony by individual foragers is lower than by group foragers.



A desert seed harvester ant (*Pogonomyrmex desertorum*) nest with a jack-knife for scale. Note the calcium carbonate granules on the nest mound transported from the caliche deposits approximately 3.5 feet below the surface.

Nest of a California harvester ant in a black grama grassland.

All three species of seed harvesters exhibit peak foraging activity at soil surface temperatures of 113^{o}F and cease foraging when the soil surface temperature reaches 125^{o}F. The critical thermal maximum temperature (average temperature at which individual animals become immobilized by temperature and are unable to escape conditions that will lead to death) for the harvester ants was 127^{o}F. These ants are immobilized by temperatures of 41^{o}F and below. Therefore colony activities such as nest cleaning and foraging do not begin until the temperature of the upper 10 inches of soil exceeds 45^{o}F, the temperature at which these ants are mobile. Rainfall stimulates intense activity in all species of seed harvesters and several other species of ants. Rainfall also stimulates surface activity of subterranean termites which are important prey species for seed harvesters.

A California seed harvester ant (*Pogonomyrmex californicus*) nest in a desert grassland.

Harvester ants frequently carry whole fruits and remove the seed or seeds from the non-edible parts in the nest. The non-edible parts: husks, calyxes, awns and florets are carried out of the nest and deposited in "chaff" dumps at the margins of the nest disk or nest mound. In order to examine forage selection and factors affecting foraging activity, we collected all ants returning to the nest in a five minute period. The ants were aspirated as they approached the nest entrance. Since the returning foragers held their forage items tightly in their mandibles, the forage items were collected along with the worker ant in the aspirator. These studies were conducted over a three year period that included a drought year, a year with above average winter and summer precipitation and a year with average precipitation. During the drought year the number of active colonies of the three harvester ant species was very low. The number of active colonies of seed harvester ants was highest the year following the drought and intermediate in the average rainfall year.

The intensity of foraging activity and numbers of colonies of seed harvesting ants that are foraging at one time are only partially determined by the physical environment. In all of our studies of seed harvesters, the physical environmental factors of temperature, air relative humidity and seed availability accounted for only half of the variability in foraging activity and numbers of active colonies. Ant colonies probably change their foraging activity in response to the development of brood (growth of larvae) and to the amount of seed storage within the granaries of the nests. Another factor is the success of scouts. Especially in column foragers, individual foragers emerge from the nest and explore areas around the nest for suitable forage. When these scouts return to the nest, they communicate their success to their nest mates by chemicals or by tactile communication with their antennae and they mark their trail with a chemical produced by glands on the gaster.

The low summer precipitation during the drought year resulted in no summer annuals. Some nests of the rugose harvester ant near the margins of a dry lake with large patches of tobosa grass at the edges of the lake were active during the summer and we were able to examine the forage items. Nine percent of the forage items were shrub seeds, 17% were insects, and the rest were seed heads of tobosa grass (a perennial). During the two years with average or above average precipitation, the harvester ants collected no shrub seeds and no seed heads of tobosa grass. In those years, the seed harvesters concentrated on the spring and summer annual buckwheats (*Eriogonum* spp.) the annual grass, six week grama (*Bouteloua aristoides*) which accounted for the largest percentage of forage items collected. In the early summer, the California harvester ant climbed into the canopy of buckwheats in order to collect the fruiting seed heads while the desert harvesters and rugose harvesters collected seeds and fruiting seed heads that had fallen to the soil surface. The seed harvesters also captured termites that accounted for between 1% and 10% of the forage items carried into the nests. A number of years later while visiting the Sevilleta Research Site north of Socorro. N. M., the day after a rain, I found that all of the colonies of the rugose seed harvester were intensively searching out and capturing grass cicadas that were emerging from the soil. The ants were able to capture cicadas before their wings were dry. The ants even climbed into the grass tussocks to capture cicadas that had climbed into the tussock in order to dry their wings and fly. The grass cicadas were virtually the only forage items returned to the nests during this time. The following day, very few of the harvester ant colonies were active and there were no grass cicadas in the vicinity of the nests.

A rugose harvester ant, *Pogonomyrmex rugosus*

A study of seed (fruit) production by annual plants provided the data necessary to examine forage selection by harvester ants. None of the harvesters collected seeds in proportion to the availability of seeds. The harvester ant species were obviously selecting seeds. Other scientists had suggested that harvester ants only collected items that they could hold tightly in their mandibles (jaws). However some of the forage items selected by these harvester ant species were small and smooth, two characteristics that should have eliminated these items as forage.

When we used bait stations consisting of a glob of honey, a glob of peanut butter, a glob of tuna fish and a small pile of cracked milo seeds to sample the number of species of ants in an area, we found that harvester ants dominated the tuna fish baits. When tuna fish bait was available, the seed-harvester ants took very few seeds and continued carrying bits of tuna back to the nest for more than an hour past the time that foraging usually ceased. The ants carrying the tuna ran very rapidly and appeared to be running on “tip-toes” in order to keep their body as far above the soil surface as possible. At that time of day the soil surface temperature exceeded 120 F and exposure to those temperatures for more than a couple of minutes would probably have been lethal.

Based on these observations we hypothesized that the ants would select seeds with higher protein content. To test this, we made artificial seeds with the same caloric (energy content) but with different protein contents. The rate at which foragers returned with artificial seeds containing five percent protein was nearly twice the rate at which foragers collected artificial seeds containing no protein. However the harvester ants did not discriminate among artificial seeds containing more than five percent protein. We also observed that harvester ants ceased foraging on the high protein artificial seeds at the same temperatures that they ceased collecting native seeds. When we considered these data in combination with the observations on foraging on grass cicadas and termites, we concluded that when “meat” was available all foragers were mobilized to obtain the high protein high caloric value food and only returned to seeds when the high quality “meat” was not available. Developing ant larvae require protein therefore the preferential foraging on insects when they are available. Seeds are stored in nest chambers and are probably sufficient to insure the survival of a colony for more than one drought year.

A honey pot ant nest with calcium carbonate
(caliche around the nest disc.

Another ant species that makes nests that are easy to identify are the honey-pot ants (*Myrmecocystus* spp.). These nest discs are 2-4 inches above the surrounding soil surface and the entrance is very large (approximately 0.3-0.6 inches in diameter). The diurnal honey-pot ants are small, black, fast moving ants. The nocturnal species is pale, almost translucent and their nest disc made of small uniform stones. Honey-pot ants were found to be the primary prey of the round-tail horned lizard and the behavior of these ants is described in the chapter dealing with horned lizards and ants.

Other species of ants that we presumed to be seed harvesters were of the genus *Novomessor* – meaning new messor. *Messor* are well-known seed harvester ants in the Mediterranean region of Africa, southern Europe and the Middle East. The size of these ants and the abundance of their colonies prompted us to undertake a series of studies of these ants. Taxonomists have now placed these species in the genus *Aphaenogaster*. These black ants with their long legs are among the most obvious ants in the northern Chihuahuan Desert. *Aphaenogaster* make large nests with relatively large openings. Nests of long-legs black ants are characterized by two or three entrances within a 20 foot diameter circle. Foragers typically exit and return from one nest entrance but may use a different entrance on another day. There is a second species of *Aphaenogaster* found in the northern Chihuahuan Desert (*A. albisetosus*). *A.* a*lbisetosus* looks like the *A. cockerelli* but is found in different locales. In the areas of our studies, there were only narrow zones of overlap in the spatial distribution of these two species. Our studies of *A. cockerelli* were on the university ranch and of *A. albisetosus* at the Aguirre Springs recreational area on the east slopes of the Organ Mountains. The average abundance of *A. cockerelli* colonies was 12 per acre and the average abundance of A. *albisetosus* was 11 colonies per acre. We estimated that the average number of foragers per colony of *A.*

albisetosus was 1590 and ranged between 722 and 2104. The average number of foragers per colony of *A. cockerelli* was 1312 and ranged between 882 and 1674. We were able to excavate six colonies of *A.cockerelli* to the depth of the cemented caliche layer. The galleries of each of the six colonies continued into the caliche but we were unable to trace the galleries to locate the queen or chambers within the caliche. The numbers of ants recovered in these excavations ranged between 840 and 1535. The numbers of ants recovered from the excavated nests was within the range estimated by the mark and recapture procedure.

Worker of *Aphaenogaster cockerelli* with a seed hull.

One aspect of the behavior of the *Aphaenogaster albisetosis* that we could not explain was the transport of pupae (development stage just before the adult ant emerges from the surrounding case) from the brood chamber to the surface. The adult ants appeared to be cleaning the pupae. The pupae were exposed to the dry warm air on the granular surface of the nest which may have been beneficial for increasing the development of the pupating ant. The surface of the nest would certainly be warmer and drier than the brood chamber.. If pupae were packed tightly in the brood chamber, the high humidity and moderate temperature may have provided environmental conditions for growth of fungi. The cleaning activity and outside exposure may have been necessary to remove fungal hyphae from the pupal cases.

Aphaenogaster albisetosis ants tending pupae that were transported to the nest surface from the brood chamber in the nest

We measured foraging intensity and forage items by collecting workers returning to the nest with booty. We estimated the number of foragers in a colony by painting dots on the gasters of collected workers. Fortunately, *Aphaenogaster* ants do not sting which makes working with them easier and much less painful. The foraging activity of both species was similar during the summer months but the time of peak activity changed during the season. Foraging appeared to depend on soil surface temperatures. These ants were not active when soil surface temperatures were below 68°F and activity ceased when soil surface temperature exceeded 104° F.

Aphaenogaster foraging intensity was greatest at night. In July after a number of rains, these ants switched to intense foraging in the morning. We speculated that the rains may have been the stimulus for the nocturnal to diurnal shift in foraging intensity. When we tested foraging behavior by providing seeds (rolled oats) or tuna fish to some colonies and comparing their behavior with ants from colonies that had not been provided additional food, we found *Aphaenogaster* behaved somewhat differently from the *Pogonomyrmex* seed harvesters. *Aphaenogaster* colonies provided with rolled oats increased their rate of returning seeds to the nest but ceased foraging at the same time and soil surface temperature as those colonies not provided with additional food. However colonies provided with tuna fish not only increased their rate of foraging, these ants continued to carry bits of tuna to the nest for more than an hour after the colonies without access to tuna quit foraging. *Aphaenogaster* foraged on tuna until soil surface temperatures reached 115°F. The response *A. cockerelli* to the tuna was more dramatic than that of *A. albisetosis*. Laboratory studies showed that temperatures greater than 110°F was lethal for *Aphaenogaster*. These field experiments showed that foragers would continue working at near lethal conditions in order to bring protein to the colony.

Other researchers had documented the importance of protein to ant colonies and protein is especially important in the rearing of brood.

Seeds were not the most important forage items for either species of *Aphaenogaster*. Seeds of grasses and annual herbs were a very small fraction of the forage items returned to the colonies by *A. cockerelli* foragers. *A. cockerelli* collected more mesquite seeds and creosotebush seeds than seeds of grasses and herbs. Leaves, stems, and flower petals were important items of forage. Arthropods and arthropod parts accounted for 46% of forage by weight and 75% of that material was ants and termites. Insect material only comprised 6% of the weight of materials transported to the nests by *A. albisetosis* while plant materials, mostly mesquite and acacia seeds accounted for 70% of the forage by weight. Twenty four percent by weight of the items carried to *A. albisetosis* nests included feces, rabbit skin, porcupine quills, and bird feathers! The inclusion of these materials in the forage taken into the nest was really surprising because we considered these items to be inedible. *A. cockerelli* also took some items into the nests that we considered inedible but these accounted for approximately 13% by weight. None of these were as strange as quills or animal skin.

A nest of the long-legs black ant, *Aphaenogaster cockerelli* on a desert pavement piedmont. Note the angular shaped pebbles that cover the soil surface.

The relatively large ants such as the seed harvesters and honey-pot ants are but a few of the many species ants that inhabit the Chihuahuan Desert. Most of the ants of the Chihuahuan Desert are small, mostly inconspicuous species. Some produce nests that can be seen as small circles of fresh soil around a tiny opening in the soil. A number of the small inconspicuous species are seed harvester ants. We found several species of *Pheidole* and a native fire ant, *Solenopsis xyloni*, that harvested seeds. These small seed harvesters were found in creosotebush shrublands, mesquite-grass mosaics, and black grama grasslands. We studied forage selection and factors affecting foraging activity of three species of *Pheidole* on a watershed. Two species, *Pheidole rugulosa* and *Pheidole xerophila* were abundant in all of the plant associations on the watershed except for the dry lake basin. The average density of *Ph. rugulosa* nests ranged from 110 nests per acre in the creosotebush shrubland to 250 nests per acre in the black grama grassland at the top of the watershed. The average density of *Ph. xerophila* nests ranged between 150 per acre in the creosotebush shrubland to 650 nests per acre in the black grama grassland. One species, *Pheidole militicida* was found only on the mid-slope shrub-grassland mosaic and occurred at a density of 50 nests per acre. Less than half of the *Pheidole* nests were active in June and September. Almost all of the nests were active and foraging in July following the beginning of monsoon rains and more than half of the nests remained active and foraging in August. Between 15% and 30% of the colonies continued foraging activities during October and November. *Pheidole* sp. Were most active for three hours after dawn and for the first three hours after sunset during the summer months. These seed harvesters ceased foraging when soil surface temperatures reached 80^{o}F. We found that the most important factors affecting foraging activity were soil surface temperature and the availability of preferred seeds.

Pheidole xerophila major workers and a minor worker. Foragers are minor workers

The *Pheidole* sp. are column foragers. Columns of *Ph. militicida* extended from 15 feet to as long as 60 feet. The columns of the other *Pheidole* were shorter; extending for 3 to 20 feet and terminating at grass tussocks or patches of herbaceous plants that had dropped seeds on the ground. *Pheidole* sp. focused their foraging on the seeds of a widely distributed grass: fluff grass which produces large numbers of seeds per plant; on the annual grama grasses, and on the annual buckwheats. Forage selection by *Pheidole* sp. was similar to that of the larger *Pogonomyrmex* sp.. We observed no aggressive competition between the *Pogonomyrmex* sp. and *Pheidole* sp.. While there was some overlap of foraging territories of these species, aggressive exclusion or interference competition of one species by another was probably avoided by temporal differences in peak foraging times.

Formica perpilosa

One of the larger ants that we collected in initial surveys of ants in the mesquite thickets at the edge of the dry lake (playa) was *Formica perpilosa*. Since there was nothing published on the ecology of this species, we conducted studies on nest distribution, numbers of workers foraging, temporal and seasonal patterns of foraging, locations of active foragers, and food selection. *F. perpilosa* produced relatively large mound nests of excavated soil, twigs of mormon tea and mesquite, and some grass segments. Most of the mounds were located at the base of large mesquite Forager populations were estimated to be between 2,000 and 3,500 workers.

F. perpilosa foraged most intensively at soil surface temperatures between 59^{o}F and 115^{o}F but exhibited limited activity to and from the nest at soil surface temperatures between 115^{o}F and 150^{o}F. Since the nests were at the base of mesquite where most of the foragers went for food, the workers were exposed to high soil temperatures for a few seconds at most while traveling from the nest entrance and climbing up a basal stem of the mesquite. *F. perpilosa* began foraging approximately two hours after sunset with increasing activity (less than one forager per minute returning to the nest between midnight and 2 AM). Foraging intensity increased from two in the morning to seven returning workers per minute one hour after sunrise. There were two time periods when there were no foragers returning to the nests: 9 AM – 3 PM and 7 PM – midnight. Since the times with no returning foragers encompassed the middle of the day and one hour before sunset until midnight, the activity of *F. perpilosa* was not regulated by temperature. Returning foragers were active when soil temperatures were highest and lowest, thus confirming that temperature was not a significant factor affecting the activity patterns of this species.

F. perpilosa were observed foraging in mesquite shrubs and on one species of annual buckwheat: *Eriogonum trichopes*. The only visible forage items recorded for *F. perpilosa* were dead insects. We concluded that this species was concentrating on liquids. Other Formica are known to be generalists that collect honey-dew from homopterans or collect liquids exuded from plant wounds or glands and that prey on a variety of insects in addition to collecting insect carrion. Our observations were consistent with the idea that *Formica perpilosa* is a generalist.

We observed several instances of predation on *F. perpilosa*. Lone workers of *F. perpilosa* were attacked by ten or more small *Forelius pruinosum*. The small ants eventually exhausted the victim and carried it off.

A *Formica perpilosa* worker

Fungus culturing ants

One species of fungus culturing ants (*Trachymyrmex smithii neomexicanus*) occupies several habitats in the northern Chihuahuan Desert in the U. S. and Mexico. These are slow moving, dull grey ants that play dead when touched. We observed *Trachymyrmex* feign death when touched by *F. perpilosa*. We saw *F. perpilosa* pick up *Trachymyrmex* workers and carry them for several feet. The *F. pepilosa* did not retrieve the forage items dropped by *Trachymyrmex* and the pretend dead ants that were curled up recovered within two to three minutes after being dropped. We could see no benefit to the *F. perpilosa* from this behavior.

We conducted studies of foraging behavior of this species and attempted to estimate numbers and castes in excavated nests. Attempts to recapture marked individuals were extremely unsuccessful. Dead marked individuals were deposited in a heap by the nest entrance. We could not determine if our handling caused the deaths or if their nest mates killed them and deposited them near the nest entrance. Attempts to excavate entire colonies of *Trachymyrmex* were unsuccessful because the tunnels were lost in a caliche layer (cemented calcium carbonate) at a depth of three feet. The soil depth to caliche in the area of our study was between twelve and twenty inches.

In the excavated nest, we recovered 168 workers and 85 larvae. The larvae were in a chamber approximately seven inches from the top of the caliche layer. The brood chamber of *Trachymyrmex* was at a depth of 28 inches whereas the brood chambers of seed harvester ants were only 4 inches from the soil surface. In summer the average temperature at the depth of brood chambers of *Trachymyrmex* is around 77^{o}F and at the shallower depth of the seed harvesters is 95^{o}F. We were unable to find the fungal garden of *Trachymyrmex*. T. A. Johnson and others from the University of Texas, El Paso, excavated several *Trachymyrmex* nests in mesquite coppice dunes near El Paso. They reported that the fungal gardens were constructed of whole mesquite leaves stacked together to resembling a “house of cards” that were covered by a thin coat of fungal mycelia. Other reports of fungal gardens of *Trachymyrmex* reported the leaf substrate in the form of tennis ball size mass of granular leaf fragments and fungal hyphae.

Shrub Removal and Intensive Grazing

We conducted several studies of ants on eighteen one acre plots established in black grama grass grassland. We removed all of the mesquite shrubs from nine of the plots. Six of the plots were subjected to intense grazing by domestic livestock in summer and six of the plots were subjected to intense grazing in winter. We used pit fall trap grids and mapping of ant nests to study the responses of the ants to shrub removal and to loss of grass cover resulting from livestock grazing. We recorded twenty-six species of ants in the plots including five species of honey-pot ants, nine species of small seed harvesters (*Pheidole* sp.), three species of large seed harvesters (*Pogonomyrmex* sp.) and three species of fire ants (*Solenopsis* sp.). The most abundant ants taken in the pit fall traps and in mapping surveys of nests were the crazy ants, *Dorymyrmex insana*. Other moderately abundant species included the tiny red ant, *Forelius pruinosus*, desert harvester ant, *Pogonomyrmex desertorum*, a native fire ant, *Solenopsis xyloni*, and one of the honey ants, *Myrmecocystus mimicus*. All of the ants exhibited differences in relative abundance among the four years of the study.

There were only three species that exhibited a significant response to the plot treatments. Crazy ants, tiny red ants, and large desert harvesters responded to shrub removal and grazing by reduced abundance and changes in spatial distribution of nests. The removal of mesquite shrubs from plots resulted in the loss of the most predictable food source for ants that collect homopteran honey-dew and plant exudates. Mesquite shrubs initiate leaf production in late April and early May and produce flowers and fruits in June and July. Although stem elongation and abundance of flowers and fruits of mesquite vary with rainfall, the green foliage produced in early summer remains green and hydrated even during the most severe drought. The second and third years of the study were characterized by early growing season drought. The green growth of the grasses during those years did not appear until September. During those years the homopterans on mesquite provided the only reliable food source for liquid feeding ants like the crazy ants.

Mesquite Coppice Dune Defoliation

We compared the ant communities in mesquite coppice dune habitat that had been treated with a defoliant (2,4, 5 T) an untreated mesquite coppice dune habitat and in an ungrazed black grama grassland. Mesquite cover on the untreated site was two to five times higher than that on the defoliant treated sites. Mesquite cover on the ungrazed grassland was very low. *Pogonomyrmex* sp. and *Pheidole* sp. were abundant only in the ungrazed grassland. *Pheidole militicida* was present on all sites, *Ph. xerophila* only on one defoliant treated site, and *Ph. rugulosa* was present on all but the untreated mesquite coppice dune site. Honey-pot ants were most abundant on the untreated dune site and in the grassland. Crazy ants and a native fire ant (*Solenopsis xyloni*) were abundant on all sites. The ant species that was most affected by the treatment was the fungus culturing ant, *Trachymyrmex smithi neomexicanus*. *Trachymyrmex* was absent from the untreated coppice dunes and from the ungrazed grassland but was relatively abundant on both sites treated with defoliant. Fungus culturing ants may have benefited from the large quantity of mesquite leaf litter resulting from the defoliation treatment. The treatment with defoliant was in June and resulted in lots of leaf litter almost six months prior to normal leaf drop. Accumulations of leaf litter may benefit incipient queens after mating flights which occur after the first summer rains. Although most of the nests of *Trachymyrmex* at the dry lake location were shaded for part of the day, a majority of the nests at the defoliant treated sites were in the open and exposed to direct sunlight for most of the day. These observations negate the conclusion that *Trachymyrmex* require shaded habitat.

Species Interactions at a Rich Food Source

In our study of *Formica perpilosa*, our attempts to examine the forage preference of that species by putting out a cafeteria choice of a sugar solution, peanut butter, dead insects and seeds failed because the tiny red ant, *Forelius pruinosum* over-ran all of the baits except the seeds and kept the *Formica* from the cafeteria. E. O. Wilson (the ant guru) reported that some species of ants recruit rapidly to rich food sources and may exclude other species from that source. *Forelius pruinosum* was found to displace the formicine honey pot ants (*Myrmecosystus* spp.) at food baits. In our study of mesquite removal and grazing in a grassland, we had an opportunity to study the interactions between several species of generalist ants that are relatively abundant in the grassland habitat. The most abundant ant species on the plots was the crazy ant (*Dorymyrmex insana*) with more than 50 colonies per acre. The other generalists in the plots were fire ants (*Solenopsis* spp.), tiny red ants (*Forelius* spp.) and honey-pot ants (*Myrmecocystus* spp.) that feed on honey dew, plant exudates and insects. In summer before the onset of monsoon rains, the only sources of liquid food are the fruits and flowers of soaptree yucca (*Yucca elata*) and flowers of honey mesquite. We studied the ants on the flowering stalks of soaptree yucca on eight plots where mesquite had been removed and on seven plots where mesquite was present. There were approximately 35 flowering yucca plants per plot. Of the 1034 yucca stalks studied, 528 had only crazy ants, 62 had only honey-pot ants and 15 had only fire ants. Three yucca stalks had both crazy ants and tiny red ants, five had crazy ants and honey-pot ants and eleven had tiny red ants and honey-pot ants. On one stalk there were a small number of crazy ants with a large number of tiny red ants. During a five minute period of observation, the crazy ants jumped from the stalk to the ground abandoning the resource to the more numerous small red ants.

We recorded one yucca stalk with tiny red ants and the Mexican honey-pot ant (*Myrmecocystus mexicanus*). We were very surprised to find Mexican honey-pot ants on a yucca stalk more than two hours after sunrise because earlier studies concluded that this species was nocturnal. The presence of Mexican honey-pot ants on yucca during the sunlight hours indicates the value of this resource for a liquid feeding species.

There were more crazy ants on yucca stalks with fruits than on stalks with flowers. The crazy ants were concentrated on the fruits and appeared to be feeding on sap exuding from small cuts in the epidermis of the fruits. Crazy ants and tiny red ants have been reported to recruit rapidly to rich food sources and to drive other ants away from the food source by aggression and by chemical means. The study of ants on the flowering stalks of soaptree yucca is consistent with rapid recruitment to rich food sources and aggressive behavior to drive other ants away from that resource.

Seed Eating Ants and Rodents

Seed eating desert rodents were reported to remove more seeds than ants in the Chihuahuan Desert. Those reports were based on seed tray studies using millet seeds to evaluate seed removal by ants and rodents. Paired seed trays were used: one with a wire mesh cover that excluded rodents but allowed access to ants. Those studies were conducted on a sloping piedmont with a creosotebush shrubland vegetation. In order to provide an independent test of those results, we repeated those studies using seed trays with large (millet) seeds and small (couch grass) seeds in grazed and ungrazed (fenced to exclude livestock) grassland, in creosotebush shrubland and mesquite shrubland. The livestock exclosures had not been grazed for more than forty years. The grass cover in the livestock exclosures (35 %) was more than double that of the grazed grassland plots (16%).

A total of twelve species of ants were recorded removing seeds from the seed trays in all habitats with nine species in creosotebush shrublands, nine species in grazed grasslands, seven species in ungrazed grasslands and four species in mesquite shrublands. The fire ant (*Solenopsis xyloni*) was the only ant collected from the seed trays in all habitats and it was the species with the highest frequency at seed trays in every habitat except the creosotebush shrubland where *Pheidole xerophila* and long-legs black ant (*Aphaenogaster cockerelli*) visited more of the seed trays. In the grassland sites, the fire ant, *S. xyloni*, a Pheidole, *Ph. militicida*, and the large desert seed harvester, *Pogonomyrmex desertorum* were the most frequent visitors to the seed trays. The small fire ant (*S. xyloni*) recruited rapidly to the dense food source. However the fire ants removed seeds only from the trays with grass seeds and did not forage on the larger millet seeds.

More seeds were removed by ants than by rodents in the grazed and ungrazed grassland but in the creosotebush shrubland, rodents removed more seeds from the seed trays than ants. Seed removal was the same for ants and rodents in the mesquite shrubland. Ants typically removed more of the smaller grass seeds than the millet seeds. Rodent trapping conducted on the sites of the seed tray study revealed that Ord’s kangaroo rat was the only rodent trapped in the grasslands with Ord’s and Merriam’s kangaroo rats in the mesquite shrubland and Merriam’s kangaroo rat plus a few pocket mice and deer mice in the creosotebush shrubland. The relative abundance of rodents (number captured in 150 trap nights) was three to four times higher in the creosotebush shrubland than in the mesquite shrubland or grasslands. Thus in habitats with low populations of seed eating rodents, ants are the most important group removing seeds from the environment. The levels of seed removal by ants in our study were considerably higher than seed removals by ants in other studies in North American deserts. This was a surprising and important finding because rodents are using stored seeds in scattered caches and in their burrows during the winter months when ants are not active. This means that ants are the most important seed harvesters in Chihuahuan Desert grasslands and that historical vegetation change resulting in shrublands occupying much of the former desert grassland is responsible for the conclusion that rodents are more important than ants as seed harvesters.

Horned Lizards and Ants

Two species of horned lizards are widely distributed in the Chihuahuan Desert. The most frequently observed species is the Texas Horned Lizard, *Phrynosoma cornutum*. Texas Horned Lizards emerge from hibernation in May when day time soil temperatures exceed 20^{o}C (68^{o}F) and remain active through September. Texas Horned Lizards feed primarily on large seed harvester ants of the genus *Pogonomyrmex.* In our studies of Texas Horned Lizards, three species of Pogonomyrmex harvester ants made up the bulk of the lizards diet: the rugose harvester ant, *Pogonomyrmex rugosus*, the desert harvester ant, *Pogonomyrmex desertorum*, and the California harvester ant, *Pogonomyrmex californicus*. Hatchling Texas Horned Lizards were observed feeding on only two species of harvester ants: rugose and desert harvesters. Honey-pot ants (*Myrmecocystus* spp.) were also taken by several of the Texas Horned Lizards in our study. Honey-pot ants and other small ant species accounted for most of the insects in the diets of the Round-tailed Horned Lizard.

A Texas Horned Lizard (photo by Al Krueger)

We discovered that horned lizard populations can suffer large losses when there is little winter rainfall and extremely dry weather in May through July. During one such dry year we noted that most harvester ant nests were inactive during the day. During most of July, we began finding emaciated Texas Horned Lizards that were very weak and moving very slowly. We also found several of the emaciated horned lizards that had died of starvation or dehydration. When the rains finally did arrive in early August, we rarely saw adult horned lizards, despite frenzied activity of the harvester ants. The observations of emaciated horned lizards earlier and the dearth of horned lizards feeding at ant colonies led us to conclude that many horned lizards had died from dehydration or starvation. The dry early summer weather did not have the same effect on Round-tailed Horned Lizards probably because their primary prey, small liquid feeding ants, continued to be active.

These observations led to measurement of water loss in adult Texas horned lizards and the average water content of seed harvester ants, the primary prey of these lizards. Average water loss of adult horned lizards in the laboratory at a controlled temperature of 100^{o}F (38^{o}C which is the average body temperature of active lizards) was 6.5 mg of water per day. The calculated average intake of water by Texas horned lizards when feeding on ants when most ant colonies were active was 372 mg of water per day. This study demonstrated that Texas horned lizards could obtain sufficient water from their ant prey even when there were few active colonies of harvester ants.

We studied the behavior of Texas Horned Lizards by capturing a lizard early in the morning, painting a colored spot at the base of the tail and releasing the lizard at the point of capture. We could then follow that individual from a distance of 10 -15 feet without disturbing the animal. With binoculars we could identify the species of ants that were eaten by the lizard. We also recorded the behaviors of the lizards. When the lizards defecated, we immediately collected the fecal pellet and placed it in a plastic vial with a cap to minimize the moisture loss from the pellet. The freshly collected fecal pellets were used to measure water loss by defecation and lost via the white uric acid blob attached to one end of the fecal pellet. Uric acid is the nitrogen waste product excreted by horned lizards and other lizards. Excreting uric acid is a water-saving trait shared by reptiles and birds. That trait is a positive adaptation in arid environments.

Texas Horned Lizards did not become active until approximately 3 – 3.5 hours after sunrise. Most of the lizards that we followed in our study were initially captured between 8 AM and 9 AM. After release, the lizards engaged in behaviors that were either thermoregulatory (getting the body temperature up to the preferred temperature of 98^{o}F to 100^{o} F, and keeping it there) and searching for prey and feeding. Thermoregulatory behavior in the morning consisted primarily of the lizard sitting with front legs extended and the rear third of the body in contact with the soil surface. The lizard would sit with its back oriented toward the sun thereby maximizing heat gain by radiation, the sun’s rays.

Once a horned lizard had warmed sufficiently, it would begin to move by walking at a deliberate pace, stopping after every four to five steps and raising the front of the body. The raised position of the head allowed the horned lizard to examine its surroundings by tilting its’ head from one side to the other. If the lizard detected ants moving in the area, it would take one or two steps toward the ant, flick out its tongue to capture the ant. The tongue flick was very rapid and difficult to see. Mostly the observer would see the ant disappear into the mouth of the horned lizard. On one occasion while following a horned lizard we observed a behavioral response by the ants in a foraging column when the lizard missed the target ant. The ant column stopped moving in both directions from the ant that had been missed by the lizard. The ants assumed an erect posture moving like rows of dominos from the horizontal position to a vertical position. The ants with seeds in their mandibles remained vertical for more than ten minutes. The lizard kept tilting its' head from side to side and seemed not to see the stationary ants. After five minutes the lizard resumed its slow deliberate walk and moved more than nine feet from the stationary ant column before the ants resumed their treks to and away from the home nest. When that lizard missed an ant, the ant must have released an alarm pheromone (a volatile chemical) that elicited a predator avoidance behavior in the other ants. Because the lizard did not attempt to capture any of the immobile ants, it is likely that horned lizards detect mobile prey but do not "see" immobile objects as prey. It is also likely that the horned lizard moved away when it did not "see" potential prey after a few minutes.

Horned lizards moved between 160 feet per day and 300 feet per day. These movements were slow with frequent direction changes until the lizard detected ants and began a feeding bout. Horned lizards ingested on average between 30 and 100 ants in a day. The ants ingested were from one to four species: desert seed harvesters (*Pogonomyrmex desertorum*), rugose seed harvester (*P. rugosus*), California seed harvesters (P. *californicus*) and honey pot ants (*Myrmecocystus* spp.). There was considerable variability in the numbers of ants of each species captured and eaten by individual horned lizards. For example, one horned lizard ingested 111 desert seed harvesters in one day, another horned lizard took 8 desert seed harvesters, 52 rugose seed harvesters, 42 California seed harvesters, and 27 honey pot ants, and a third took 16 desert seeed harvesters, 15 rugose seed harvesters, 3 California seed harvesters, and 4 honey pot ants. This variability in numbers and species taken by Texas horned lizards demonstrates that these lizards are opportunistic predators that move through the environment until suitable prey are encountered and then use a "sit and wait" predatory behavior.

In addition to observing feeding behaviors, we had several opportunities to observe territorial behaviors when our marked horned lizard encountered another horned lizard. When another lizard was within a few feet from the marked lizard, both animals would begin "push-ups" with body tilting toward the other lizard. If the "push-up" display did not cause the other lizard to retreat, the encounter became more physical with head butting, biting and chasing until one of the animals retreated.

After feeding through the morning, the lizards most frequently sought shelter in the canopy of small shrubs. This was a behavior that we did not expect because other species of lizards seek shelter in shallow burrows, or in the shaded areas under large objects such as yucca logs, rocks, or large cacti. Watching a Texas Horned Lizard climb into a small *Ephedra* (Mormon Tea) or soaptree yucca, was almost shocking! During the hottest part of the day, a horned lizard would move in the canopy of the plant from the partially shaded part to the sunny part. This behavior would allow the lizard to maintain a high core temperature which is necessary to digest prey like ants with their chitinous armor. The fecal pellets contain the head capsules, hollowed thorax and legs as identifiable ant parts. The digestive process obviously requires that enzymes enter these structures and break-down the muscle and other tissues within the exoskeleton.

The other horned lizard found in the Chihuahuan Desert is the Round-tailed Horned Lizard, *Phrynosoma modestum*. The Round-tailed Horned Lizard is much smaller than the Texas Horned Lizard and its coloration matches the soil background much more than the Texas Horned Lizard. Round-tailed horned lizards typically initiate activity approximately 2 hours after sunrise. These lizards spend the night under the cover of a thin layer of soil that results from the animal swimming into the soil.

A Round-tailed Horned Lizard placed on a dark patch for contrast.

Round-tailed Horned Lizards spend their active periods moving between sun and shade in order to keep a relatively constant body temperature. Active round-tailed lizards maintain relatively high body temperatures between 37 and 39^{o}C (98.6 – 102.2^{o}F). Their daily thermoregulatory behavior is similar to that of the Texas Horned Lizard. High body temperatures are essential for a lizard that feeds primarily on ants because the indigestible chitin exoskeleton of the ants must be broken open for the digestive enzymes of the lizard to access the internal tissues.

Round-tailed horned Horned Lizards exhibit two behavioral sitting postures when thermoregulating during the day. In the early morning hours the lizards most frequently use the “up” position with the legs slightly extended and with the body not touching the ground. In the “up” position, the animal is typically oriented with its’ back to the sun which allows for maximum heat gain from the sun’s rays. In the “down” position, the lizards’ legs are bent and the ventral surface is touching the surface of the soil. The “down” position may be used to gain heat from the warm soil surface or when the lizard moves into shade, may be used to lose heat to the cooler shaded soil. During the middle of the day when soil surface temperatures exceeded 110 F, this horned lizard species remained active in the shade of large shrubs where they behaved as “sit and wait” predators. Sit and wait round-tailed horned lizards were constantly alert and were relatively successful at capturing small ants that wandered into their “kill zone.” Their primary prey species were honey-pot ants.

Honey-pot ants collect honey-dew from several species of insects that feed by inserting their hypodermic needle-like mouth part into the middle of a leaf and sucking out the cell sap. One result of this feeding behavior is the production of a drop of honey-dew that exudes from the anus of the insect. When round-tailed horned lizards captured honey pot foragers returning to the nest, the lizard not only gained the protein in the muscle of the ants but also the watery sugar in the buccal cavity of the ants.

Honey-pot foragers left the nest in waves of 200-500 workers during the morning hours. Upon leaving the nest, the workers dispersed to all directions. These ants did not follow a specific trunk trail to the target shrub where they would forage. Their behavior was random movement on the ground followed by rapid ascent up the trunk or stem of a shrub. During the hottest part of the day, honey-pot ants remained in the canopies of mesquite, soaptree yucca and other shrubs. If a passing cloud momentarily lowered the soil surface temperature the workers would descend and either return to the home nest or climb into another shrub.

Peak feeding times for round-tailed horned lizards were between 10 AM and 1 PM which corresponds to the peak activity periods of the honey pot ants. Most frequently, the horned lizards captured honey pot ants that were descending from the shrubs to return to the nest with their crops filled with honey-dew. When startled, or signaled that an attack had missed, the ants either remained motionless or ran away with surprising speed. Although honey-pot ants made up the bulk of the round-tailed horned lizard diet, other ants (seed harvesters, *Pogonomyrmex* spp. and *Pheidole* spp.) made up almost half of the ants identified in the lizard scats. Other insects that comprised less than 2% of the diet included two other ant species (*Conomyrma* spp. and *Aphaenogaster* spp. and some small beetles.

Predators of Horned Lizards

The Texas Horned Lizard is fairly immune to predation by snakes. The long spines on the back of the head and the flattened wide body prevent most snakes from attempting to swallow this horned lizard. Any snake that tries to swallow a Texas Horned Lizard, will probably die in that attempt because once the snake has the head of the lizard in its mouth, the snake cannot eject the prey because the long spines at the back of the lizard's head stick into the snake's mouth and throat. We were able to observe the consequences of an attempt by a glossy snake, a constrictor, to kill and swallow a Texas Horned Lizard. When we found the snake and lizard, both were dead, the lizard probably from having its body constricted which caused the lungs to collapse and the snake from blood loss from the wounds in its mouth and throat or from overheating in the sun. In this instance both the predator and prey were killed.

A glossy snake that died while attempting to swallow a Texas Horned Lizard.

The most important predator on the Texas Horned Lizard is the Swainsons Hawk. This large hawk arrives from Argentina in early May, establishes a nest in a tall Soaptree Yucca (*Yucca elata*) or tall Mesquite. All of the nests of the Swainsons Hawks were located in shrubs that were more than 10 feet tall. The Swainsons Hawks need a large foraging area to capture sufficient prey to feed their young. We estimated that a breeding pair of Swainsons Hawks needed an area of between five and ten square miles in order to feed an average of 1.6 young per nest. Two lizards accounted for almost half of the prey taken to feed the young hawks: the tiger whiptail lizard (*Cnemidophorus tigris*) and the Texas Horned Lizard which accounted for 28% and 19 % of the prey items respectively. The hawks ripped open the belly of the horned lizards to get at the internal organs and the muscle. They did not ingest the head or skin with its spiny margin. Whiptail lizards are more numerous in the northern Chihuahuan Desert than horned lizards.

The Round-tail Horned Lizard lacks the protection of long spines and wide body that offers some protection to the Texas Horned Lizard. The Round-tail Horned Lizard is more cryptic that the Texas Horned Lizard but is probably susceptible to predation by diurnal snakes such as Coachwhip snakes and Patch-nose snakes. There was no evidence that round-tail horned lizards were taken by Swainsons Hawks.

Insect Communities on Plants

Our first studies of Chihuahuan Desert insect communities were initiated by the Desert Biome section of the International Biological Program (IBP) (1970-1975). The focus of that program was to work out energy flow from the producers (plants) through the consumers (vertebrate and invertebrates) and through the predators (vertebrate and invertebrate). As the only zoologist on the project, I had responsibility for all of the vertebrate and invertebrate studies. My experience up to that point in time was limited to research on vertebrates. Because I was responsible for all of the invertebrate research, I began to learn as much as possible from colleagues and from some very bright and talented students. We learned a great deal about the structure of desert insect communities that inhabited a number of the dominant shrubs and grasses on the watershed near the NMSU ranch. After the IBP ended, funded research took precedence over completion of past research and most of the data on insect communities remained in the IBP reports and was never published in the peer-reviewed literature. Here the essential findings of those studies are summarized.

Until the IBP program, most of the research on insects was conducted on species that were pests on economically valuable crop plants. There was very little published information on insects that live on native plants or on the effects that insects have on those plants or the role of insects in the ecosystem. One paper that caught the attention of many biologists addressed the question of why the world is green. The authors hypothesized that there were so many predatory insects and other predators to keep the herbivorous insects in check that the foliage of native plants while damaged were not destroyed by insects and therefore the world remained green. Soon after that paper appeared, other scientists reported on the chemical defenses of plants that curtail the activities of insects and help to keep insect populations in check. For example, some plants like braken ferns are known to produce cyanide during susceptible early growth stages and in later stages to protect tissues with compounds like tannins (digestion inhibitors) or complex toxins. Most anti-herbivore compounds are located in the cells of leaf surfaces or surface of stems which protects plants from chewing herbivores. The story of plants and insects is one of an evolutionary arms race with insect species developing ways to avoid, remove, or neutralize toxins, or shunt toxins to resistant glands. Plants continually evolve newer chemical weapons to stave off the insect onslaught. We studied the insect faunas of a number of shrubs plus the two grasses on the dry lake. Season and among year differences in the insects on plants probably reflect the physiology and life cycle stage (phenology) including vegetative growth, flowering, and fruit set responses of plants to variations in temperature and rainfall.

Insects on Shrubs

We collected the insect fauna on a variety of shrubs at different seasons and years with very different rainfall patterns. We sampled insects on Mariola (*Parthenium incanum*), Mormon Tea (*Ephedra trifurca*), Apache Plume (*Fallugia paradoxa*), and Desert Willow (*Chilopsis linearis*). Arthropods on shrubs were most abundant in the spring and summer growing seasons but there were some arthropods on shrubs even during the winter months. The insect fauna during the growing season was dominated by insects of two orders of bugs that feed by sucking fluids from cell contents or vascular tissues: Homoptera and Hemiptera. Both of these orders have piercing-sucking mouth parts that are in the form of a slender segmented beak which encloses four piercing stylets. On Mariola (*Parthenium incanum*) two families of homopterans: Cicadellid leaf hoppers and Issid plant hoppers were most abundant. Mormon Tea (*Ephedra trifurca*) is an evergreen gymnosperm which we thought would have an insect fauna different from that on other shrubs. Homopteran leaf hoppers (Cicadellidae), tree hoppers (Membracidae), and jumping plant lice (Psyllidae) were the most abundant on mormon tea in spring. In midsummer (June-August) the tree hoppers and leaf hoppers were replaced by homopterans of two other families of plant hoppers (Issidae and Fulgoridae). In October, two families of homopterans: (Issidae and Psyllidae) were most abundant. In spring when mormon tea was flowering, two species of ants: small crazy ants (*Dorymyrmex insana*) and tiny red ants (*Forelius pruinosum*) were on the flowers. Apache plume (*Fallugia paradoxa*) generally grows along the margins of dry washes (arroyos). It produces two types of flowers: simple white rose flowers and reddish feather-like flowers. Two homopteran fluid feeders: flatid plant hoppers (Flatidae) and leaf hoppers (Cicadellidae) were the most abundant insects on apache plume. There were also gall midges (Diptera: Cecidomyidae) on this plant. Gall midges cause the growth of small swellings on the leaves in which the midges lay eggs. Gall formation probably eliminates chemical toxins and allows for development of the midge larvae. The same species of small ants found on mormon tea were also on Apache plume visiting the flowers. In October the only piercing-sucking insects were lace bugs, (Hemiptera:Tingidae).

Mormon Tea (*Ephedra trifurca*) growing on an old lava flow.

Insects that chew on leaves or flowers of plants occurred in low numbers on shrubs and never accounted for more than one to fifteen percent of the total number of arthropods in the sample   Chewing insects on the shrubs we sampled included inch worm caterpillars (Geometridae), metallic wood boring beetles (Buprestidae), leaf beetles (Chrysomelidae), snout beetles (Curculionidae) and soft wing flower beetles (Malachiidae).

Jumping spiders (Salticidae) and crab spiders (Thomisidae) were the only predators that were found on shrubs in every season. In spring and summer there were ladybird beetles (Coccinellidae), and common lacewings (Neuroptera: Chrysopidae) on most of the shrubs sampled Spiders, lacewings and ladybird beetles never accounted for more than ten percent of the numbers of arthropods in samples.

A jumping spider. Note the large eyes.

A crab spider on a finger (finger for scale)

Insects on Grasses

Arthropods on tobosa (*Pleuraphis mutica*) and vine mesquite (*Panicum obtusum*) grasses were sampled during each season for two years. There was essentially no effective rainfall during the summer growing season of year one because most storms only delivered between 0.1 and 0.2 inches of rainfall. During the winter and following spring, summer, and autumn, rainfall was average or above average resulting in new foliage growth of the grasses. Insects with piercing-sucking mouth parts accounted for more than seventy percent of the total arthropods on grasses. Cicadellid leaf hoppers, membracid tree hoppers and psyllid jumping plant lice were the most abundant insects on vine mesquite grass in the first year. The remaining insects on vine mesquite grass were five ant species: honey-pot ants (*Myrmecocystus* spp.), tiny red ants (*Iridomyrmex pruinosum*), the fungal garden black ant (*Trachymyrmex smithii neomexicanus*), *Formica perpilosa* and crazy ants (*Dorymyrmex insana*). When vine mesquite grass was sampled in the second year, the insect fauna was more diverse. In May, cicadellid leaf hoppers accounted for ninety percent of the insects collected from vine mesquite with mirid bugs and thrips as the other fluid feeding insects. In summer, tetranychid spider mites and stout thrips accounted for most of the arthropods on vine mesquite. In October, the plant feeding insects on vine mesquite were staphlinid beetles and thrips. . Other arthropods on vine mequite included snout beetles, flower beetles, muscoid flies, leaf miner flies, midges, damsel bugs, chalcid parasitic wasps, plant hoppers, butterflies and moths. Predators were jumping spiders and crab spiders.

In the first year, tobosa grass did not begin to produce green foliage until September. Thrips (Thysonoptera) accounted for forty percent of the total number of arthropods in September. Thrips are plant feeders that attack flowers, leaves, fruit, twigs, and buds of many types of plants. That summer there were few insects on tobosa grass with some grass hoppers (Acrididae) and walking sticks (Phasmatidae) plus ants and spiders.

In the second growing season, above average winter rainfall produced abundant spring annuals which carpeted the spaces between tobosa grass tussocks. Some of the arthropods captured from tobosa grass tussocks probably fed on the annuals and sought shelter in the dense grass tussocks. Cicadellid leaf hoppers accounted for sixty four percent of the total. Scale insects (Coccoidea) and common thrips added to the plant fluid feeders on tobosa grass in April. In July, psyllid plant lice made up nearly half and stout thrips (Phlaeothripidae) which are plant fluid sucking insects contributed nearly seventy percent of all arthropods sampled. Plant sucking cicadellid leaf hoppers, delphaed leaf hoppers and psyllid jumping plant lice dominated the October samples. The winter samples included two families of homopterans that were not captured in the summer or autumn samples: cicadellid leaf hoppers and psyllid jumping plant lice.

In the second year, there were few chewing insects on tobosa grass and these were caterpillars (Lepidoptera) and grasshoppers (Acrididae). There were several types of predators including spiders, beetles, predatory hemipteran bugs and two lace wings (Neuroptera): dusty lacewings and brown lacewings,and dance flies (Empididae) that accounted for a small portion of the total arthropods sampled. Chalcid parasitic wasps and ants were sampled in the spring but were not on tobosa grass in the other seasons.

Soaptree Yucca (*Yucca elata*)

Soaptree yucca is the state flower of New Mexico and is widely distributed in the Chihuahuan Desert in the United States and Mexico. Soaptree yucca, a member of the lily family, has fibrous leaves that form an ovoid crown of leaves. Mature soaptree yucca may reach more than twelve feet in height on a caudex (fibrous stem). Soaptree produces large numbers of white flowers near the top of an inflorescence stalk that grows out of the center of the leaf crown. It flowers in June to mid-July and produces large numbers of flat, black seeds that are released from dry pods. The pods are produced only from pollinated flowers that grow on small branches of the main flowering stalks (see photo of *Yucca elata* with flowers). Many of the flowers are not pollinated and there are no seed pods produced on those stems. Pollination in several species of *Yucca* was attributed to a moth which led to several studies of the potential pollinators of this plant. The insects on soaptree yucca during flowering and fruit set were equal numbers of leaf beetles (Chrysomelidae) and snout beetles (Curculionidae) that feed on leaves and flowers. Two families of insects associated with flowers: bee flies (Bombyliidae) and soldier flies (Stratiomyidae) were also abundant when flowers were present.

Flowering soaptree yucca (*Yucca elata*) in a black-grama grassland

The obligate association between yucca plants and yucca moths was first described in the 1890's of yucca species in the Mojave Desert. Additional studies of yucca species and yucca moths reported similar obligate associations of yucca moths and yucca plants. The yucca flower is deliberately pollinated by a female yucca moth after she has laid an egg on the ovary of the flower. This behavior results in fertilization of the flower, and production of up to six columns of seeds in the yucca fruit. The yucca moth larvae feed on the yucca seeds in the fruit. The absences of information on soaptree yucca pollination and the large numbers of insects that could potentially pollinate soaptree yucca flowers, prompted an experimenta led by two post-doctoral associates (Dr. Craig James – Australia and Dr. M. Timm Hoffman – South Africa). Their study documented three species of moths, twelve species of bees and wasps, nine species of flies, and eighteen species of beetles that could potentially pollinate soaptree yucca flowers. Together these potential pollinators accounted for more than ninety percent of all of the insects on the yucca flowers. The large numbers of thrips and aphids on the flowers were not included because they were not potential pollinators. Because yucca moths only fly after sunset, flowering stalks were bagged with fine mesh bags to exclude either day- time (diurnal) or night- time (nocturnal) insect groups. None of the flowers exposed to only diurnal insects produced fruits. However approximately 5% of the flowers exposed to nocturnal insects produced fruits and that was not different from the flowers that had not been bagged. Two kinds of hand pollination were performed to evaluate the effectiveness of floral visitors. When yucca pollen was brushed over the top of the stigma tubes, there was no fruit production. Yucca pollen formed into small balls and pushed into the stigma tubes resulted in production of fruits.

The intense observations of the behavior of the yucca moths (*Tegeticula yuccasella*) on soaptree yucca flowers provided interesting details on the reproductive behavior of the moths. During daylight hours, the moths were motionless at the base of old flowers that had partially closed. When these moths were examined, more than a third of the moths had yucca pollen in their mouthparts. This yucca moth did not start flying until 40 minutes after sunset and tapered off after one hour.

Male yucca moths flew into a flower and rapidly ran about in a flower and if no female was present quickly flew into another flower on that flowering stalk. If a female was present in a flower the male would attempt to mate often unsuccessfully. Female moths after entering a flower would circle around the base of the flower ovary. Most females would insert the ovipositor deep into the tissue at the base of the ovary and remain stationary for short time. We assumed that the insertion of the ovipositor resulted in an egg being placed at the base of the ovary. The only females that were observed to pollinate a flower were females that appeared tooviposit (lay an egg) in the flower. Yucca flower ovaries have six segments called locules. Female moths normally oviposited eggs in one or two locules and then departed. Approximately one quarter of the yucca flowers were oviposited in and pollinated by more than one female.

Soaptree yucca flowers covered with aphids.

Creosotebush Insect Communities

Large areas of the Chihuahuan Desert are dominated by creosotebush (*Larrea tridentata*) and most of our ecological studies were in creosotebush areas. Evergreen creosotebush shrubs are important habitats for some organisms providing important resources during stress periods of the year. The leaves of creosotebushes produce a number of volatile chemicals and resins that deter many animals from chewing on the leaves. Creosotebush leaves also contain some large molecules known as antiherbivore compounds that are toxic to most animals. These molecules include some tannins and phenolic compounds. Despite this elaborate set of defenses, many arthropods obtain needed energy and nutrients from cresotebush. Those herbivores serve as prey for a diverse group of predators. Some ant species provide protection for the most sedentary species of plant sucking insects: a relationship that provides mutual benefits e.g. sugary liquids from the insects to the ants and the ants provide protection of the immobile insects from predators. The foliage of creosotebushes is home to a number of different kinds of sucking insects: insects with piercing mouthparts that allow them to avoid the chemicals on the leaf surface and to pierce the cells of the internal (mesodermal) tissues of the leaf thereby avoiding the toxins. Sucking insects of two orders (Hemiptera – true bugs, and Homoptera which includes cicadas, leaf hoppers, jumping plant lice, aphids and scale insects) are the most abundant insects on creosotebushes. The abundance of all insects and spiders on creosotebush plants varies with the physiological condition of the plants.

The physiological condition of creosotebush varies among years. In a year with little effective summer rainfall, the July samples were dominated by hemipteran bugs: leaf bugs (Miridae), seed bugs (Lygaeidae), stink bugs (Pentatomidae) and homopterans including plant hoppers (Fulgoridae), leaf hoppers (Cicadellidae), and jumping plant lice (Psyllidae). Thrips

(Thysanoptera) which are plant fluid sucking insects were also abundant. In October after some effective September rainfall, hemipteran stink bugs (Pentatomidae) and homopteran jumping plant lice (Psyllidae) were most abundant. Grasshoppers accounted for nearly twenty percent of the insects on creosotebush in October. Leaf bugs (Hemiptera: Miridae) and jumping plant lice (Homoptera: Psyllidae) made up more than seventy percent of all of the insects on creosotebush in late November.

The second year that the arthropods on creosotebush were sampled was characterized by good winter rainfall and above average rainfall in the growing season. The May samples were dominated by leaf bugs (Hemiptera: Miridae) and three types of homopterans: leaf hoppers (Cicadellidae), tree hoppers (Membracidae) and jumping plant lice (Psyllidae) that together accounted for more than sixty five percent of the total number of arthropods in the samples. The July samples had fewer leaf bugs, but more tree hoppers and jumping plant lice. Plant fluid sucking insects accounted for thirty five percent of the total number of arthropods in the samples. The only chewing insects were inch worm caterpillars (Lepidoptera: Geometridae).

Irrigation Experiments

In studies where creosotebush were subjected to sprinkler irrigation to mimic small storms (approximately .25 inches each week) and large storms (approximately 1.0 inches each month) and application of nitrogen fertilizer, the sucking insects were most abundant on the plants receiving irrigation plus nitrogen. Application of water without fertilizer had no effect on the abundance of sucking insects or chewing insects. Leaf chewing insects did not respond to either irrigation or nitrogen fertilizer. There were dramatic seasonal fluctuations in the abundance of insects on creosotebush. Numbers of insects were highest in late spring, and lowest in mid-summer and early autumn. It is likely that creosotebush foliage quality is highest during the cooler temperatures of early spring when the shrubs are exposed for longer periods of sunlight at optimum temperatures for photosynthesis. Higher abundance of insects on the plants fertilized with nitrogen probably resulted from higher amino acid content in the cell sap or sap in the vascular tissues.

Rain out shelters in a creosotebush shrubland on the upper slopes of a piedmont.

There are two hypotheses that have been offered to explain the abundance of insects on plants. One is the Plant Stress Hypothesis that states that stressed plants are more suitable hosts for plant feeding insects and the second is the Plant Vigor Hypothesis that states that vigorous plants are the most suitable hosts for plant feeding insects. We evaluated these hypotheses for the insect assemblages on creosotebushes. We applied stress by building “rain-out” shelters over plants in eight plots. The “rain-out” shelters consisted of a steel frame covered with green house plastic. The rain-out shelters were designed to produce extreme drought during the summer growing season (June through October). We applied sprinkler irrigation to creosotebush shrubs in eight plots and had a similar number of plants in eight plots that had no experimental treatment. Sampling consisted of vigorously shaking randomly selected branches into a muslin sweep net, closing the net and transferring the insects into labeled plastic zip lock bags. Because scale insects (Homoptera: Coccoidea) and gall forming insects (Diptera: Cecidomyiidae) were not dislodged from shaken branches, in May and September, we examined three branches from each shrub and counted all of the scales and gall formers. The arthropods were sorted and counted by mophospecies (arthropods that look alike) and identified to the lowest taxonomic rank possible.

Territorial Behavior of Creosotebush Grasshoppers

A study of territorial behavior of creosotebush grasshoppers showed that the largest creosotebushes harbored four to six males and three females. More than one male was found on many shrubs but females were found on only one out of four creosotebushes. When more than a single male was present, only one of the males called (by rubbing legs) producing a short buzz that lasted about half a second. Subsequent calls were produced at intervals between one and two minutes. Male creosotebush grasshoppers in shrubs that had no females left those shrubs within half an hour. When there was more than one male in a shrub with one female, there were confrontations. Both males would signal by sharp ticks and the rivals would move toward each other. Physical contact was generally avoided when one of the rival males retreated. Generally the first male to call or signal won such encounters. When a singing male from one shrub was introduced into a shrub with a singing male, the results were variable, introduced male ran-off resident male three times, resident males ran-off introduced males three times and once the intruder remained silent in the shrub avoiding a response from the resident male.

A creosotebush branch with a "creosotebush grasshopper" (*Boetettix argentatus*)

We recorded 44 groups of arthropods in our samples. Three types of spiders were the only non-insect arthropods in the samples. A type of jumping spider, (Salticidae) was significantly more abundant on the irrigated shrubs than on shrubs in the other plots. The abundance of the other spiders was not affected by irrigation or drought. Nine groups of insects were more abundant on the irrigated shrubs than on shrubs in the other plots. Among the insects that responded as suggested by the Plant Vigor Hypothesis were four species of gall forming insects of the genus *Asphondylia*, a mirid bug (*Parthenicus* sp.), a membracid bug (*Multireoides* sp.) and two scale insects. The positive response of scale insects and other sap-suckers to amount of rainfall reflects the water-dependent sap flow upon which these insects depend. One foliage feeder exhibited a non-linear response which did not support either hypothesis.

There were only two types of insects that occurred in higher numbers on the drought stressed plants, a moth larva (*Semiothesia* sp.) and a species of thrips (*Frankliniella* sp.) that feed on flowers. These were the only insects that responded as predicted by the plant stress hypothesis. There were more flowers on the drought stressed plants than on untreated or irrigated creosotebushes. It is known that creosotebush produces more flowers when drought stressed than when receiving average rainfall. Since drought stressed plants produce fewer antiherbivore compounds in the epidermal cells of the leaves, more moth larvae that feed by chewing the leaves from the leaf margin inward could make a living on the drought stressed plants.

While there were more arthropod groups that responded as predicted by the Plant Vigor Hypothesis, most of the morphospecies of insects and spiders were unaffected by either drought or by irrigation. Many of the arthropods occurred too infrequently for us to detect responses to drought or simulated rainfall. Combinations of rare species into a single morphotype or functional group probably masked differences in responses of individual species that were lumped into a functional group. This study showed that the creosotebush arthropod community exhibits a wide diversity of responses to precipitation levels and cannot be predicted by the stress or vigor hypotheses.

A mutilid wasp that mimics the fruit of a creosotebush

There are many predatory and parasitic insects that are associated with creosotebushes. One of the most unusual insects is a mutilid wasp that resides in the leaf litter under mature creosotebushes. This wasp mimics the light grey, hairy fruits of the creosotebush.

Insect Associates of Mesquite

Our initial studies of arthropods on mesquite were conducted over two years. In the first year of the study, rain events were mostly too small to be effective during most of the summer monsoon season. There was several effective rain events in September of the first year followed by above average rainfall during the winter that continued through the growing season of the second year. Mesquite produces new foliage in late April to early May and produces flowers in late May and June. There were twenty two groups of arthropods recorded in the mesquite samples in May. Three fluid sucking homopterans accounted for eighty percent of the arthropods in the May samples. Jumping plant lice (Homoptera: Psyllidae) were the most abundant, making up seventy percent of the individuals sampled. The other homopterans were Issid plant hoppers and Membracid plant hoppers (Homoptera: Issidae and Membracidae). Thrips (Thysonoptera) added to the list of plant fluid sucking insects. There were a small number of beetles of several families: branch and twig beetles (Bostrichidae), metallic wood boring beetles (Buprestidae), leaf beetles (Chrysomelidae), and checkered beetles (Cleridae) that together accounted for only one percent of the total. Several generalist ant species were found on mesquite in the spring.

The July samples had forty one different groups of arthropods taken from mesquite. Scale insects (Coccidea), membracid plant hoppers (Membracidae), leaf hoppers (Cicadellidae), aphids (Aphidae) were the fluid sucking homopterans which with the fluid sucking hemipteran mirid bugs (Miridae) accounted for twenty three percent of the insects in the samples. Ants dominated the samples and made up more than sixty four percent of the insects in the samples. Small numbers of flies, bees and wasps were associated with the flowers and fruits of mesquite in the July samples. The October samples had only twelve groups of arthropods. The most numerous were plant fluid sucking jumping plant lice (45%) and leaf hoppers (16%) of the total number of arthropods. Generalist ants contributed thirty four percent of the total.

Mesquite still had leaves when arthropods were sampled in mid-November. There were only three taxa of arthropods in the November samples: jumping plant lice (Homoptera: Psyllidae) accounted for ninety seven percent of the arthropods in the sample. Membracid plant hoppers and generalist ants made up the rest of the November sample.

In May of the second year, the arthropods on mesquite were less diverse than the previous year with only jumping plant lice (Homoptera: Psyllidae) and plant chewing leaf beetles (Coleoptera: Chrysomelidae) in the samples. The July samples of the second year were also less diverse with only five groups of arthropods. Jumping plant lice accounted for ninety eight percent of the arthropods in the July sample with small numbers of ants, caterpillars, hemipteran bugs and spiders making up the remainder of the sample. The October samples in the second year had ten different groups of arthropods but jumping plant lice accounted for nearly ninety percent of the arthropods in the sample. Spiders, flies, leaf hoppers, membracid plant hoppers, chalcid parasitic wasps, ants, halictid wasps, and caterpillars made up the rest of the sample.

A walking stick on a mesquite stem.

Mesquite Stem Girdlers

One of the more impressive insects of the Chihauhan Desert is the mesquite stem girdler beetle (*Oncideres rhodostica*). The stem girdler belongs to a family of beetles known as long-horn beetles (Cerambycidae). The long-horn beetles get their name from the long antennae that are characteristic of members of this family. Most members of this family are wood boring in the larval stages. The larvae are elongate, cylindrical, whitish and almost legless. The larvae of stem girdlers are round-headed borers which makes them different from other wood borers that have flat heads. Although the adult stem-girdlers are small and not easily seen, they leave ample evidence of their presence in the form of dying branches on mesquite plants. The leaves on the stem above the girdle turn yellowish brown after the water and nutrient supply is disrupted by the girdle. The mesquite stem-girdler utilizes mesquite stems for oviposition (lay eggs) and larval development sites. Female beetles chew girdles around mesquite stems severing the phloem and xylem, disrupting water and nutrient transport; killing the affected stem above the girdle. The beetle then oviposits distally from the girdle, which protects its egg from being coated in sap flowing up the stem in response to the girdle. Mesquite is known to produce a viscous (thick sticky liquid) sap that exudes from a wound when the stem tissue is disturbed. Female beetles girdle and oviposit in only one branch, and have been reported to lay 8.1 eggs per stem.

It has been reported that the mesquite stem girdler occurs at an average density of 4.7 beetles per mesquite plant in the Trans-Pecos region of Texas. Adult beetles kept in field cages lived only 20-30 days. The eggs hatch within one month of oviposition and the larvae overwinter by feeding on the dying mesquite stem. The larvae pupate within the stem and the adults emerge in early autumn, mate, and the females girdle fresh mesquite stems prior to the onset of freezing temperatures. Mesquite stem girdlers are insects that have benefitted from the expansion of mesquite into the Chihuahuan Desert grasslands in the past century. The abundance of multi-stem mesquite provides an ample resource base for this beetle. While we have no density estimates of stem girdler beetles on mesquite in southern New Mexico, the high levels of stem death from girdling beetles on mesquite suggests that densities of this beetle may be as high or higher than those reported from Texas. Our early studies of mesquite stem girdlers revealed that the beetles killed stems on approximately 45% of the mesquite plants on the upper slopes of a desert watershed. Recent studies in a basin grassland found girdled stems on more than 70% of the mesquites.

Tarbush Insects

The name of tarbush is based on the resinous leaves that contain a suite of chemical compounds that are distasteful and/or toxic to livestock, rabbits, and many insects. Since tarbush is frequently winter deciduous, we sampled the insects on tarbush between May and November. Insects were sampled by enclosing a branch in a plastic bag, severing the branch from the main stem and sealing the bag. Virtually all insects including highly mobile wasps and flies were captured by this method. The insects were knocked out by cold temperatures and the immobile insects sorted and classified.

We estimated the proportion of leaf area that was missing and attributable to insect herbivory by assessing the proportion of each leaf that had been chewed relative to the total number of leaves in the sample. Some leaves were completely consumed but could be identified by the presence of petioles or abscission scars. The percent defoliation in May was only 1% but increased to between 23% and 30% in August, September and November. There was a relatively high diversity of chewing herbivores on tarbush in comparison to mesquite and creosotebush. Chewing herbivores included three generalist grasshoppers, seven beetles, and eight butterfly or moth larvae. Chewing herbivores exhibited similar abundance May through August and declined dramatically in November. The numbers of chewing herbivores and the estimated loss of leaf area by defoliation could have a significant effect on photosynthesis and the growth potential of the shrubs. This could be especially important during periods of water stress and may account for the low average height of tarbush in the northern Chihuahuan Desert.

There were 10 species of sap-sucking herbivores on tarbush. These included three species of thrips, a *Lygus* bug, three scale insects, and three true bugs. There were approximately two to four times the number of sap sucking herbivores than chewing herbivores and there was no significant reduction in abundance of sucking herbivores in November. The predators on tarbush included three beetles and two spiders. The beetles were only present on tarbush in August. The density of spiders did not vary significantly at any of the sampling dates. There were two generalist species of ants that were found on the tarbush foliage throughout the growing season: a *Pheidole* sp. and *Forelius pruinosus*. Five other species of ants were also recorded on the tarbush branches.

Egg case of a praying mantis on a tarbush stem.

Insect Fauna of Chihuahuan Desert Shrubs – Conclusions

The most numerous insects on desert shrubs are plant fluid sucking homopterans and hemipterans. While the families and species of fluid sucking Homoptera and Hemiptera vary among shrub species, among years, and among seasons, they are almost always present on shrubs with foliage only in the growing season and they also occur on shrubs that retain foliage in the winter months. These two groups of insects have modified mouth parts that form hypodermic needle like structures that can penetrate the leaves. The feeding method of these insects allow them to bypass the toxins and feeding deterrents of the epidermal cells of the leaves in order to get at the cell contents of mesophyll cells (internal layers of cells in leaves) or the fluids in the vascular tissues.

Photos of several species of leaf hoppers (Homoptera: Cicadellidae)

Insects that chew on leaves removing tissue from the edges of leaves or chewing holes in leaves are present on most desert shrubs during the growing season. However the numbers of chewers are generally much lower than the number of fluid suckers. Chewers are primarily beetles and a few specialized grasshoppers. The predators on shrubs are mostly spiders and the most common spiders in the foliage of shrubs are jumping spiders (Salticidae) and crab spiders (Thomisidae).

A jumping spider. Note the large eyes.

A crab spider on a finger (finger for scale)

Insects on flowers of rubber rabbit brush (*Ericameria nauseosa*, old name *Chrysothamnus nauseosa*). Insects on flowers primarily butterflies (Lepidoptera) and bees (Hymenoptera).

Sulfur butterflies congregating on a moist patch of clay soil.

Effects of Summer and Winter Grazing on Insect Diversity in a Grassland

As part of a study designed to test hypotheses about the effects of seasonal grazing and mesquite shrub removal on a black grama desert grassland ecosystem, we sampled the insect populations on the grass and herbaceous plant layer, on snakeweed and on mesquite over a five year period. We sampled grasses and snakeweed by sweep net. We sampled mesquite insects by knocking insects from the foliage of a fixed canopy area into a net. Insects were sorted by family and morphospecies (insects of a family that were visually different when examined under a microscope).

The number of families of insects on the grass-herbaceous plant layer varied with the growing season rainfall (June through August). In years with growing season rainfall of more than 150 mm, we recorded 110 families of insects on the grasses. During the driest year with growing season rainfall of 47.5 mm, there were only 72 families of insects recorded from the gass-herbaceous layer. In the years with more than 70 mm of growing season rainfall, there was an average of 94 families living on the grass layer. The insects on snakeweed, (*Gutierrezia sarothrae*), exhibited a pattern similar to that on the grasses with the largest number of insect families, 89, occurring in years with more than 150 mm of rainfall during the June through

August period. In the driest year there were only 62 insect families recorded on snakeweed and in the years with more than 70 mm of growing season rainfall there were 69 families of insects collected from snakeweed. The number of insect families on mesquite exhibited much less variation among years and there was no significant relationship of numbers of families and rainfall. The number of insect families recorded on mesquite ranged from 42 to 68.

Species Studies

Carpenter bees

The large shiny black bees flying in loops in the late spring are carpenter bees (*Xylocopa californica arizonensis*). We think that these flights are a type of lek display of male bees or mating flights of newly emerged adult bees. Carpenter bees are a little larger than bumblebees and feed on nectar and pollen of a variety of desert flowers. In the Chihuahuan Desert, carpenter bees nest primarily in dried flowering stalks of soaptree yucca (*Yucca elata*) or stool flowering stalks (*Dasylirion wheeleri*). Mated female bees seek nest sites in yucca stalks containing empty carpenter bee nests or in dried yucca or stool flowering stalks of appropriate size for a nest. When constructing a nest, carpenter bees chew a round hole near the base of the flowering stalk that becomes the entrance to the nest chamber. The entrance hole is just above the leaf crown or partially hidden by the leaf crown. Once an entrance hole has been made into the center of a stalk, the bee turns ninety degrees and begins to excavate a hole up the center of the stem. Carpenter bee mandibles are sharp and strong allowing the bee to cut through the woody tissue. The fine pieces of material resulting from the chewing are pushed out of the entrance hole. The hollowed out nest chamber is approximately ten to14 inches long with a diameter a little larger than the girth of the bee. Once the nest chamber is completed, the female bee begins to collect pollen and nectar. In the region of the Chihuahuan Desert where we studied carpenter bees, most of the pollen and nectar was collected from creosotebush flowers. The timing of emergence young adult bees from the nest, mating flights and nest chamber construction is coincident with the late spring flowering of creosotebush.

Ground Dwelling Arthropods

The largest ground dwelling arthropods include the desert centipede (*Scolopendra polymorpha*), a desert millipede (*Orthoporus ornata*) and the vinagaroon or whip scorpion (*Mastigoprocctus giganteus*). Desert centipedes are active only at night and are very active following summer rains.

Many of the ground dwelling arthropods may be encountered any time of the year. In summer, many of the arthropods are active only at night, early morning, or at dusk. Some like darkling or stink beetles (Tenebrionidae) are conspicuous and readily seen depending upon the season and time of day. Darkling beetles are found in most Chihuahuan Desert habitats and are relatively abundant. Darkling beetles are one of the most common insects seen at White Sands on the gypsum dunes and in the inter-dune areas. Their wide distribution and abundance is probably because they feed on detritus or dead plant parts. Tenebrionid beetles (*Eleodes* spp.) are known for their behavior of standing on their head with their posterior in the air. These darkling beetles squirt a brown fluid, chemical quinones, from their anus. That is a chemical defense that keeps most predators at bay. There is one predator, the grasshopper mouse, is not deterred by the liquid quinones. The grasshopper mouse sticks the beetle into the soil, posterior end first, then proceeds to eat the beetle like an ice cream cone.

We studied water loss and seasonal activity of four species of *Eleodes*. The two species (*Eleodes gracilis* and *E. tenuipes*) with the lowest rates of water loss at temperatures between 90^{o}F and 100^{o}F were the most abundant in the pit fall traps during the hot summer months. The two species with rates of water more than double those of *E. gracilis* and *E tenuipes* at high temperatures accounted for most of the tenebrionid beetles trapped in spring and autumn when air temperatures between 70^{o}F and 80^{o}F prevailed. Since detritivores have plentiful food available all year, the seasonal abundance and activity of *Eleodes* spp. is a function of environmental temperatures.

Another detritivore, the desert millipede (*Orthoporus ornatus*) is relatively abundant and frequently seen after rains. Desert millipedes are segmented, reddish brown to black with two pairs of legs per segment. Average size (length) is four inches, with a range from three inches to more than six inches. When disturbed *Orthoropus ornatus* curls into a coil and secretes a bad smelling fluid. That liquid is made up of benzoquinones, aldehydes, hydrocyanic acid, phenols and terpenoids. That behavior and the secretion apparently protect desert millipedes from most predators. We have observed desert millipedes being attacked by a beetle larva (family Phengodidae) which basically unzipped the millipede by cutting through the thin chitin between segements. The beetle attacked the ventral side of the millipede and left only the cuticle which looked like a hollow spring. This beetle will completely consume the entire millipede which is usually several times larger than the beetle larva. The desert millipede was found to coexist in captivity for several months with a large centipede (*Scolopendra polymorpha*) which quickly dispatched arthropods like desert roaches, crickets, and grasshoppers. There is no evidence that birds like roadrunners or mammals prey on desert millipedes.

After heavy rains, millipedes are most active in the early hours after sunrise; are not very active at dusk and not active at all after sundown. Desert millipedes were studied by Dr. Cliff Crawford and his students from the University of New Mexico. They studied desert millipedes in the vicinity of a playa lake on the watershed near the Chihuahuan Desert Rangeland Research Station headquarters. Using counts of millipedes on the roads, he estimated an abundance of approximately 35 per acre. Millipedes spend most of their time feeding on organic detritus that accumulates around the bases of some shrubs and in small drainages. Millipede gut contents consisted of large amount of sand grains and shredded organic matter plus some chitinous remains of small insects. Identifiable organic materials were small sticks, grass stems, and pieces of leaves. Desert millipedes actively fed on dead bark of mormon tea (*Ephedra trifurca*) often removing considerable amounts from a single branch. Dead bark of other shrubs was rarely eaten. During the middle of the day, many of the larger millipedes climbed up into shrubs and were most numerous on mormon tea. Millipedes that did not climb into shrubs entered rodent burrows and holes made by other animals. By entering existing burrows or climbing into shrubs, the millipedes escape the high temperatures mid-day soil surface temperatures.

A band-wing grasshopper (one of the most common grasshoppers in the desert)

A tarantula on the side of a house – crawled up the stucco.

A lubber grasshopper

A tarantula hawk (*Pepsis* spp.) dragging a paralyzed tarantula to a suitable burial location. The tarantula hawk has red wings.

A tarantula hawk (*Pepsis* spp.) feeding on nectar and pollen.

A camel cricket

A camel cricket

The Living Soil

Because the models driving the International Biological Program were based on energy flow in ecosystems, there was a push by the program lead scientists for studies on the decomposition of dead plant material (leaves, stems,and flowers) because the detritus (dead material) pool accounted for most of the energy in terrestrial ecosystems. We had studies of ants and termites that process dead plant material and a microbiologist who focused on microbial decomposition. When an airplane crash claimed the life of the microbiologist that had been leading the Chihuahuan Desert efforts, we had no person to assume responsibility for that work. Our lab undertook studies of the role of all soil biota on decomposition and later nutrient cycling processes. Those studies were supported by additional funding from the U. S. National Science Foundation

Most of the literature on the breakdown of organic materials in the soil was from agricultural and forest studies in rain-fed systems. Soil biological communities in moist environments were extremely diverse and included large (visible to the naked eye) invertebrates such as earthworms, snails and slugs, wood lice, millipededes, centipedes,beetles and collembolans plus microscopic biota such as mites, nematodes, protozoans, bacteria and fungi. In a book published in 1976 there were no data cited for the soil fauna in hot deserts. Organisms that live in soil are difficult to study because soil is an opaque medium. Animals that live in burrows such as ants, termites, millipedes, centipedes, and adult beetles can be observed and studied when they are active on the soil surface. Animals such as insect larvae and soil microfauna require indirect techniques to extract these organisms from the soil.

At the end of the International Biological Program, we had studies of a Chihuahuan desert millipede, *Orthoporus ornata*, conducted by a colleague, Dr. Clifford Crawford and some studies of termites and ants. We had tested some of the techniques developed by European scientists for studies of microscopic soil biota and had found that our Chihuahuan Desert soils were suitable habitats for mites, collembolans, nematodes Our initial studies of soil microarthropods (mites and isotomid collembolans) were enhanced by the discovery of one of the graduate students, Perseu Santos, that extracting microarthropods by Tullgren funnel produced higher numbers and diversity when the fluid in the extraction container was water. Tullgren funnels are cylinders with a cheese cloth bottom. Soil cores are placed in cylinder which is supported on a funnel that empties into a small container. Microarthropods are driven to the underside of the soil core by a 60 watt bulb that is hung at the top of the cylinder. As the soil heats and dries, the microarthropods move through the cloth and fall down the funnel into the water. Previous studies of extraction of soil microarthropods used alcohol or picric acid as the fluid in the collection vial. The large quantities of fine sand that passed through the cheese cloth obscured organisms at the bottom of vials of alcohol or picric acid which made them virtually impossible to see or count. The microarthropods extracted in Tullgren funnels using water, were largely confined to the surface of the water because the surface tension of the water kept them on top of the water where they were visible without being obstructed by sand grains.

Initial surveys of microarthropods and nematodes found that the abundance and diversity of these organisms were a function of the quantity of plant litter. Large plants like mesquite and desert willow growing at the edges of arroyos had the largest accumulations of dead leaves, stems, and the highest abundance and diversity of mites and nematodes. Litter layers under creosote bushes varied with the morphology of the shrub but were always nearly 10 times less than that under arroyo mesquite and desert willow. Open spaces between shrubs, bare arroyo bottoms had very little plant litter mixed in the sand and very few microarthropods and nematodes. When we sampled in grassland, microarthropods and nematodes were abundant and diverse under grasses with dense root systems and much less abundant and diverse in spaces between grass tussocks. Chihuahuan Desert microarthropod populations are dominated by small prostigmatid mites in the families: Tydeidae, Paratydeidae and Pyemotidae that feed on fungi and nematodes. Another abundant prostigmatid mite of the family Nanorchestidae feeds on soil algae and probably other soil microorganisms. Oribatid mites that are dominant and abundant in forests, pasturelands, and some agricultural lands are found in low abundance and diversity in virtually all Chihuahuan Desert environments.

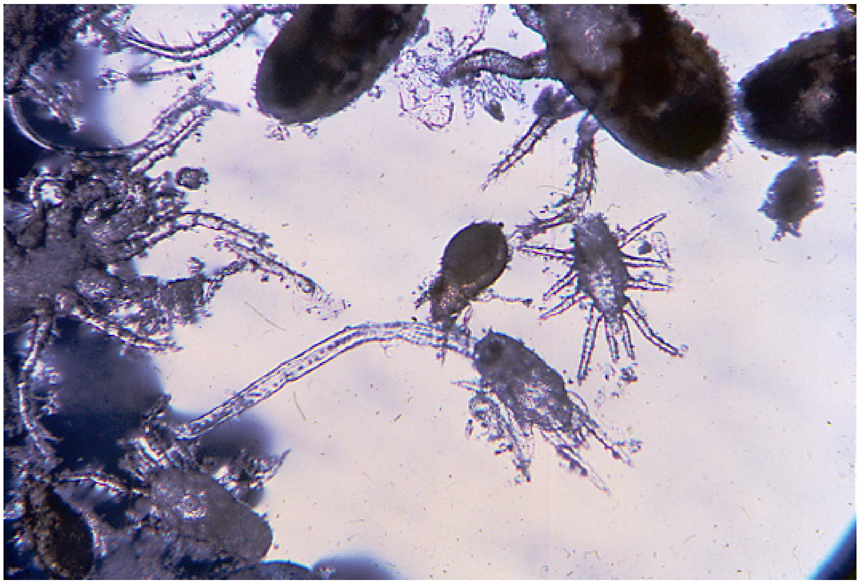
When the results of our initial studies were presented at a meeting on soil biota, we met Professor J. A. (Tony) Wallwork who accepted an invitation to work with us on the soil biota of the Chihuahuan Desert. Professor Wallwork (University of London) and Dr. Diana Wall (Freckman) from University of California- Riverside) enabled us to bring taxonomic expertise to our studies of soil fauna and their role in the processing of dead plant materials. We conducted studies in the gypsum sand dunes at White Sands National Monument to determine if the chemistry of the substrate had any effect on the microarthropod community or on the decomposition process. The microarthropod community at White Sands differed from the Jornada basin watershed not in the families of mites but the most abundant mites. At White Sands the most abundant mites were nanorchestid mites probably as a result of the algae that developed in the surface sands of the dunes. The other mites that were relatively abundant were the smaller prostigmatid mites that were dominant in the Jornada soils. The rates of decomposition at White Sands were similar to those reported for the Jornada experiments..

Our first experimental studies were focused on the role of soil fauna on the rates of decomposition in our desert environment. When microarthropods were chemically excluded, the rate of plant litter decomposition was reduced in the early (first couple of months) stages of the process. We then learned that removal of microarthropods resulted in exponential growth of the soil nematode populations. The nematodes that exhibited exponential growth were bacteria-feeding nematodes. Bacteria- feeding nematodes are distinguished by a round mouth and a muscular pump at the back of the mouth. These nematodes feed by sucking up bacteria from the surfaces of stem fragments, leaf fragments and the surface of soil particles. The most abundant soil mites in the litter in the early stages were small tydeids that were predators on nematodes.

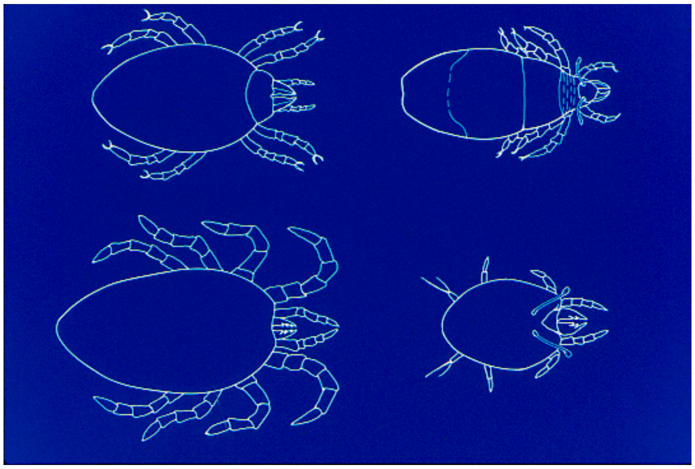
When the predatory mites were removed, the bacteria – feeding, cephalobid nematodes overgrazed the bacteria that were breaking down the plant litter thereby reducing the rate of decomposition.

The soil fauna of the Chihuahuan Desert is poorly known taxonomically with few Genera and even fewer species that have been described by experts. We have reasonable data on the relative abundance of the different morpho-types of soil protozoans. The most abundant soil protozoans in Chihuahuan Desert soils are naked amoebae.

We set up a major study to examine the decomposition of roots and the role of the soil biota in that process. We used the roots of a spring annual pepper weed (*Lepidium lasiocarpum*) that was common in the creosotebush area on the Jornada watershed. The major finding of that study was the following the initial rapid mass loss in the first month, the rate of decomposition leveled out and over time the nitrogen concentration in the roots increased. The increase in nitrogen concentration during decomposition is referred to as "nitrogen immobilization". Fungal hyphae growing in and on the roots scavange ammonium and nitrate from the soil which appears as increased concentration of nitrogen in the roots.



Soil mites extracted onto the surface of water in an extraction vial. Photo at 400 magnification.



Drawings of four different types of prostigmatid mites.

Alien Species: Problems and Pluses

South African gemsbok (*Oryx gazella*) were established on White Sands Missile Range by the New Mexico Game and Fish Department in the early 1960's. The Oryx as they are called, came from the winter rainfall Kalahari Desert in South Africa. The Game and Fish Department hoped to establish a sufficiently large population of Oryx on the missile range that these animals could be hunted and bring revenue to the department. The introduction of Oryx was very successful and hunting permits were issued based on the population models for this species in the Kalahari. No one anticipated the rapid increase in numbers or that Oryx would disperse over a mountain range into the Jornada basin and the southern Rio Grande area of New Mexico. Oryx in New Mexico experience much more nutrient rich vegetation than was available in the Kalahari as well as higher rainfall that is spread over most of the year. The reason for the higher nutrient content of Chihuahuan Desert vegetation than the vegetation in the Kalahari is that the Kalahari soils are very ancient and most of the water soluble nutrients have been leached from the soils of southern Africa.

The Oryx is a superbly adapted large desert animal. Oryx do not sweat and have reduced water losses from respiratory surfaces, and feces. Oryx do not have to spend water to regulate their body temperature and in mid-summer have body temperatures as high as 108^{o}F. They survive the high body temperature because their brain temperature is maintained at 98-99^{o}F. Their brain temperature stays at this level because of a counter-current heat exchange arrangement of blood vessels from the heart and from the nasal passages. This arrangement of blood vessels regulates the temperature of the blood supplied to the brain. This anatomical feature allows the Oryx to survive on fresh vegetation for several days without the necessity of going to a source of water such as a well, stream, or lake because the animal has not used water to maintain its body temperature

Our first sightings of Oryx in the Jornada Basin were in the late 1970's. We were really surprised to see this animal on the research ranches because all of the public information suggested that these animals would not cross mountains. We initially passed off the sightings as strays and did not believe that there were sufficient numbers of animals to establish a breeding population. Less than a decade later, we were regularly seeing Oryx or fresh sign of Oryx in virtually every habitat in the Jornada Basin. During that time, several studies of Oryx were conducted by students in the Wildlife Department at New Mexico State University. They found that Oryx eat a much wider variety of plants than domestic livestock and have established populations in some areas that have little in the way of forage for cattle. Their studies also showed that Oryx produce calves at almost any time during the year.

Oryx are now as far north as the Bosque del Apache near Socorro, N. M. and may have expanded south into the rangelands east of El Paso Texas. N. M. Game and Fish now issue permits for depredation hunts on areas outside the missile range. However, that hunting pressure has not been very effective at stopping the spread of this animal. If ranchers in the Chihuahuan

Desert could benefit from Oryx on their ranches, they could produce several times more meat from Oryx than from cattle. In my opinion and that of many of my friends who have eaten Oryx meat, the meat is better than any beef and a much healthier source of protein. It is good that we have learned about an animal that is well adapted to the Chihuahuan Desert environment and has the potential to provide an economic benefit to the rancher in this region.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Oryx with calves on a grassland at the Chihuahuan Desert Rangeland Research Ranch. One of the Oryx has a bent horn but that is not unusual in the New Mexico population. Photo by Amilee Pasco.

However another introduction from South Africa, gets very different reviews. Lehmann’s lovegrass (*Eragrostis lehmannii*) was introduced at the Santa Rita Experimental Range south of Tucson, Arizona as one of several grass accessions from arid areas around the world that were thought to have the potential to provide grass cover for erosion control on areas where native grasses had been greatly reduced by drought and grazing by livestock. The introduction of Lehmann’s lovegrass in the early years of the twentieth century resulted in virtual monocultures of this grass on the Santa Rita. By the early 1990's Lehmann's lovegrass expanded into the Wilcox basin and the San Simon Valley of Arizona where it is rapidly replacing native grasses. In southeastern Arizona, the presence of Lehmann's lovegrass decreased the abundance of native grasses. At that location certain species of grasshoppers, rodents, and birds were found in lower abundance in the lovegrass dominated area than in patches of native grassland. In New Mexico, Lehmann's lovegrass was used to stabilize road cuts and to re-vegetate areas that were disturbed by construction of power lines etc. In the Jornada basin, Lehmann's lovegrass expanded into black grama grassland at the base of the Dona Ana mountains from the power line corridor where it had been used to recover areas cleared during the construction of the power line. In the 1960's Lehmann's lovegrass was limited to the edges of the power line road and the area around the tower structures that had been cleared for the installation of the towers. In the mid-1980's when we were doing studies in the grassland at the base of the mountain, approximately half of the grass cover was Lehmann's lovegrass which had spread up to the base of the mountain and down-slope into the creosotebush shrubland. Over the next thirty years, Lehmann's lovegrass increased to more than ninety percent of the grass tussocks in this area. At present, there are scattered patches of Lehmann's lovegrass on the mid-

Lehmann's lovegrass (*Eragrostis lehmannii*) on mid-slope of a piedmont at the Chihuahuan Desert Rangeland Research Ranch near Las Cruces New Mexico. Photo taken in early March. Note the green foliage at the base of the grass. Photo by Amilee Pasco.

A photo taken in early March of black-grama grass (*Bouteloua eriopoda*) growing on mid-slope of a piedmont at the Chihuahuan Desert Rangeland Research Ranch near Las Cruces New Mexico. Photo by Amilee Pasco. .

slopes and lower slopes of the watershed and it is likely that most of the grassland area of this watershed will be dominated by this alien grass species within the next fifty years.

Colleagues that have been monitoring vegetation change at a number of locations in Big Bend National Park recently reported that Lehmann's lovegrass has expanded into many of the grasslands and is the dominant grass in some of their monitoring areas. We found several patches of Lehmann's lovegrass on the Jornada Basin and it will probably continue to expand into the desert grassland areas. Where Lehmann's lovegrass has been planted to stabilize road cuts or control roadside erosion, it has expanded from the planted areas into the native vegetation wherever there are suitable soils. We predict that this alien grass species will increase and out-compete the native grasses with the result that Lehmann's lovegrass will dominate many of the grasslands in the Chihuahuan Desert.

We conducted studies at the Santa Rita Experimental Range south of Tucson and at the USDA-ARS Jornada Experimental Range to evaluate the effects of Lehmann's lovegrass dominance on animal populations. We measured the abundance and diversity of the ant fauna and estimated the abundance and diversity of small mammals by measuring the abundance and size of pits and excavations made by rodents. At the Santa Rita, there were significantly fewer colonies of large, seed harvester ants (*Pogonomyrmex* spp.) in the Lehmann's monoculture compared to native grassland with sparse Lehmann's cover. The leaf-cutter ants (*Atta Mexicana*) that had large colonies in the native grassland were absent from the Lehmann's monoculture.

There was far less soil disturbance and burrow systems in the Lehmann's monoculture than in the native grassland. The burrow complexes of ground squirrels: Yuma antelope squirrel (*Ammospermophilus harrisii*) and the round-tail ground squirrel (*Citellus tereticaudus*) were abundant in native grassland and sparse or absent in the Lehmann's monoculture plots. While there were fewer ant colonies and less soil disturbance on the Lehmann's lovegrass plots than in native grassland on the Jornada Experimental Range at some dates, these differences were not consistent at all dates when the estimates were made. The differences among and between study areas were attributed to site history in addition to geographic and topographic position. The degree to which this alien grass species affects the fauna appears to be related to the time elapsed since Lehmann's lovegrass was first established.

Restoring Missing Pieces

In the early years of the twentieth century, black tailed prairie dogs (*Cynomys ludovicianus*) were found in many areas of the Chihuahuan Deset. Prairie dog colonies were found on many areas with clay loam soils on the run-on areas of many watersheds. Because they were believed to compete with cattle and sheep for grasses and to present a hazard to horses and cattle, there were concerted efforts by government agents to extirpate these animals from western rangelands. However there is little hard evidence of these perceptions. The result of the government – rancher efforts has been the virtual elimination of prairie dogs from Chihuahuan Desert rangelands in the U. S.

We had an opportunity to study black tailed prairie dog colonies that had been reintroduced into areas where colonies of prairie dogs had been poisoned out. Reintroduction of prairie dogs was one of the goals of the Turner Foundation on the Armendariz Ranch north east of Truth or Consequences, N. M. Prairie dog colonies were established in alkali sacaton (*Sporobolus airoides*), tobosa grass – burro grass (*Pleuraphis mutica – Scleropogon brevifolius*) and burro grass areas. Colonies in the burro grass areas reduced the height of the grass to approximately one inch whereas the burro grass height outside the colony averaged seven inches. The height of tobosa grass and alkali sacaton on the colonies averaged 1.5 inches. The height of tobosa grass and alkali sacaton off colonies is about sixteen inches. The foliar cover of grasses on the colonies was much lower than that off the colonies. Cover of burro grass on the colonies was around three percent and in burro grass patches off colonies was approximately seventeen percent. The percent foliar cover of tobosa grass and alkali sacaton on colonies ranged from 1.5 to 3.5 %. Percent foliar cover of these grasses off prairie dog colonies ranged from 13.4 -18.7%. By reducing the cover and height of perennial grasses, prairie dogs open the site for annual forbs (herbaceous plants) and improve the ability of the residents to detect predators such as rattlesnakes.

We studied the effects of prairie dog colonies on ground-dwelling arthropods by establishing pit fall traps on five colonies and in the grassland at least 400 feet from the edge of the prairie dog colony. Traps were emptied weekly and the arthropods identified to at least the family level. There were differences in arthropod species among prairie dog colonies and among sites that appeared to be related to soil differences and differences in species composition of the grassland. The largest differences in arthropod abundance in the grassland versus the prairie dog colonies were two genera of ants (*Crematogaster* and *Solenopsis*). There were higher numbers of *Crematogaster* spp. colonies on prairie dog colonies than in the grasslands and higher numbers of colonies of fire ants (*Solenopsis* spp.) in the grassland than on the prairie dog colonies. Seventy percent of the prey items were from four families of arthropods: ground beetles (Carabidae), ants (Formicidae), sun spiders or wind scorpions (Eremobatidae), and darkling beetles (Tenebrionidae). Sun spiders and darkling beetles were more abundant on prairie dog colonies than in the adjacent unmodified grassland. . There were no differences in rodent abundance on colonies and in the surrounding grasslands. Small rodents accounted for approximately ten percent of the prey items found in the pellets. The rodent remains in the burrowing owl pellets were those of pocket mice (*Perognathus* spp.). Adult pocket mice weigh between 6 – 10 grams. In comparison, the average weight of one of the most frequent prey items, darkling beetles (Tenebrionidae) is 0.6 grams. Given these mass differences owls would need ten to fifteen beetles in order to equal the mass of one pocket mouse. Since arthropods accounted for approximately 90% of the prey items brought to feed the young, it is obvious that arthropods are important prey for burrowing owls.

In less than a year after successful reintroduction of prairie dogs, burrowing owls (*Athene cunicularia*) took up residence in the prairie dog colonies and there was at least one nesting pair of owls on each of the colonies. We studied burrowing owl foraging behavior on five prairie dog towns between early June and the end of July which represented the nesting season. We selected one nest burrow at the center of each colony and one nest burrow at the edge of each colony. We observed the adult owls from a vehicle approximately 75 yards from the edge of the prairie dog colonies and recorded foraging success and time foraging on the colony or in the grassland around the prairie dog colony.

A prairie dog on a fresh mound.

A Burrowing Owl (*Athene cunicularia*)

A burrowing owl on a prairie dog colony on the Armendariz Ranch north of Engle, N. M. Note the bison dung pats and lack of vegetation.

Burrowing owls foraged more frequently on prairie dog colonies than in the surrounding grasslands independent of the location of the nest burrow (center or edge of prairie dog colony). Owls spent less time in pursuit of suitable prey on colonies than owls that foraged in the grasslands. Successful pursuits, defined as an owl returning to the nest with a prey item, took much less time on colonies than in the surrounding grassland. This study demonstrated that the relationship between burrowing owls and prairie dogs is symbiotic. Owls benefit by using abandoned burrows as nesting sites. The shorter vegetation of the prairie dog town allow the owls to make shorter, quicker flights in order to locate prey than is required when owls forage in the surrounding grassland. In addition, several of the primary arthropod species that burrowing owls feed to their chicks are more abundant on the prairie dog towns than in the unmodified grassland. It is thought that burrowing owls warning calls of approaching predators are perceived by the prairie dogs which invokes defensive or avoidance behavior. This study also demonstrates the importance of prairie dog towns for successful breeding populations of burrowing owls and indirect evidence that the decline in burrowing owl numbers is related to the extirpation of most of the prairie dog colonies in the Chihuahuan Desert.

A burrowing owl at the edge of a reintroduced prairie dog colony on the Armendariz Ranch north of Engle N. M.. Note the large bison dung pats scattered around the open area of the prairie dog colony. The tall grass in the background is alkali sacaton (*Sporobolus airoides*).

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